Philosophy of Plant Biology Workshop

Egenis, the Centre for the Study of Life Sciences, University of Exeter 5-7 May 2021

Organisers: Özlem Yılmaz and John Dupré

Philosophy of Plant Biology Workshop (Virtual)

Book of Abstracts

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* This workshop is a part of the Plant Phenome Project that has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No:833353.

Workshop Website: http://sites.exeter.ac.uk/plantphenome/phil-plant-bio-workshop/

Hashtags: #PhilPlantBio2021 #PlantPhenomeProject

Contents

*Abstracts are ordered according to the program.

*Photograph on the cover page: Özlem Yilmaz

Call for Papers: Philosophy of Plant Biology Workshop

Egenis, the Centre for the Study of Life Sciences, University of Exeter, 5-7 May 2021

Organisers: Özlem Yilmaz and John Dupré

Plants are very interesting organisms. They implement unique internal processes and modes of interaction with their environments. Needless to say, as the primary harvesters of solar energy they are vital parts of ecosystems. Serious attention to plants provides novel and interesting perspectives on many topics in philosophy of biology, including individuality, organisation, cognition, and disease. For example, the growth of plants requires us to stretch the concept of organism. If vegetative spread, for example via suckers from roots, is counted as mere growth, a forest can be considered a single organism, as is the case with 'Pando', a *Populus tremuloides* forest in Utah. And although there seems to be no centre of the coordination in a plant body as in animals, there is usually a highly-tuned coordination of the body parts that has led some theorists to attribute cognitive capacities to plants. Plant scientists use diverse methodologies and approaches, some of which are uniquely applicable to these organisms.

A workshop to consider philosophical issues arising in plant science will be held at Egenis, the Centre for the Study of Life Sciences, University of Exeter on May 5-7, 2021. We hope to hold the meeting in person, but it will also be accessible through Zoom. If the state of the Covid-19 pandemic requires this, the workshop will be held fully online. This workshop is a part of the Plant Phenome Project that has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No:833353.

We welcome abstracts from philosophers, historians and biologists. Although we are interested in the full range of topics pertaining to plant sciences, we have a particular interest in topics that bear on plant phenomes. Please send a word file abstract with no more than 600 words to o.yilmaz2@exeter.ac.uk before 15 January 2021. Please include four keywords, name of the author(s), affiliation(s) and email address.

Topics of the talk can be any subject on the **philosophy of plant biology**, including:

Plant individuality; History of plant biology; Data management in plant sciences; Plant biotic and abiotic stress; Plant relations with microorganisms; Plant cognition; Plant nutrition; Plant physiology; Plant evolution; Plant ecology; Plant-soil interactions.

Philosophy of Plant Biology Workshop

Egenis, the Centre for the Study of Life Sciences, University of Exeter, 5-7 May 2021 (Virtual)
Organisers: Özlem Yilmaz and John Dupré

05 May 2021

14:30-16:00

Opening Talks- Özlem Yılmaz and John Dupré (University of Exeter)

17:00-19:00

Process-Sensitive Naming: Crop Descriptors and the Shifting Semantics of Plant (Data) Science
Sabina Leonelli (University of Exeter)

Ontological commitments and the working worlds of plant DNA barcoding
James W. E. Lowe and David Ingram (University of Edinburgh and The Royal Botanic Garden Edinburgh)

Putting Markers in Their Place: Population Construction and Improvement in Contemporary Plant Breeding
Hugh F. Williamson (University of Exeter)

The proximate-ultimate causation distinction is still relevant: examples from plant hydraulics
Mark E. Olson et al. (Universidad Nacional Autónoma de México)

06 May 2021

14:00-16:00

Resisting the biotic/abiotic division – The case of plant immune systems
Sophie Juliane Veigl (Cohn Institute for the History and Philosophy of Science and Ideas)

My plant teacher: what can we learn from plant immunology about our own immune system?
Gregor P. Greslehner (University of Vienna)

Delineating the Boundaries of Self: Modularity, Regeneration, and Individuality in Plants
Auguste Nahas and Zoe Nahas (University of Toronto and University of Cambridge)

Is a Plant a Genetic Mosaic? An Insight into Plants' Individuality
Sophie Gerber and Thibault Leroy (UMR Biogeco Inrae-Univ Bordeaux and University of Vienna)

17:00-18:30

Keynote talk: Multi-generation plant plasticity and unscripted development
Sonia E. Sultan (Wesleyan University)

07 May 2021

14:00-16:00

Theophrastus' Philosophy of Plants and Aristotle's influence
Thomas McCloughlin (DCU Herbarium, Dublin City University)

Tree phenomes and the phenomenology of extinction
Ramsey Affifi (University of Edinburgh)

Living Fossils as Paleoclimate Proxies: The Case of Ginkgo biloba
Aja Watkins (Boston University)

What Shall We Make of "The Weather Plant"?
Susan G. Sterrett (Wichita State University)

17:00-19:00

How to understand and discriminate plant cognition?
Quentin Hiernaux (University of Brussels)

From signaling systems to intentionality: approaching adaptive agentivity in plants in Eco-Devo
Tiago Rama (Autonomous University of Barcelona)

Plants as agents: Against gradualism about the mind
Bendik Hellem Aaby (KU Leuven)

Closing

Note: The program is in UK time (GMT)

Opening Talks Özlem Yılmaz and John Dupré

Plant Phenome Project

Plant Phenomes and Climate Change

Plant Individuality: A Cognitive-Physiological Approach

Özlem Yilmaz[1] (a) **and John Dupré**[2] (a)

(a) **University of Exeter**

All organisms have cognitive capacities, sufficiently broadly construed. By minimal cognition we mean that there are processes in the organism that respond systematically to features of the environment ("perception"), that perceptions can leave some trace in the organism, systematically related to the perception ("memory"), and that the organism has the capacity to produce an action appropriate in the light of a perception that contributes to maintaining the coordination of the whole. This paper examines these processes in plants, particularly focusing on the coordination aspect. But this perspective on plant cognition requires distinguishing the individual plant that is coordinated as a whole. Although they do produce systemic responses even to a local stimulus, considering plants as wholes, as individuals, is problematic. Plants are modular organisms, they can constitute clones, etc. And also, we need to consider the interactions with mycorrhiza, microbiota... So how do we determine the boundaries of the individual plant? There are many ways of individuating plants and plant parts employed in scientific experiments, depending on the experiment and the purpose of the research. We have particularly focused on research on the coordination between plant parts involved in the regulation of source-sink balance and how or if this is regulated by the whole organism. Whereas in the case of animals this kind of regulation and coordination is accomplished by the nervous system, in plants it is achieved rather by the flow of hormones and other information-bearing molecules around the system. We propose a cognitive-physiological approach for understanding plants as individual organisms.

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Multi-generation plant plasticity and unscripted development

Sonia E. Sultan[3]

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Developmental flexibility or *plasticity* in response to environmental conditions is a characteristic property of organisms. Plants are well suited to plasticity studies because, in many taxa, genetically identical individuals can be produced and grown in contrasting environments to determine the repertoire of alternative outcomes a given genotype can express. The resulting 'eco-devo' data reveal that adaptive adjustments take place in individual organisms, through active processes of developmental response. Yet biologists have generally accounted for plasticity by assuming that such responses are genetically programmed, thus maintaining a view of development as pre-scripted in the genome. Studies of *transgenerational plasticity* (using the study species *Polygonum persicaria*) provide new insights to the nature of development that challenge this view. Experimental tests of contrasting parental soil moisture and light environments show that parental conditions affect development and fitness of progeny. Moreover, the parent plant's environment affects how offspring respond to their own environment, showing that individual plastic responses are not determined by genotype. These complex, multigeneration plastic responses point to a different view of development across the life-cycle as an unscripted process of developmental integration that takes place, in real time, in progeny individuals.

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Process-Sensitive Naming:
Crop Descriptors and the Shifting Semantics of Plant (Data) Science

Sabina Leonelli[4]

University of Exeter

Philosophical discussions of plant naming practices have largely focused on research fields concerned with the conservation of biodiversity, such as evolutionary biology and systematics, leaving aside taxonomic questions raised by fields that study how plants can be domesticated and manipulated for consumption, including experimental biology, gene editing and other technologies of intervention, field trials and breeding practices. As a step towards redressing that balance, this paper investigates the epistemic commitments underpinning the naming of plant traits in the context of the collection and management of phenomic data. This is often referred by curators and participants in plant data infrastructures as the domain of "plant data semantics". The effort to share phenomic data about crops across different locations, and particularly between high-resourced and low-resourced research environments, places in sharp relief the complexity and diversity of biological and environmental characteristics, the methods used to generate and process data, and the goals, skills and expectations of the stakeholders involved. Focusing on naming initiatives that negotiated this diversity upfront, and particularly the Crop Ontology, I argue that attention to what I call "process-sensitive" naming of traits can go a long way towards facilitating interoperability, comparability and visualisability of plant data, and at the same time enable a dialogue between the semantic systems developed within data science and more traditional taxonomic systems focusing on species. I conclude that focusing on data semantics and related descriptors constitutes a productive and underexplored way to think about broader questions of naming and taxonomy within plant science. The attempt to articulate semantic differences among plant varieties and methods of data collection, sharing and analysis is generating new ways to develop and communicate biological knowledge; in turn, such practices defy existing understandings of both systematisation and expertise in biology.

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Ontological commitments and the working worlds of plant DNA barcoding

James W. E. Lowe[5] (a) **and David Ingram**[6] (b)

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(b) **The Royal Botanic Garden Edinburgh**

This paper explores the ontological consequences of species-discrimination practices employed in biological communities studying various higher-level taxa. We characterise these as distinct 'ethnobiologies', each reflecting the supervenience of classifications and classificatory practices to ontological commitments (Kendig, 2020). These commitments owe something to the historical objectives of the communities working on particular taxa, the materiality of the biological entities and processes that they engaged with, and their specific working world problems (after Agar, 2012). These generate particular theoretical articulations of biological variation – and practical means for its apprehension, analysis and interpretation – that affect the criteria by which markers of species-discrimination are selected and used: we term this *varipraxis*. In this theoretical background, we draw on Kendig (2020) and Minelli (2019), who highlight non-Linnaean 'grey nomenclatures' manifested, for example, in DNA barcoding and the long-established 'promiscuous realism' set out by Dupré (1993).

First, we identify the relationship of DNA barcoding – a method by which a set of informative genetic markers associated with DNA sequence variation in a number of genes can be used to discriminate between species – to existing taxonomic practices and outcomes. We then demonstrate how DNA barcoding has operated distinctly for different higher-level taxa, comparing plant DNA barcoding with that of protists. Although protists do not constitute a monophyletic clade, a working group coalesced around them to establish standard markers and barcoding procedures. We compare the means by which this was achieved, and the particular outcomes. These outcomes include criteria used to identify markers to use in barcodes and data infrastructures established to enable the identification of species-specific barcodes. We focus on how this relates to the ontological commitments and working worlds associated with the different groups of organisms represented by distinct barcoding efforts. We pay especial attention to the variety of potential uses to which plant DNA barcoding can be put as conditioning the forging of its standards and protocols, and examine one protist group in particular, the photosynthetic and phytoplanktonic algae called diatoms, whose primary taxonomic interest lies in their role in environmental monitoring. Finally, we relate how these barcoding efforts reflect back on the *varipraxis* that underpinned them, encouraging an interpretation of genomic variation within particular higher-level taxa that centres on a processual conceptualisation of taxonomic discrimination. This leads to 'thicker' explorations of the wider biology of the organisms involved, in a quest to understand the processes by which the nature of genomic variation is shaped between and within putative taxa.

We conclude by adumbrating how, in investigating processes and objects that necessitate encounters between different ethnobiologies in the study of 'plant-focused communities', various

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practical, epistemic and ontological problems are managed. In plant-focused communities, plants constitute a nexus of interactions among different organisms including: plant-plant inter-specific epiphytic and parasitic interactions; and plant-microorganism symbioses, as in lichens, mycorrhizal associations and parasitic/pathogenic interactions, and the complex interrelationships of the phyllosphere and rhizosphere. These final considerations allow us to build on the findings detailed earlier, to suggest further avenues for exploration of the concept of *varipraxis*.

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Keywords: DNA barcoding; taxonomy; classification; variation

Putting Markers in Their Place:
Population Construction and Improvement in Contemporary Plant Breeding

Hugh F. Williamson[7]

University of Exeter

Recent philosophical work has identified a shift towards "marker-centric biology" in livestock and, we may add, crop genetics, in which genetic markers and the mapping thereof have come to serve as a focal point for research and breeding applications, without necessarily requiring the identification or functional knowledge of associated genes (Lowe and Bruce 2019). Much of the prominence given to markers depends on their association with phenotypic traits under quantitative genetic assumptions, notably the infinitesimal model of gene effects, and with an emphasis on population- rather than individual-level variation and change. This is particularly driven by the rise of genomic selection methods, which utilise models of marker-trait associations together with genotyping data from individual plants or animals in order to provide estimated breeding values that can inform selection decisions.

This paper argues that in order to appreciate the importance of marker-centric methods in plant science, we need to understand, firstly, the wider set of quantitative genetic principles and, secondly, the construction and conceptualisation of populations in the practical fields of plant breeding to which marker-centric research is oriented.

It has been noted that markers are relational entities, with highly variable relations to (known or assumed) gene loci and to phenotypic traits, and in this sense their particular qualities are very population-dependent. But more than this, populations are a significant object of interest(s) and manipulation. Population-level improvement is a key goal for plant breeding programmes, especially within contemporary breeding priorities, given a widely recognised exhaustion of breeding strategies based on the introduction of single alleles with major effects (such as the well-known dwarfing gene in wheat) into relatively homogeneous lines. Moreover, this is a goal with a clear method of monitoring: Namely, the rate of genetic gain (or 'response to selection'). This statistical tool measures the change over time in average value for a given trait within a population owing to selection. It is also grounded in quantitative genetic assumptions, in particular that improvement results from increasing additive genetic variance within populations. This in turn is predicated on the repeated recombination of existing alleles within a population that is by necessity relatively closed (in genetic terms), to access hidden "depths" of genetic variation. Given this, the selection and management of initial source populations is critical to establishing the parameters and aims of phenotypic improvement. (Indeed, the utility of genomic selection and, by extension, markers come in large part from their ability simply to speed up breeding, by utilising genotyping data to make selection decisions well before phenotypic evaluation.)

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This paper identifies two principles of population construction that have been given particular significance in recent years—the identification of relevant source material based on envirotyping and the exclusive use of elite varieties as source materials—and explores several implications of these. More broadly, I will address the degree to which a wider range of quantitative genetic concepts and population-construction work underpin marker-centric biology. This leads me to contextualise marker-centric methods in the plant sciences less as representative of a contemporary shift in genetic reasoning and practice than as a set of methods associated with one activity (population improvement) within the wider process of plant breeding, that spans pre-breeding to variety release.

Key words: plant breeding; populations; quantitative genetics; marker-centric biology

The proximate-ultimate causation distinction is still relevant: examples from plant hydraulics

Mark E. Olson[8](a), **Sean Gleason**[9](b), **Kate McCulloh**[10](c), **Rachel Spicer**[11](d), **Kasia Zieminska**[12](e)
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(c) **University of Wisconsin,** (d) **Connecticut College,** (e) **Uppsala University**

The validity of the proximate-ultimate distinction in biology has been rightly challenged in current evolutionary biology. Traditionally, "proximate" causation is regarded as ontogeny, seen by Modern Synthesis practitioners as being the unfolding of the information in the genetic program. "Ultimate" causation is regarded as being the factors of natural selection that explain the presence of a given trait in a population. Thus, proximate causation has traditionally been regarded as providing the "how" a given trait comes to be expressed and ultimate causation its "why." This dichotomy is most defensible if development and evolution are truly separate, as envisioned by the Synthesis. However, natural selection itself is the biasing of development such that favored outcomes are produced. Moreover, it is increasingly clear that notions of genes as autonomous causal agents is indefensible and instead DNA is a necessary but not sufficient participant in developmental systems (the collection of resources, environmental and otherwise, necessary for a developing individual to reconstruct a configuration similar to its progenitors), and it is the developmental system that is inherited and changes in evolution. As a result, the proximate-ultimate distinction does not provide bedrock on which fundamental biological theory can be constructed. However, there are fields in which the proximate-ultimate distinction in a more or less traditional form still promises to provide key insights. We present an example here from our field of plant hydraulics. Plant hydraulics studies how plants move water from the soil to the leaves through the tubes in their wood (xylem conduits). A distinguishing feature of much work in plant hydraulics is appeal to proximate, developmental factors to explain patterns of putative functional (i.e. adaptive) significance, where inclusion of ultimate factors (natural selection) would be essential. We trace the proximate-ultimate disconnect in plant hydraulics to the scientific traditions that its practitioners come from. Most plant hydraulics researchers come from plant physiology and to some extent from plant ecology. In both cases, these fields stem from traditions that have origins largely separate from evolutionary biology. This becomes important when studies of plant hydraulics focus on the functional relevance of plant hydraulic variation – here they encounter the proximate-ultimate distinction. Function in biology implies adaptation,

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and adaptation falls under the purview of evolutionary biology. Because plant hydraulics has as its starting points outside of evolutionary biology, it lacks key conceptual tools necessary for testing hypotheses regarding adaptation, especially those gained over the past 40 years post-*Spandrels of San Marco*. We explore ways in which the proximate-ultimate distinction would provide useful guidance for testing the hypotheses that plant hydraulic scientists are interested in examining, leading to greater clarity in the way that explanations are built in the field, and leading to fruitful collaboration across experimental physiology, comparative biology, and developmental perspectives on woody plant structure. Plant hydraulics thus provides an example of an area in which the proximate-ultimate distinction can still provide useful insight and improve biological practice.

Keywords: adaptation, causality, plant hydraulics, plant physiology

Resisting the biotic/abiotic division – The case of plant immune systems

Sophie Juliane Veigl[13]

Cohn Institute for the History and Philosophy of Science and Ideas

The philosophy of immunology is currently experiencing its heyday within the philosophy of science. After a surge of feminist critique regarding sexist, racist, and capitalist biases in the imagery and concepts of immunology in the last decades of the previous century (e.g., Haraway, 1991; Martin, 1990; Weasel, 2001), a new wave of philosophy of immunology, characterized by its rejection of the self/nonself dichotomy (e.g., Pradeu, 2012) is on the rise. What constitutes both bodies of knowledge is an almost exclusive focus on mammalian immune systems.

Ideas and concepts guiding the current philosophy of immunology are anthropocentric, or at least mammal-centric. They display taxonomic chauvinism (Bonnet et al., 2002). Concepts and ideas for talking about immunity-related phenomena, such as memory, self/nonself, innate/adaptive, and what defines immunogenicity, are developed from a mammalian perspective: Immune systems are generally regarded to only respond to biotic triggers. Invertebrates and plants are generally believed to lack an adaptive immune system, not displaying processes akin to the clonal selection and expansion of B- and T-cells.

Browsing the literature, plant immune systems are most often characterized by "lack of x," compared to mammalian immune systems (e.g., Jones & Dangl, 2006). Given that plants are mostly sessile organisms, shouldn't we expect that plant immune systems operate radically different from those organisms, who can avoid specific triggers by changing location? And, owing to this sessile nature, wouldn't it make sense that plants inherit immune responses (Molnier et al. 2006)? In my talk, I will try to continue the groundwork laid by early feminist scholarship regarding bias in immunology and apply it to provide an alternative position that resists taxonomic chauvinism. Ideally, a framework that resists biases is also a framework that describes the processes studied more accurately.

I will examine plant immune systems to demonstrate the inaptness of mammalian-centric preconceptions and urge a more open way of classifying immune systems across species. I will argue that 1) if one examines plant immune systems, the distinction between biotic and abiotic stressors fails, as both triggers are immunogenic. Drought, salinity, cold, heat, light, oxidative stress, and nutritional deficiency are triggers of immune responses (Khraiwesh et al., 2013). 2) I will argue that if one looks at a particular set of effectors in the response against biotic and abiotic stressors, small RNAs, it is tempting to consider small RNAs capable of instantiating an immune response that could be considered adaptive. Furthermore, as small RNA responses to stressors are heritable (Bond & Baulcombe, 2014), they operate at the intersection of genetic and immune systems. 3) Reframing some aspects of plant interactions with their biotic and abiotic environment as (possibly heritable) immune responses will also contribute to understanding the many interactions of environment and the plant phenome, and particularly how certain phenotypes persist transgenerationally.

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Keywords: plant immune system, biotic and abiotic stress responses, philosophy of immunology, heritable stress responses

My plant teacher:
what can we learn from plant immunology about our own immune system?

Gregor P. Greslehner[14]

University of Vienna

When we think about immune systems, most people have been brought up with the idea of defense mechanisms and the distinction between "self" and "non-self". However, as is becoming increasingly clear in recent years, immune systems are much more than just defense mechanisms (Tauber 2017). They also play a crucial role in development, repair, and normal physiological processes (Pradeu 2020). Another important conceptual change has been the appreciation of microorganisms not only as infectious pathogens, but often as useful and essential symbiotic partners, known as the "microbiota" (O'Malley & Dupré 2007).

Without dedicated immune cells and working less centralized than animal immune systems, it could be disputed whether plants do have an immune system at all. While this is being widely acknowledged nowadays, plant immunology being an accepted fact and topic, a huge gap between researchers working on different model systems remains. While having different benefits and drawbacks, the choice of model organisms is an important one (Ankeny & Leonelli 2020). A lot of research and experimental results in immunology are based on mouse models. Given the differences between rodents and primates, there are significant differences that have given rise to a call for "rebooting human immunology" (Davis & Brodin 2018). What might we learn from plants, an even more distantly related phylum?

Looking at differences and commonalities in how immune systems work in plants, as compared to other organisms, can provide a fresh perspective. Especially when it comes to the different ways in which immunological recognition works, plants might help us understand some puzzles and open questions about similar mechanisms in other organism. While most known mechanism of immunological recognition are based on pattern-recognition receptors, there are other, indirect ways in which immune systems recognize pathogens, process and respond to all sorts of inputs and conditions. Immune systems might not only monitor and respond to certain structural features, but rather activities and effects (Greslehner 2020). "Effector-triggered immunity" had been first observed in plants and is currently also investigated in animals (Stuart et al. 2013). Similarly, nucleotide binding (NB) and leucine rich repeat (LRR) proteins can be activated indirectly by effects rather than merely structural features of pathogens or damage (Dangl & McDowell 2006). These results are not only interesting from a scientific point of view, but also raise many conceptual questions about the nature of these processes, biological individuality, and many other issues from philosophy of immunology.

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Taken together, trying to understand immune systems in plants also has implications for the way immune systems work in other organisms – and what they have been selected for.

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Keywords: immunology; microbiota; systems biology; model organism

Delineating the Boundaries of Self: Modularity, Regeneration, and Individuality in Plants

Auguste Nahas[15] (a) **and Zoe Nahas**[16] (b)

(a) **University of Toronto,** (b) **University of Cambridge**

This paper is concerned with the status of plants as biological individuals; a question which has been much debated in light of their modular architecture and regenerative capacities (Clarke, 2012). Unlike complex animals, plants lack unique parts, which makes them more resilient to the risks of predation that come from their sessile lifestyle. Alongside this modularity is a remarkable capacity for regeneration. To achieve this, plant cells (e.g., from a shoot) dedifferentiate before redifferentiating into a different cell type (to become e.g., root tissue). These phenomena have long been used to argue that plants are less individuated than other organisms, with some claiming that these features make plants more like colonies than individuals (e.g.: Mancuso & Viola, 2015, p. 125).

This kind of argument has a long history, dating at least to the Enlightenment. In his *Philosophy of Nature*, Hegel argues for an Aristotelean vision of organisms as highly individuated, "concrete unities", composed of unique parts which exist and act as such only within the context of the whole. When detached from such a whole, these parts also cease to be properly *organic*, and rather become merely chemical or physical in nature (Gambarotto & Illetterati, 2020). As he argued, plants fail to meet such stringent criteria for organismality because their parts are much closer to individuals in their own right, rather than uniquely specialised parts. The interchangeability and modularity of these parts make it such that the whole can be divided without losing its essential nature, which, in Hegel's view, puts into question whether it was ever a true individual to begin with. Since then, many others (among them, Erasmus Darwin) have espoused similar views.

In our view, the relationship between modularity, regeneration, and individuality requires clarification. By thinking of biological individuality or selfhood in physiological terms, specifically in terms of informational integration (Levin, 2019), we can see how regenerative capacities are distinct from the question of individuality. Our central contention is that just because a part of a plant has the *possibility* of becoming a separate individual, does not mean that it is less tightly integrated into the larger whole. In other words, we must distinguish the question of how clearly individuated a system is from its capacities to alter these boundaries. By thinking about individuality processually, whereby the boundary of the self is determined by the goals that a system can pursue as a whole (*ibid*), regeneration, i.e. the *potential* ability for a part to survive if it becomes detached, does not blur the plants' *current* boundary.

This information-based view of the self focuses on the emergence of large scale orchestrated outputs or goals from the integration of parts, regardless of whether these parts are morphologically identical (as is the case in plants) or unique (as in many animals). Accordingly, the development of redundant plant modules is tightly integrated, as exemplified by the ability of shoots to tune each other's

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growth. Central to the regulation of shoot branching is the phytohormone auxin and its self-organising transport network. Auxin is a small molecule involved in virtually all developmental processes (Leyser 2017). As an engineering solution, auxin transport is poorly suited to carry specific signals, which suggests that its role could be one of connectivity rather than targeted signal propagation (Bennett & Leyser, 2014). The most useful framework of auxin may be as an organism-wide integrator, making it a good candidate for delineating the self.

In sum, modularity and regeneration do not blur the boundary of the self but rather endow plants with the possibility of a *flexible* boundary that makes them resilient to damage from their environment. In fact, given plant development is indeterminate, their boundary of the self *must* be flexible in order to continuously accommodate new parts.

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Keywords: individuality, modularity, regeneration, auxin

Is a Plant a Genetic Mosaic? An Insight into Plants' Individuality

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Biologists study different basic living units, from genes to biotopes, including cells, tissues, individuals or species. Definitions of these units can be discussed, and their exact boundaries are generally open to questions. One typical example is individuality. This unit is notably affected by the usual human anthropocentric bias. Hence, among non-animals, plants particularly call for new ways of considering individuality. Genetic homogeneity is one of the main criteria commonly related to individuality and plants are historically considered to be different from animals for this criterion. A single plant was constantly considered, through a long history[19], as a population of fragments, of units; hence buds were for instance supposed to bear individuality rather than the plant as a whole. Plants are alleged to be heterogeneous in nature because of, among other traits, their particular cell functioning, the assumed very late differentiation of their germlines, their modular growth, their multicellular propagation (clonality), their long lifespan. Additionally, these features make somatic mutations non-fatal for plant life. However, this genetic heterogeneity, seen through potential mosaic, might be more present in cultivated plants, that were modified by human intervention since the beginning of domestication, than in wild specimen (Herrera 2009, Gerber 2018a,b).

Phenotypic mosaic plants are indeed very rarely described in non-domesticated species (except in Padovan *et al.* 2013). Studies based on molecular biology, on DNA sequencing and on epigenetic markers (genetic and epigenetic markers being probably intertwined evolutionary factors in plants Herrera *et al.* 2014) have provided new light on plant functioning. The amount of intraindividual genetic variation, due to somatic mutations, remains in fact low in several wild plant species and in trees in particular. Environment, and especially stress, acts on the accumulation of mutations and epimutations (Jiang *et al.* 2014). Phylogenetic trees reconstructed from somatic mutations are following the architecture of trees/plants (Schmid-Siegert *et al.* 2017, Plomion *et al.* 2018, Wang *et al.* 2019, Orr et al. 2020). Differences of rates between organs were also found, and the existence of protected cell lines appears now probable in several plant species, based both on cell, model and genetic observations (Lanfear *et al.* 2013, Burian *et al.* 2016, Watson *et al.* 2016, Schmid-Siegert *et al.* 2017, Wang *et al.* 2019). Links were shown between epigenetic modifications and some phenotypic traits (Zhong *et al.* 2013, Alonso *et al.* 2018), the phenotypic expression of mutations is not easy to decipher, and is yet important to analyse the potential effect of selection on the fate of mutations (Exposito-Alonso *et al.* 2018).

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[19] Among others, Theophrastus ~300BC, Grew 1672, Malpighi 1675, Bradley 1721, Goethe 1879, Darwin E 1800, Candolle 1827, Gaudichaud-Beaupré 1841, Darwin C 1845, Braun 1853, Gray 1876, Whitham and Slobodchikoff 1981, Hallé 2005

Scientific knowledge acquired on intra-plant genetic diversity is growing since some years, and suggests that the drivers of new mutations and their inheritance are more complex than previously thought. For instance, the early segregation in development between germinal and somatic cells (Weismann theory), was classically observed in animals but did not include plants till recently (Lanfear 2018). Our vision of plant can therefore evolve thanks to the scientific perspectives opened by these new findings (Leroy *et al.* 2020), shedding light on the philosophical question of plant individuality.

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Keywords: trees, individuality, genetic heterogeneity

Theophrastus' Philosophy of Plants and Aristotle's influence

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Theophrastos, née Tyrtamos in Eresos on the Aegean island of Lesvos (c.371 – c.287 BC), Latinized as 'Theophrastus', was the successor of Aristotle of the Peripatetic School, and contemporary in studies relating to the natural world. He was a student at Plato's Academy as a young person, where he met the older Aristotle with whom he maintained a lifelong friendship. After Aristotle imposed self-exile from Athens c. 347/8, he went to Lesvos around 337/8, at least because of his connection to Theophrastus, and there advanced, if not started, his scientific study. It has been assumed that Theophrastus and Aristotle divided the living world between themselves as domains of study - Theophrastus for plants, Aristotle for animals. It is notable that Aristotle produced texts on plants, but also that they did not survive. Scholars of Theophrastus have suggested a broad range of views concerning Aristotle's influence - 'the less or more' and the role of *differentiae*; and the technical veracity of Theophrastus' botany, whether akin to a modern classification system or a jumble of facts. Importantly, despite the early strict conformity between *Historia Animalium and Historia Plantarum* in language and purpose, Theophrastus makes important contributions to the study of plants for its own sake.

Given Aristotle's zoological texts and their place within his overall philosophical project, this paper will determine how Theophrastus' texts on plants either fits with Aristotle's project or wholly Theophrastus'. It is concluded that Theophrastus' work was broader, and of himself, and emphasised the study of plants from an economical botanical perspective. Theophrastus is concerned with the causes of food and materials from plant sources and recognises that humanity intervened in the generation of plants, and that generation *per se* was a definite area of study. Theophrastus makes the important departure concerning the immutability of plants whereby he acknowledged reversion, mutation, as well as new reproducible forms (Aristotle is less definite in this regard).

He was the first to recognise that plants do not easily coalesce into totally exclusive categories, which in studies of phenology continues as a problem today. Theophrastus deliberated on the possible *megista* gene and chose as a model the main habits of vascular land plants: trees, shrubs (and sub-shrubs), and herbaceous plants; however, he was impaired by an absence of the understanding of the whorls of floral parts as a pre-Linnaean botanist. Like Aristotle taking humans as the best form of the animal, Theophrastus took 'tree' as the best form of the plant. Despite Linnaeus reverence for Theophrastus (it was he who applied the moniker 'father of botany' to Theophrastus), and who held the best editions of Theophrastus' works in his personal library, Linnaeus developed a model of *megista* gene aligned initially purely with plant whorl numbers - as artificial as using habits, but fortunately for Linnaeus closer to a natural classification. Notwithstanding retrospective views of Theophrastus' work from a botanical

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perspective, Theophrastus would offer the first model of classification of plants, and what was presented represents the intuitive 'life-form' distinctions that botanical novices produce in everyday life. He then discusses the local interpretations ("as so and so of X says") of such a model. In modern discussions on 'plant blindness', Theophrastus may have something to offer today in terms of engaging novices in plant awareness and enhancing biodiversity literacy.

Tree phenomes and the phenomenology of extinction

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This paper describes how plant phenomes force a reconsideration of genocentric conceptions of extinction.

A phenotype is the ongoing expression of a particular developing being and its particular history. For perennial plants, sessile and slow growing, an individual phenotype is also an expression of a particular organism-environment transactions that make a particular place. This is especially evident in long-lived trees, with forms that simultaneously manifest their history into spatial configuration while offering semi-stable possibilities and constraints for the ongoing dynamics of the ecosystem, such as connecting different trees together in specific ways for animals, lightening and darkening the understory, etc. The phenotypic record of the past shapes how the tree place-makes in the present.

Most conservationists follow a *genocentric* conception of evolution framed by the modern evolutionary synthesis. Evolution, from this perspective, is characterised as the intergenerational change of gene frequency within a population (e.g. Fisher 1918). The modern synthesis is a successful but incomplete model of evolution. It is facing a shake up by diverse organism and systems centered theories and approaches (e.g. Pigliuicci and Müller, 2010), including developmental plasticity (West-Eberhard, 2003), developmental systems theory (Oyama et al.), and niche construction theories (Odling-Smee et al, 2003). A broad commonality underlying many of these theories is the claim that evolutionary process cannot be understood without the positive contribution various phenotypic levels make as causal agents (Walsh 2015). If evolutionary theory needs to transcend genocentrism, why not extinction theory too?

Notably, the particular features of long-lived tree phenotypic diversity foregrounds the role that individual make in ecological systems (Affifi 2020). This draws attention away from treating entities as merely instances of a class (say a variety, species, or family), which is supposed (but perhaps not a necessary feature) in genocentric models. For instance, even if a particular species of tree is allowed to grow long enough to seed and propagate, if it is never able to reach maturity, a number of diverse ways in which it reorganises spatiotemporal relations, regulates the rate of being and becoming in that environment, enabling homes and habitats, in a forest would still be obliterated. In this case, the genotype would not be extinct, but a realm of its phenotypic possibilities would. The emphasis on the extinction of classes of beings seems not merely genocentric, but also animalcentric. Insofar as the ways conservationists spot and track animals in an ecosystem are based on fleeting encounters and signs, the mobility of animals lends themselves to being treated categorically and in terms of species-typical behaviour. We speak of the extinction of the loss of a category, such as a species, genus or a family. But some plant phenomes reveal (*phenome*nologically) that extinction is also the loss of an event. This reveals an ecological dimension of 'processual philosophy of biology' (Nicholson and Dupre, 2018) concerned

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with sustainability issues. What such plants project into lived experience is the awareness that individuality is a property of life – and with this, the insight that extinction is both an idiographic and a nomothetic process.

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Keywords: tree phenomes; extinction; nomothetic; idiographic

Living Fossils as Paleoclimate Proxies: The Case of *Ginkgo biloba*

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Paleoclimate proxies are invaluable sources of data for reconstructing past climates. Ice cores, lake and ocean sediment cores, and various stable isotopes can all serve as proxies to track different features of the climate. As expected, given the plasticity of plants in response to changing environmental conditions, plant fossils provide a number of paleoclimate proxies. Tree rings can provide data on temperature, precipitation, and atmospheric levels of CO_2. Fossilized grains of pollen can serve as proxies for various measures of biodiversity.[23]

Leaves of vascular (i.e., respirating) plants can serve as proxies for CO_2 concentration as well. The cuticles on these leaves contain stomata, small pores through which the plant respirates. The number and density of the stomata are negatively correlated with CO_2 concentration. Fossils of plants in the genus *Ginkgo* are often studied in this context.[24] Ginkgo plants appear in the fossil record more than 200 million years ago, providing a long, sustained record of climate that extends into the present, with the extant *Ginkgo biloba* species. Ginkgo's extensive evolutionary history has earned the taxon its status as a "living fossil."

Living fossils have received some recent philosophical attention.[25] In particular, living fossils can be used to make inferences about the past.[26] Relevant here is the inference from "members of a living fossil taxon share morphological trait X" to "members of this living fossil taxon share some other phenotypic trait Y." In the case of ginkgo as a paleoclimate proxy, the idea is that we can use the morphological similarities between past and extant species of ginkgo to infer that their stomatal density changes similarly in response to CO_2. We apply what we know about extant ginkgo plants to fossilized ginkgo, and reconstruct atmospheric CO_2 based on the relationship between stomatal density and CO_2.[27]

This paper has two objectives. First, I will spell out exactly how ginkgo's living fossil status contributes to our ability to successfully use it as a paleoclimate proxy. In brief, this will come down to inferences based on homology (rather than mere analogy[28]) between past and present ginkgo plants, and the experimental tractability of extant ginkgo plants. By controlling for climate, our ability to experiment on extant ginkgo plants helps us to identify other factors that are prone to affect stomatal density, such as natural variation,[29] and can help us to develop a mechanistic understanding to bolster the purported relationship between stomatal density and CO_2.[30]

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[23] For a review of many paleoclimate proxies, see Bradley (2015).
[24] Note that ginkgo can be used as a proxy in other ways; see Zhang et al. (2019).
[25] Lidgard & Love (2018); Turner (2019).
[26] Watkins (forthcoming).
[27] Of course, multi-proxy reconstructions are common, so ginkgo is rarely used alone. See Kowalczyk et al. (2018).
[28] Regarding analogy versus homology, see Currie (2016).
[29] Sun et al. (2003).
[30] Jordan (2011).

The second aim of the paper is to show how ginkgo's status as a living fossil makes it useful not only for developing paleoclimate reconstructions, but also for developing climate *projections*. The idea here is that ginkgo's extensive fossil record makes it the case that we can study a single taxon's response to a range of climate conditions, a range which exceeds that ever experienced by many extant taxa (including humans).[31] Ginkgo is thus well-equipped to help us predict the biotic response to ongoing climate change.[32] Although the usefulness of paleoclimatology for making climate projections has been underappreciated by scientists and philosophers alike, more researchers are turning to paleodata to make predictions about future climate states.[33]

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Key words: living fossil, paleoclimate, proxy, ginkgo

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[31] Sun et al. (2008).

[32] Guo et al. (2019).

[33] National Research Council (2012); Tierney et al. (2020).

What Shall We Make of "The Weather Plant"?

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My title has double meaning: The first meaning is: What shall we as philosophers of science make of a certain episode in the history of science: an attempt in the late nineteenth century to use "The Weather Plant" as an instrument of weather prediction? The second meaning is a question asked from the standpoint of the protagonist; as he saw the situation, there was a plant that had a certain cultural role, and he wanted to make a scientific instrument out of it. Should the lesson be that he went about his investigations inexpertly, or that the very project was scientifically misguided? And, if so, what about it was misguided?

Over a hundred years ago, the Austrian baron J. Nowak spent vast amounts of money and time performing experiments on the plant Abrus peregrinus, in what he called "a matter of the deepest scientific study." He rallied people of various professions and ranks, including royalty, in his cause, and eventually was given space in London for an experimental 'Weather Plant Observatory' consisting of a greenhouse of hundreds of such plants.

Nowak argued that he had found the physiological basis for the plant's ability: it was an "electro-magnetic" plant. There are some striking aspects to Nowak's attempts to see the plant as a scientific instrument that seem to have no justification except for ideological commitments about how instruments work, such as his view about how the plant's predictive abilities are affected by its immediate environment. He also argued that the plant's development must be supervised in the manner he prescribed in order to function properly as an instrument of weather prediction.

In this talk, I'll examine the different kinds of evidence available, from indigenous knowledge of the plant in its natural habitat in South America, to time series of weather and sunspot data and laboratory experiments in England and Europe, and consider how they were regarded at the time. I'll examine whether Nowak's ill-fated investigations might be analogous to the kinds of negative cases in animal comparative psychology that led Frans de Waal to ask whether we are smart enough to know how smart 'they' are.

Keywords: plant cognition, plant intelligence, history of science, experimental botany

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How to understand and discriminate plant cognition?

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It is more and more common to hear about plant cognition, even plant consciousness. What credibility should be given to these perspectives? An enquiry into plant consciousness requires, on the one hand, taking into account recent experiments in plant biology and, on the other hand, refining the theoretical framework of behaviour and the various degrees of cognition. The main goal of this contribution is to advance such a framework by comparing classical animal and human cognition approaches with the theories of minimal cognition. This leads us to interpret more carefully the various plant activities (e.g. tropisms, but also memory and learning) and to highlight the limits of classical theories of zoocentric cognition. In particular, the notions of cognition and consciousness are often abusively confused, and with that of behaviour. Once this ambiguity is removed, it is possible to better distinguish several meanings of consciousness and to evaluate their relevance to plant activities.

Keywords: cognition, plant biology, behaviour, consciousness

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From signaling systems to intentionality: approaching adaptive agentivity in plants in Eco-Devo

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Ecological Developmental Biology (Eco-Devo) pursues an alternative picture of development than the gene-center one drawn by neo-Darwinian biology (for central textbooks, cf. Gilbert and Epel 2009, 2015; Lewontin 2001; Sultan 2015; West-Eberhard 2003). Development is mediated by ecological variables during epigenesis. The environment of any developmental resource -the gene, the genome, the cell, the body, and the outside- is always regulating and conditioning the ontogenetic pathway. Rather than as a master molecule, the genome should be understood as "a highly sensitive organ of the cell."[37] The sensitiveness of development calls for the introduction of *signals as key elements in organismal regulation of ontogeny*. Signaling networks -at different levels of the organism- orchestrate the holistic view of development that Eco-Devoists empathize with.

Many authors that adopt this view of development hugs the idea of *organisms as adaptive agents* (for instance, Levins and Lewontin 1985; Sultan 2015; Walsh 2015). Adaptiveness means that, at any stage of development, the route that the organism take would be adaptive according to its inner and outer conditions. Importantly, signaling systems are responsible for informing the outer and inner situation, so as the development fits and dialogues with the environment, i.e., it makes development an adaptively-directed process. Moreover, *agentivity* lies in the fact that the organism is active in front of its conditions for existence. Hence it can self-guide its developmental trajectory by regulation, inhibition, behavior, motility, compensation, or any activity that the organism itself performs to stay adaptive.

Our central thesis is that the Eco-Devo stance requires to take *organisms as intentional systems*. The notion of intentionality comes from the philosophy of mind and language. It concerns the capacity of a system to bear referential relationships with the world -through signs or representations- that makes agentive behavior in cognitive systems adaptive/intelligent. We believe that such referential relationships are crucial to understanding plant development from an ecological viewpoint, even though it doesn't mean that cognition must be extended beyond the animal kingdom. The centrality of signaling networks for the sensitiveness of development constitutes intentional systems as they are a fundamental ingredient to make organisms adaptive agents.

This view applies throughout the living systems, from unicellular organisms to complex animals. However, we will try to see these properties in plants based on the prominent work of Sonia Sultan, a

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[37] Quoted in Keller (2000, p. 34), from Barbara McClintock's acceptance remarks of the Noble prize in 1983. (cf. also Gri_ths and Stotz 2013; Keller 2014; Sultan 2015)

pioneering in plants development from an Eco-Devo perspective.[38] Firstly, (i) I will present some examples of ecological mediations of development where the place of genes becomes decentralized. Secondly, (ii) I will highlight the role of signaling systems and signaling networks in such cases. Consequently, (iii) the agential and adaptive dimension of plants will emerge from the sensitiveness, plastic, and contingent dimension of their development. Finally, (iv) I will argue that the adaptive agentivity of plants implies an *intention towards* the ecological situation informed by signals.

The adaptive agentivity of developing organisms sometimes is taken as a mark of intrinsic teleology. The organism is constantly goal-directed to an adaptive port where its thermodynamical equilibrium and organizational closure are dependent on its agential capacities (cf. Moreno and Mossio (2015) and Walsh (2015)). The teleosemantic project in cognitive science aims to naturalize intentionality by appealing to natural teleology (Millikan 1984 ; Neander 2017). But, contrary to this picture, we would like to ask, as an *open question*, whether intentionality is not indeed a necessary ingredient for natural, intrinsic teleology. It could be so insofar as intentionality is a key to understanding how the organism regulates its activity through signaling systems interacting with the environment. Intentionality would be a requirement for intrinsic teleology because it settles the directedness of the goals that organisms pursue.

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[38] Some of her work, with collaborators, are Ackerly and Sultan (2006), Baker et al. (2018), Griffith and Sultan (2006), Herman and Sultan (2011), Sultan (1995, 2000, 2003, 2004, 2007, 2010, 2017, 2019), Sultan, Horgan-Kobelski, et al. (2012), and Sultan and Stearns (2005); pretty well presented in Sultan (2015).

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Keywords: Ecological Developmental Biology; signaling systems; plant intentionality; adaptivity and agentivity in plants.

Plants as agents: Against gradualism about the mind

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Mainstream behavioral biology and analytic philosophy commonly treat plants as patients. Since plants are (most of their life-cycle) sessile organisms and lack central nervous systems, they are often thought to be bound to a passive existence without much need complex behavior, and consequently without need for the cognitive and mental properties that often accompanies such behaviors. However, research in plant signaling and communication, and on plant phenomes more generally, has uncovered capacities in plants that challenge this view. Not only do plants show an impressive range of goal-directed behaviors, they are also capable of behaviors that are generally seen as cognitive (e.g., habitual and associative learning, memory and recollection, cross-modal perception). There is thus a need to reconsider how we treat plants, whether we should treat them as agents—as organisms that purposely act on and in their world in a multitude of ways. Philosophy of plant behavior and cognition has hitherto primarily been concerned with establishing how the non-neural physiological signaling mechanisms found in plants can give rise to cognition. A central philosophical obstacle for this research is the concept of representation. The standard representationalist story of mind and cognition consist in a three-step process. First, information in the form of physical signals are received through the perceptual systems and transmitted to the brain. Second, these physical signals are translated into mental representations (beliefs, intentions, concepts, etc.) and processed as such by the mind. Finally, the motor system is employed to perform the will of the mind. It is similar in the philosophy of action. Agency is understood as the capacity to perform intentional actions, and an action counts as intentional when an initial mental state (e.g., wanting beer) causes a behavioral output (e.g., going to the fridge) through a mental representation (e.g., the belief that there is beer in the fridge).

Such approaches are obviously problematic in the case of plants, primarily because they lack a brain (or a functionally equivalent central processing unit) in which we can locate such representations. However, it is by no means clear that we should hold on to the commitments of the mainstream approach when studying plant minds and cognition. Thinking that we should stems from a gradualist approach to mind—the view that mental and cognitive properties are instantiated according to similar principles across the tree of life, and that the differences between organisms is one of degree, and not kind. These principles are best understood in the higher animals, most notably in humans, which then serves as the starting point for thinking about mind and cognition in other beings.

But why should we think that having a mind or exhibiting cognitive or mental capacities will work according to similar principles in plants as in higher animals? I argue that it is gradualism which invites us to treat plants as patients, as plants lack most of the central ingredients of mind exhibited by the higher

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animals—e.g., brains and mental representations. Instead, we should view the concepts of mind, cognition, and agency as being constituted by capacities and abilities which guide behavior. Understood as such, plants can be treated as agents in virtue of exhibiting the behaviors indicative of these capacities, and not by having the "right" mental representations. I conclude by arguing that gradualism about the mind (at best) should be restricted to specific taxa of our phylogenetic tree.

Keywords: (I) Plant cognition, (II) (Non-)Representationalism, (III) Gradualism, (IV) Mind and behavior.