On Mushroom Individuality

This paper is an application of the principles of individuality found in Guay and Pradeu (2016a) to illuminate biological individuality in mushrooms. I begin with the distinction between logico-cognitive individuals and ontological individuals (Chauvier 2016), and then I argue for genidentity (Lewin 1922, Guay and Pradeu 2016b) plus material continuity, as a minimum conception of ontological individuality in biology. Of the many materially-continuous genidenticals found in fungi, only those with functional roles in biological theory, either evolutionary or physiological, warrant consideration. Given numerous ways that theory picks out materially-continuous genidenticals in fungi, I argue for a pluralistic account of mushroom individuality.

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1. Introduction

Mushrooms play an essential role in many terrestrial ecosystems, but they have historically received less attention from biologists than their plant and animal counterparts. This lack of attention to mushrooms, and to fungi more generally, is also evident in the philosophy of biology literature, where fungi are often completely ignored, or mentioned only as pathogens of plants and animals, Booth (2014) being an exception. In this article I apply the principles of individuality from several chapters in Guay and Pradeu (2016a), *Individuals Across the Sciences*, in order to elucidate individuality in a single example from mycology, a patch of chanterelle mushrooms.

I begin by noting the distinction between *logico-cognitive individuals* and *ontological individuals* (Chauvier 2016), and then I argue for genidentity (Lewin 1922, Guay and Pradeu 2016b), coupled with material continuity (Griesemer 2000), as a minimum conception of biological individuality. I then employ evolutionary and physiological theory to sort out notable biological individuals from the multitude of non-notable materially-continuous genidenticals. In closing, I argue for a kind of pluralism that recognizes individuals of greater and lesser degree, but considers any materially-continuous genidentical which plays a role in biological theory to be an individual.

2. Individuals in Thought and Nature

P*henomenal individuation* (Pradeu 2012, 230) is a process by which a particular thing, such as a rock, a tree, or a bird, stands out from the background clutter as one individual in a world composed of many other individuals. Phenomenal individuation automatically generates a *logico-cognitive individual* from sensory input, but the logico-cognitive individuals generated by phenomenal individuation often fail to map onto *ontological individuals* in the world (Chauvier 2016). In other words, our intuitive notions of individuality can fail to carve nature at its joints. Unmasking the real joints between ontological individuals requires that the natural world be viewed through the lens of scientific theory (Hull 1992). In biology, individuating theories fall into two broad categories: evolutionary theories and physiological theories (Guay and Pradeu 2016a). This article considers individuation in mushrooms from multiple theoretical perspectives, with the aim of generating logico-cognitive individuals which map onto notable ontological individuals in fungi.

3. The Minimum Conception of Biological Individuality

Every biological individual is a whole composed of parts, so it might be natural to think that, at minimum, a biological individual must be a mereological sum. However, as Haber (2016) observes, an organism, the paradigm biological individual (Hull 1976, Pradeu 2012), continuously exchanges parts with its environment, and is therefore constituted by different

parts from one moment to the next. The principle of identity for a mereological sum just is its parts, so if one conceives of an organism as a mereological sum, then one must countenance a series of organisms coming into and passing out of being with each breath and each meal. Because an organism is composed of different parts as it persists through time, mereology cannot ground the identity of an organism. Species-level biological individuals present another problem for a mereological account of biological individuality. Sober (1984) observes that the species *Homo sapiens* would still exist, even if he had never been born. The identity of a species is not dependent upon the existence of any one organism, so a species cannot be a set of organisms defined by its extension. While Sober's objection is directed toward conceiving of species as sets (Kitcher 1984), the objection from counterfactual constitution is equally problematic for species conceived of as mereological sums; neither a set nor a mereological sum would maintain its identity if it happened to be constituted by different members or different parts, as both sets and mereological sums are defined by their constituents. Because the identity of a biological individual is not determined by its parts, mereology cannot serve to ground a minimum conception of biological individuality.

Genidentity (Lewin 1922, Guay and Pradeu 2016b) is a better candidate for a minimum conception of ontological individuality within biology. A genidentical is any spatiotemporally-continuous series of events, in which event E1 causes E2, E2 causes E3, and so on. A wave propagating down a beach is an example of a genidentical. The wave occupies different places at different times and is composed of different water molecules at

each place and time, but each spatiotemporal wave stage is caused by the wave stage that precedes it and causes the wave stage that follows it. A spatiotemporally-continuous *world-line* of causes and effects marks the progress of the wave as it propagates down the beach, and it is this world-line, not the wave's mereological composition, which accounts for the wave's identity through time. Biological individuals, such as organisms, cells, and species, are similar to a wave, in that each biological individual occupies a continuous region of space as it persists through time, and, like the wave, each spatiotemporal stage of a biological individual causes the existence of the next spatiotemporal stage. Insofar as every biological individual traces a unique world-line of cause and effect through the space time continuum, every biological individual is also a genidentical.

Genidentity by itself, however, does not suffice for a minimum conception of biological individuality, as many genidenticals with biological stages are clearly not biological individuals. A mushroom and a mycologist's drawing of the mushroom, for example, are both stages of one genidentical, whose other stages include the log from which the mushroom is growing, photons bouncing off the mushroom, and the mycologist's eyes, brain, and hands. The mushroom specimen and the drawing are not, however, parts of one biological individual, even though each is a stage of one genidentical.

Guay and Pradeu (2016b) cite momentum transfer through a series of billiard ball collisions, as an example of a genidentical whose successive stages share no material components, but in the case of a water wave, each stage of the wave shares some matter,

some water molecules, with its preceding and subsequent stages. Biological individuals are more like the water wave than they are like the billiard ball collisions, in that each stage of a biological individual inherits some material components from the stage that precedes it, and transfers some of its matter to the next stage. While an organism continuously exchanges matter with its environment, the change in material composition is never wholesale in a single moment – some matter is always held in common by proximal stages, even though all material might be completely replaced in the long run. Pam, who is ten years old, for example, might share no material parts with her one year-old self, but one year-old Pam shares some matter with two-year old Pam, and two year-old Pam shares some matter with three year-old Pam, and so on; the lineage from one year-old Pam to ten year-old Pam is materially-continuous, even if the beginning and end stages of the lineage hold no material parts in common.

Species are likewise materially-continuous. Gametes, which originate as parts of parental organisms, supply the material which composes the first stage of the next generation (Griesemer 2002), so genidenticals that trace reproductive lineages are materially-continuous in the same way as genidenticals that trace persistence and growth in organisms. There can be no continuity of a biological lineage, at any level of organization, unless there is material overlap between spatiotemporal stages of the lineage, so biological individuality requires some continuity of material composition, though not unchanging composition, as is required for mereological identity.

Combining the elements of spatiotemporally continuity, cause and effect, and material overlap, we arrive at the minimum conception of a biological individual. A biological individual is, at minimum, a materially-continuous genidentical.

4. Theoretical Individuation

Though every biological individual is necessarily a materially-continuous genidentical (from here forward a McG), it would be a mistake to count every McG as a biological individual, not only because there are obvious non-biological counterexamples, but also because doing so would lead to an ontology bloated with non-notable biological individuals. Consider, for example, a herd of buffalo grazing in a field of grass. There exist in the world many spatiotemporally-continuous lineages of cause and effect, composed partly of buffalo stages and partly of grass stages. When a buffalo eats some grass, the grass becomes a cause of buffalo persistence and reproduction, and when a buffalo dies, its rotting carcass fertilizes the growth of new grass. A spatiotemporally-continuous world-line of causes and effects makes for a genidentical, and because grass material becomes buffalo material, and vice versa, each grass-buffalo genidentical is a McG, and therefore meets the minimum conception of biological individuality.

While ecologists are certainly interested in the relations between grass and grazing animals, few if any would consider such a material recycling relation between two species to be a biological individual; none would consider every particular causal lineage, composed of particular buffalo and particular blades of grass, to be its own biological individual, as to do

so would result in an unworkably exploding ontology of individuals. Other more complex nutrient cycles, which involve numerous organisms of many different species, also meet the minimum conception of biological individuality, but biologists do not consider them to be individuals, because they do not function as individuals in any biological theory.

While every McG could in principle function as an individual in a biological theory, biological individuality is usually cashed out in terms of evolutionary role or physiological integration. Hull (1976) cites three different evolutionary roles: unit of mutation, unit of selection, and unit of evolution, and he notes that, "dogmatically", genes are the units of mutation, organisms are the units of selection, and species are the units of evolution. While Hull admits that mutation, selection, and evolution can happen at multiple levels of biological organization, he argues that wherever they occur, there is a biological individual. Others have argued that individuality lies in physiological integration (Pradeu 2012) or in the coincidence of physiological integration and evolutionary role (Pepper and Herron 2008, Godfrey-Smith 2009, Guay and Pradeu 2016). In what follows, I consider physiological integration and evolutionary roles in a case from mycology, in order to illuminate various kinds of mushroom individuals.

5. Mushroom Individuals

Though once considered to be plants, mushrooms are actually the spore-producing fruit bodies of a polyphyletic group of species in the kingdom *Fungi*, which is more closely related to animals than it is to plants (Shalchian-Tabrizi, 2008). Mushroom-producing

species belong either to the phylum *Ascomycota* or *Basidiomycota*, but not all species in these phyla produce mushrooms. So, "*The Mushrooms"* denotes a class, or a set, or a mereological sum, rather than a genidentical, as non-mushroom producing fungi constitute evolutionary links between different species of mushrooms. As a whole, *The Mushrooms* does not meet the minimum conception of biological individuality, but within any given species of mushroom there are numerous McGs to be found. Determining which of these to consider as individuals requires the application of biological theory. Unsurprisingly, the kinds of individuals which biological theories unmask in mushrooms differ quite a bit from the kinds of individuals the same theories uncover when applied to animals and plants. Different kinds of biological individuals result from different mechanisms of physiological integration and different evolutionary strategies deployed in widely divergent sections of the genealogical nexus.

Consider the following example. Walking through a forest you come upon a patch of fragrant yellow mushrooms, poking up through the twigs and leaves under a scarlet oak. Thumbing through your field guide you find a match. The mushrooms are chanterelles, but how many chanterelle individuals are there? You count, 1, 2, 3… 14, wait there is one hiding under a leaf, 15. There are a total of fifteen golden chanterelles sprouting from the ground under the oak tree.

Someone unfamiliar with the physiology of chanterelles could easily mistake these fifteen phenomenal individuals for a population of fifteen chanterelle organisms, but a look

under the ground reveals that each mushroom is connected to the others by a web of delicate white fibers; each mushroom is actually a part of a single physiologically-integrated mycelium. Once one recognizes the mushroom patch as a single physiologically-integrated whole, a new logico-cognitive individual is generated to complement the fifteen phenomenal individuals. Indeed, consideration of physiology calls into question the reality of the phenomenal individuals. At first there appeared to be 15 chanterelle individuals, but when viewed through the lens of physiological theory, the mushroom patch appears to be only one individual, as each mushroom is understood to be a part of a single physiologically-integrated whole. Where phenomenal individuation picked out 15, physiological theory indicates that the mushroom patch consists of only one chanterelle individual.

While physiology recognizes one chanterelle individual, evolutionary theory carves the mushroom patch in complex ways. The chanterelle patch as a whole, the mycelium, is one member of a population of many chanterelle mycelia living in the forest, and as such, it exhibits differential fitness compared to other mycelia in the population. This makes the patch as a whole one unit of selection, one evolutionary individual (Hull 1992), and one Darwinian individual (Godfrey-Smith 2009). Here evolutionary theory agrees with physiological theory in determining the mycelium to be one biological individual, but the mycelium is not the only level of biological organization which functions as a unit of selection in a mushroom patch.

As Booth (2014) observes, in Basidiomycetes, such as chanterelles, a fruiting mycelium is composed of numerous heterokaryotic hyphae, whose nuclei function as Darwinian individuals in a Darwinian population constituted by other nuclei in the mycelium. To understand why nuclei function as evolutionary individuals, we have to look at the way a mycelium forms and how it is organized.

A mycelium is composed of interconnected cell-like structures called hyphae (pl.). A hypha (sing.) is like an elongated cell composed of cell walls, cytoplasm, and various organelles, but unlike the walls of cells, the walls of hyphae have openings at each end, which allow for cytoplasm and some organelles to flow freely throughout the mycelium, while nuclei usually[1] remain confined within a single hyphal chamber.

A mycelium begins its life when a haploid spore lands on a suitable substrate and germinates into a hypha that contains a single haploid nucleus. This original hypha propagates vegetatively by mitosis to form a monokaryotic mycelium, composed of many interconnected chambers, each containing one nucleus that is a clone of the nucleus from the original spore. When two monokaryotic mycelia of compatible mating types come into contact, cell walls at the growing tips of each parental hypha fuse to form a new hyphal chamber into which cytoplasm and one nucleus from each parental mycelium flows. This process of hyphal fusion, called plasmogamy, is similar to the first stages of fertilization in

[1] Very few claims are true of every species of mushroom in every situation, so I qualify this claim with "usually". Exceptions to the rule, while interesting, are beyond the scope of this paper.

plants and animals, but fusion of the two nuclei into a single diploid nucleus does not immediately follow plasmogamy. Instead, the new dikaryotic hypha propagates vegetatively by mitosis to form a dikaryotic mycelium, in which each hyphal chamber contains two haploid nuclei, one from each parental monokaryotic mycelium. When environmental conditions are right, the dikaryotic mycelium forms mushrooms, and only on the fertile surface of a mushroom, moments before spores are produced, do the two nuclei fuse in a process called karyogamy, to form one diploid nucleus. This diploid nucleus then immediately undergoes meiosis to produce the next generation of haploid spores.

The dikaryotic mycelium just described has only two parents, but the genealogical makeup of a mycelium is often complicated by parasexual recombination (Alexopoulos et al. 1996), which occurs when a tertiary monokaryotic mycelium encounters a dikaryotic mycelium and temporarily fuses with it, displacing one nucleus in a dikaryotic hypha with one of its own. The dikaryotic hypha which trades one of its nuclei with the third partner then propagates vegetatively, resulting in a heterokaryotic mycelium composed of nuclei from three parental lineages. A single mycelium can engage in numerous parasexual couplings, resulting in a mycelium composed of many more than two parental lineages. Consequently, numerous genetically-distinct pairs of nuclei can occupy the hyphal chambers of a single dikaryotic mycelium, where they exhibit differential fitness along multiple parameters. This differential fitness among the nuclei is eventually expressed in different numbers of spores of varying viability produced by the mycelium's mushrooms. Because the genetically-distinct nuclei have differential fitness and engage in reproductive competition,

each nucleus is a Darwinian individual in a Darwinian population that includes other nuclei in the mycelium.

Evolutionary theory has thus far illuminated one fungal individual at the level of the mycelium, and unaccountably many fungal individuals at the level of the nucleus, but there is yet another way in which evolutionary theory carves the mushroom patch into individuals.

Ellen Clarke (2012) notes that mutation can occur as a plant propagates vegetatively, such that one shoot can be genetically distinct from another that arises from the same seed and the same root. Genetic differences between parts of a single plant, coupled with a lack of germ-soma separation in plants, can lead to differential fitness between the parts, and thus different shoots of a single plant can function as different evolutionary individuals. A similar mosaicism can result from mutation in a vegetatively propagating section of a mycelium, which, like a plant, lacks germ-soma separation. This mosaicism can lead to differential fitness in different parts of a mycelium, including the fruit bodies. Some mushrooms will be large, well-formed, and well-suited for dispersing spores, while others will be smaller and misshapen. Yet other mushrooms will abort before they reach maturity and will produce no spores at all. Consequently, on evolutionary theory, particular mushrooms arising from a common mycelium might really be different evolutionary individuals, as mutations occurring in some hyphal lineages can result in fruit bodies which exhibit differential reproductive fitness.

So far, evolutionary theory has picked out at least three distinct levels of biological individuality in one patch of mushrooms: the mycelium, the nuclei, and, if mutations result in mosaicism, the fruit bodies. While there may be other cryptic levels of selection yet to be discovered within a chanterelle patch, there might also be an evolutionary individual that transcends the mycelium and includes a nearby individual of a different species.

Like most species of woodland mushrooms, chanterelles derive their sustenance from mycorrhizal symbiosis with trees. A chanterelle mycelium envelopes its host tree's roots and exchanges phosphorus and other trace minerals which it collects from the soil for carbohydrates produced by photosynthesis in the tree's leaves. Because the oak and the chanterelle mycelium depend on each other for their nutrition, their evolutionary fates are linked, and because chanterelles live only in association with trees, every chanterelle mycelium in the Darwinian population of mycelia has an obligate arboreal partner. The chanterelle-oak partnership maps onto a spatiotemporally-continuous line of cause and effect, and nutrient exchange accomplishes material overlap between the stages, so the symbiotic collective is a McG, and thus meets the minimum conception of biological individuality. If this one oak-chanterelle McG happens to function as a Darwinian individual in a population of other oak-chanterelle pairs, then the chanterelle mycelium and the oak taken together will constitute a forth kind of evolutionary individual, in addition to the mycelium by itself, the nuclei, and the fruit bodies.

Of course the collective entity composed of part chanterelle and part oak also counts as a physiological individual, as the tree and the mycelium perform different roles in a single metabolic process that benefits both symbionts. Whenever evolutionary theory and physiological theory coincide to pick out the same McG, as is the case for the mycelium by itself, and maybe for the mycelium-tree symbiotic collective, the biological individual picked out is more robustly individual than when a McG functions in only one theoretical role. In addition to differences in degree of individuality imparted by theoretical robustness, a physiological individual's degree of individuality also turns on how tightly its physiological processes are integrated and how autonomous those processes are. A nucleus, for example, is physiologically-integrated to a certain degree, but it cannot perform its metabolic function or replicate itself without aid from other organelles in its hypha. As such, a nucleus has a lower degree of physiological autonomy and integration than the hypha of which it is a functional part. From the perspective of physiological theory, a nucleus has a lower degree of *ontological autonomy* than its hypha, just as the corner of a door has a lower degree of ontological autonomy than the door of which it is a part (Chauvier 2016). Because physiological integration and functional autonomy comes in degrees, and because physiological theory and evolutionary theory can coincide to make a biological individual more robust, it follows that biological individuality comes not only in different kinds, but also in different degrees.

Our application of theoretical considerations has revealed a number of different kinds of materially-continuous genidenticals, which function as individuals in a mushroom

patch. These theoretical individuals fall into two broad categories: physiological individuals and evolutionary individuals. Physiological individuality comes in degrees, such that some physiologically-individuated McGs have more individuality than others. Evolutionary individuality, on the other hand, appears to be a bivalent condition – either a McG is an evolutionary individual or it is not, but as we have seen, evolutionary individuality occurs at multiple levels of biological organization. Complicating things further, a single McG sometimes functions as both a physiological individual and an evolutionary individual, in which case it is more robustly individual than a McG which functions in a single theoretical role.

In light of the complexity of mushroom individuality revealed by biological theory, one might be tempted to search for the kind of McG that exhibits the greatest degree of individuality, and then call that one kind of McG *the* mushroom individual. While this move would simplify our ontology, I think it would be a mistake, as singling out one kind of mushroom individual at the expense of all the others would yield an incomplete picture of theoretically-interesting components of mushrooms. Instead, I argue for pluralism in our concepts of mushroom individuality, not a promiscuous pluralism that would count every McG composed of biological stages as a biological individual, but rather a theoretical pluralism, which counts as an individual every materially-continuous genidentical which theory warrants as notable.

6. Conclusion

This examination of mushroom individuality, like any consideration of individuality in nature, has endeavored to map logic-cognitive individuals onto ontological individuals, so as to make our concepts of mushroom individuality match real divisions in nature. We cannot carve nature at its joints, because the joints between ontological individuals are determined by natural processes beyond our control, but we can use philosophical principles and scientific theory to bring our conceptual individuals into line with real individuals in the world. I have argued that biological individuals, and hence mushroom individuals, are, at minimum, materially-continuous genidenticals (McGs). To consider every biological McG as an individual would result in an unworkably bloated ontology, so I have further argued that we should apply biological theory to identify noteworthy biological individuals from among the multitude of genidenticals which meet the minimum conception of biological individuality. Theoretical considerations reveal numerous kinds of physiological integration and evolutionary roles in mushrooms, and I have argued for a pluralism that recognizes the individuality of any materially-continuous genidentical that functions in one of these theoretical roles.

For the sake of brevity, I have applied these principles of individuality to only one example, a patch of chanterelles, but these same principles could be used to understand individuality in any number of examples from mycology, and biology more generally. Whereas theoretical considerations identify nuclei, mycelia, and fruit bodies as individuals

in a mushroom patch, these same theoretical considerations might pick out genets and ramets in a plant population, or particular organisms, family groups, and populations in an animal species. The principles of biological individuality that I have applied here to mushrooms will likely yield different kinds of biological individuals when applied to other living things, but the principles themselves are universal in their biological scope.

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