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Matthew Sims
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1 Introduction

Physarum polycephalum (henceforth Physarum), also known more colloquially as ‘the blob’, ‘acellular slime mould’, or simply ‘slime mould’, is a unicellular protist that has continued to attract the interest of biologists over the past century because of its complex life cycle, unique physiology, morphology, and behaviour. It has been used as a model organism for numerous studies, some of which include the investigation of various mechanisms that underpin synchronous nuclear division, the development of drugs for the treatment of cancerous tumours, and the investigation of putative cognitive capacities such as decision making, learning, and memory in organisms that lack nervous systems. More recently, biologists have even used Physarum to study the effects of microgravity on growth and behaviour in outer space.

Although Physarum has much to offer in terms of being a model organism for biological research, as the non-exhaustive list of uses above should make apparent, the aim of this Element is to illustrate how Physarum can be a valuable *tool* for approaching various issues in the philosophy of biology. Physarum’s unique features not only pose a challenge to some of the received views of biological processes but also, I shall argue, provide an opportunity to clarify and appropriately sharpen the concepts underlying such received views. For example, the notion of ‘niche construction’ has become an important – yet not fully agreed upon – concept within the context of evolutionary biology. Roughly, niche construction refers to the idea that evolution is influenced not only by how (genetic) variation allows organisms to differentially adapt to the challenges of their environment but also by how organisms modify their environments and thus alter which selection pressures they are exposed to. By looking closely at Physarum*’s* complex life cycle, an opportunity arises to understand how different kinds of niche construction are exemplified and, more generally, how those different kinds of niche construction often dynamically interact.

Each section of this Element is organised around a distinct philosophical issue as contextualised by Physarum. Using Physarum’s life cycle as a concrete example, Section 2 focuses on the issue of how attention to complex life cycles can provide insights into the intricacies of niche construction. Section 3 addresses the tension between the idea that metabolic exchange is a necessary feature of all known life and the fact that biologists classify spores as a form of life despite their being metabolically inert for long periods of time. Section 4 turns to a central concept in biology – ‘biological individuality’ – and how Physarum’s fragmentation and fusion behaviour forces us to rethink at least one way of understanding that concept. Lastly, Section 5 turns to the issue of whether to understand

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Physarum's use of its extracellular slime trails as a form of memory – and if so whether such memory is subject to explanation in terms of cognition.

In addition to providing a context for investigating various concepts and puzzling issues in the philosophy of biology, the abundance of empirical research on Physarum provides a rich resource for constraining how such issues might be addressed. This is, however, not to say that these issues can be addressed without philosophically getting one's hands dirty – they cannot. One additional important aspect of using Physarum as a tool to approach difficult questions regarding niche construction, biological individuality, and cognition in non-neuronal organisms is that many answers can be used to generate testable hypotheses. In other words, although philosophising is a necessary step in addressing many of these issues, it is not the only or the last step.

Although I will argue that certain ways of addressing the focal issues brought to the fore in this Element are more plausible than others, the conceptual revisions proposed, and conclusions drawn by no means represent anything like a final word – they are tentative in that they can be both revised and/or overturned on the basis of further empirical evidence. This kind of openness to empirical amenability should not be seen as a defect but should rather be seen as an instance of how philosophy and biology are a mutually guiding endeavour; an empirically informed philosophy may be used to generate testable hypotheses and the results of such hypothesis testing should feed back into altering the very philosophical accounts which generated the initial hypotheses. This may be seen as an instance of what Pradeu et al. (2021) have called 'philosophy in science' as opposed to 'philosophy on science'. By throwing into relief some perplexing issues in the philosophy of biology that *P. polycephalum* both raises and can be used to investigate, this Element serves as both an illustration of how this outlier model organism can be used as a tool for the philosophy of biology, and an invitation for both philosophers and biologists to do so. Although the aim of this Element is not to provide a sustained argument for one particular philosophical issue, one might extrapolate from the useful role that Physarum is shown to play in each section to the more general claim that advancing the philosophy of biology requires investigating both typical and atypical model organisms. Concepts and theories based exclusively on the former may be more intuitive but less representative of the incredible diversity found in the biological world.

A few preliminary remarks: each section of this Element begins with some background information that frames the issue at hand and then unpacks the various details required to grapple with the issue. Given the nature of this Element – a book centred upon the philosophy of biology – many of the details will involve both biological descriptions and theoretical concepts: the arsenal of philosophers of biology. I will do my best, however, to avoid bogging the reader down with any unnecessary details for fear of not seeing the forest for the trees. There are also a fair number of figures throughout the Element. These are intended to supplement some of the more abstract concepts and descriptions that are introduced in each section. They are by no means intended as replacements for the text.

I have personally been fascinated – unabashedly so – by Physarum and its behaviour for some years now and I hope this Element can also serve to awaken a level of fascination for Physarum in both readers who are familiar and those who are unfamiliar with this organism that is at least on par with my own.

1.1 What Is *P. polycephalum*?

In order to understand how to use Physarum as a tool, it is important to firstly have a general understanding of what the proposed tool is. *P. polycephalum* is an amoebozoan protist belonging to the class myxomycetes (i.e., the 'acellular slime moulds' or 'true slime moulds') (Stephenson and Stempen, 1994) (see Table 1).

It is a eukaryote (i.e., having a nucleus and other membrane-bound organelles), and like other myxomycetes members, Physarum remains unicellular over the course of its whole life cycle, developing from an uninucleate cell into a multinucleate unicellular mass – a 'plasmodium'.[1] In this life cycle stage transition, Physarum goes from being a microorganism to a bright yellow, giant cell that is visible with the naked eye (see Figure 1). A species with a broad geographic distribution, Physarum lives in wooded areas, taking up residence in/on dead tree stumps and logs that offer the shade, cool temperature, and moisture it needs to survive. Physarum's diet consists of living microorganisms such as

Table 1 Taxonomic classification of *P. polycephalum*

Domain	**Eukaryota**
Kingdom	Protista
Phylum	Amoebozoa
Class	Myxomycetes
Order	Physarales
Family	Physaraceae
Genus	*Physarum*
Species	*P. polycephalum*

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[1] Acellular slime moulds should not be confused with cellular slime moulds of the class *Dictyostelia* (e.g., *Dictyostelium discoideum*). The latter are social amoeba that aggregate at a stage in their life cycle, forming a multicellular vegetative slug.

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Figure 1 *P. polycephalum* plasmodium: a giant, yellow, unicellular mass on a log. (Credit: Rich Hoyer. https://creativecommons.org/licenses/by-sa/3.0/. Unaltered photo). The colour version of this figure is available at www.cambridge.org/Sims

bacteria, yeast, amoeba, and also decomposing organic matter. Small spore-eating beetle species, woodlice, land slugs, and other myxomycetes species are among Physarum's predators (and more broadly, the predators of myxomycetes).

Physarum – in its plasmodial stage – has proven to be easy to culture in labs under conditions roughly mimicking those in which it thrives in the wild. This entails being kept in a humid and dark enclosure and having a steady food supply – usually store-bought dried oats. In addition to its unique features, the ease with which Physarum is cultured has added to its popularity as a model organism.

Having a basic understanding of what Physarum is, let us without further ado put this fascinating organism to work.

2 Niche Construction and Complex Life Cycles

According to Darwinian evolution by natural selection, whether some phenotypes (i.e., observable traits) are selected for and as a result spread through a population over time is largely determined by how well those phenotypes allow individual organisms to cope with environmental selection pressures they encounter (e.g., predation, changes in food availability, changes in exposure to physical stressors, etc.). Different kinds of niche construction may be understood roughly as distinct ways that organisms systematically affect the selection pressures that they, their offspring, and/or cohabitants face. Since whether some phenotypes evolve in a population is at least partly a response to selection pressures *as affected by niche construction*, understanding different kinds of niche construction is required for a more complete account of evolution by natural selection. This presumably involves not only understanding how each kind of niche construction is exemplified in isolation (an abstraction) but also understanding how different kinds of niche construction interact over time in broader natural contexts.

Using Physarum's complex life cycle as one such context, the aim of this section is to investigate different kinds of niche construction and to identify some of the ways that they are causally related. The broader perspective that niche construction brings into focus is how organisms not only plastically adapt to their environments but by doing so also modify their relation to environmental selective pressures in ways that can potentially affect their own evolution, and/or the evolution of other taxa which they regularly interact with. By investigating Physarum's different life cycle stages and the transitions between them through the lens of niche construction, the emphasis is placed upon how those stages, given variation in specific phenotypic parameter values, can go onto influence evolutionary dynamics *and* are quite possibly the outcomes of prior niche construction and ongoing evolutionary dynamics. My aim in this section is not to speculate about any particular role that a form of niche construction has played in Physarum's evolutionary history; rather, it is to exhume the differential importance of different kinds of niche construction and their causally interweaving relations that are specific to different stages of Physarum's complex life cycle. In doing so, this section provides an impetus for future investigation and modelling of the evolutionary dynamics associated with the different kinds of niche construction and their relative significance to the stages of Physarum's complex life cycle.

I will firstly discuss the concept of niche construction and what it was initially a response to. I shall then look at the three kinds of niche construction proposed by Aaby and Ramsey (2019) as a manner of expanding the categories of canonical niche construction theory. After articulating the notion of complex life cycles, I will then describe the details of Physarum's complex multigenerational life cycle. Lastly, I will turn to the task of identifying both the different kinds of niche construction as they arise in the various stages of Physarum's complex life cycle and how those different kinds of niche construction often dynamically interact between and within various life cycle stages.

2.1 Niche Construction: An Overview

Beavers use mud, stones, and tree branches to build dams in rivers. This seems to be common knowledge. However, what are the implications of building dams

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for the evolution of those large rodents we know as beavers? By constructing dams, beavers create small, controlled aquatic pools in which they can easily access primary food sources and nest. The behaviour of dam-building has been so effective in contributing to the beaver's fitness (i.e., survival and fecundity) that this behavioural phenotype has become characteristic of beavers.[2] Moreover, and importantly, at some point in their evolutionary history beavers developed other phenotypes that made aquatic life and dam building easier: webbed feet and a flat, mud-packing tail. In other words, beavers have modified their physical environments in ways that have affected the impact of selection pressures upon them, and this in turn has affected which phenotypes have been selected for. Dam construction on the part of beavers is a paradigm example of niche construction (or at least one type of it as we shall soon see).

Niche construction is 'the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other's niches' (Odling-Smee et al., 2003: 419). From an evolutionary perspective, *niches* may be construed as the collection of all selection pressures that populations regularly encounter (Odling-Smee et al., 2003). Niche construction thus describes how organisms affect their own (and other's) evolution. This kind of approach to evolutionary explanation may be contrasted to those that are known as 'externalist explanations' (Lewontin, 1983) (see also Godfrey-Smith, 1996). Externalist explanations, it is argued, are founded on the supposition that evolutionary change is solely an adaptive response to environmental challenges – a supposition that has found its way in much of neo-Darwinian evolutionary thinking. These explanations emphasise organismal evolution as a function of the organism and the environment while simultaneously relegating the environment to a background condition. The environment, in other words, is viewed as something that is not affected by the organism in any way that is relevant to evolution.

Departing from explanatory externalism, niche construction stresses the idea that organisms are active causes of their own evolution.[3] Whether it is beavers modifying their river habitats by constructing dams, burrowing worms altering the composition of the soil in which they live, or trees shedding leaves and modifying the soil substrate around them, organisms routinely affect their selective environment. To this, proponents of niche construction view inheritance as something that outstrips mere genetic inheritance (i.e., the transmission of DNA across parent–offspring lineages or through bacterial DNA exchange),

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[2] I will continue to use the term 'fitness' to refer to the combination of viability and fecundity, following the convention of how the term is understood in life history.

[3] Some of the key figures in biology and ecology that laid the groundwork for the development of niche construction theory were Darwin (1881), Clements (1916), Schrödinger (1944), and Waddington (1969).

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acknowledging what is called 'ecological inheritance'. This refers to 'the modified environmental states that niche-constructing organisms bequeath to their descendants' (Scott-Phillips et al., 2014: 1233). In acknowledging the importance of the organism's impact upon evolution, the niche construction approach has been viewed as a manner of supplementing standard evolutionary theory, offering a more complete evolutionary explanation than externalist explanations can provide alone (Odling-Smee et al., 2003).

Canonical niche construction theory (Laland et al., 2000; Odling-Smee et al., 2003) recognises two ways that organisms can construct their niches: 'perturbation', occurs when organisms modify their physical environment (think of the beaver and its dam-building); and 'relocation', occurs when organisms modify their spatio-temporal relation to the selective environment (think of birds that migrate every winter to warmer climates to avoid freezing and/or starvation). More recently, Bendik Hellem Aaby and Grant Ramsey (2019) have put forth a tripartite niche construction taxonomy, expanding these two niche construction categories.[4] Although the scope of this section does not permit a detailed treatment of their arguments, a brief description should serve to make explicit their rationale for developing the kind of tripartite taxonomy that they put forth.

Firstly, Aaby and Ramsey note that organisms not only relocate to accommodate changing resource conditions (e.g., temperature, food, predators, etc.) but they also often physically change their spatio-temporal relation to other organisms to maintain and control the flow of information between them. For instance, an antelope might follow a nearby lion in order to remain informed of its potential predator's location, thereby reducing its uncertainty about an attack. This kind of relational modification, although having something in common with relocation, is not covered by it; it is an indirect epistemic pay-off that the antelope's change of spatial location in relation to the lion affords and not a direct pay-off of escape. Thus, the first line of reasoning motivates a broadening of the relocation category.

Aaby and Ramsey's second line of reasoning for an expansion is based upon the idea that in order for canonical niche construction theory to be consistent with the notion of niche that it adopts from Odling-Smee et al. (2003), a third kind of niche construction must be acknowledged. Odling-Smee et al. (2003), in developing the niche construction approach, deploy Walter J. Bock's (1980) *factor–feature interactions* analysis of niche. According to this analysis, 'factors' are selection pressures and 'features' are organismal phenotypes. If a niche consists of the sum of all selection pressures faced by a population, then

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[4] Also see (Sultan, 2015) and (Chiu, 2019) for similar efforts to expand the categories of canonical niche construction theory.

this is just to say that a niche consists of the sum of factors faced by a population that select for organismal features. If something like this is assumed correct, which it is by canonical niche construction theory, then organisms can alter their niche in three ways: (1) modifying factors (i.e., perturbation), (2) modifying the relation between factors and features (e.g., relocation), and (3) modifying their own features. Thus, for niche construction to be consistent with the *factor–feature interactions* conception of niche*, constitutive modifications* to the features of the organism must be taken on as a third category of niche construction.

2.2 Three Kinds of Niche Construction

Aaby and Ramsey refer to the various ways (1–3 in the previous paragraph) that factor–feature relations can be modified, respectively, *as external niche construction, relational niche construction, and constitutive niche construction*. External niche construction (ENC) refers to the modification of the biotic and abiotic environmental factors made by a focal organism, which thereby changes its selective environment, that of its offspring, and/or cohabitants. ENC is equivalent to perturbation of canonical niche construction theory. Paradigmatic examples of ENC include the construction of dams by beavers or the construction of nests by birds. Relational niche construction (RNC) refers to the modification of a focal organism's spatio-temporal location relative to environmental factors but also the modification in relation to other organisms which alter a focal organism's epistemic niche. This latter kind of modification – amongst other things – allows for the maintenance of information flow from one organism to another and is particularly crucial for organised social behaviour that is structured according to a division of labour (Sterelny, 2003). Thus, RNC conceptually includes relocation but represents a broader category than relocation.

Lastly, constitutive niche construction (CNC) refers to the modification of a focal organism's features that alter its causal relation(s) to environmental factors, and thus alters its (or its offspring and/or cohabitants) relation to selection pressures.[5] CNC occurs via the mechanism of phenotypic plasticity – environmentally induced, non-heritable trait modifications that include reversible and nonreversible behavioural and morphological changes.[6] For instance, a plant, being sessile, cannot move to a different location if deprived of light. Instead, it will modify the effects of environmental factors by way of phenotypically plastic responses, sometimes drastically changing its morphology. This might include growing broader leaves to compensate for less light or growing narrower leaves to

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[5] Similar to CNC, the notion of 'experiential niche construction' has been extensively developed by Sultan (2015).

[6] Epigenetic modifications are recognised as one of the key molecular mechanisms contributing to phenotypic plasticity (see Bateson and Gluckman, 2011).

compensate for exposure to excess light (Sultan, 2015). Importantly, such differences in leaf shape amongst members of the same species are not due to genetic differences; they are different environmentally induced forms that genetically identical plants (or the same plant) may take over the course of their (its) development.

Some proponents of niche construction have expressed scepticism regarding such an expansion (see Godfrey-Smith, 1996, 2001; Baedke et al., 2021; Trappes et al., 2022). Part of such scepticism may be seen as stemming from a general worry concerning the ubiquity of niche construction, namely: if every selection-relevant biotic or environmental modification that an organism makes is a form of niche construction, then the concept becomes trivial and of no explanatory use. Discussing and responding to this criticism, Abby and Ramsey remind us that both selection and genetic drift are equally ubiquitous phenomena and that this case does not make them any less useful. Their usefulness in evolutionary theory stems from recognising that not every instance of selection or drift is equally important in every evolutionary process. That is, there are explanatory contexts in which specific forms of selection or drift should be foregrounded, whilst others are backgrounded and this differential importance across different contexts allows selection and drift to remain useful notions. According to Abby and Ramsey, niche construction is similar in this manner. Despite niche construction's ubiquity, the differential importance of different types of niche construction relative to a particular explanatory context can help us to understand and model evolutionary processes. In one particular stage that makes up Physarum's complex life cycle (or transitions to and/or from that stage), a number of different types of niche construction are possibly at play. However, understanding the differential importance of ENC, RNC, CNC, or any combination thereof relative to that stage can be useful in understanding (and informing models of) the evolutionary dynamics that have stabilised that stage within the sequence of stages that make up Physarum's life cycle.[7]

Another worry that some sceptics have raised has to do with the idea that describing a plastic response in terms of something like CNC fails to provide any additional information about that response and, thus, to do so is unwarranted. This worry, however, overlooks the fact that although phenotypic plasticity is a mechanism that underwrites niche construction, considering the evolutionary consequences of plastic responses is extrinsic to any accurate description of a response as such. Describing some variable response as a form of phenotypic plasticity is to acknowledge that it is a change in phenotype in response to an environmental or internal cue without any accompanying

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[7] I would like to thank an anonymous reviewer for pushing me to clarify this point.