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Is evolution fundamental when it comes to defining biological ontology?

Yes

To make a case for an affirmative answer to the title question I should say something about what ontology, especially biological ontology, is; Something about what sort of criteria we might use in evaluating different approaches to defining biological ontology; And, finally, what it would mean to take evolution as fundamental in the latter activity. Most of the discussion will centre on a particular item of biological ontology – the *individual* – and on the merits of an evolutionary definition of that item, as opposed to a metabolic definition.

1. Ontology – what are concepts for?

Ontology is the study of what there is; of what sorts of things exist. It describes the attempt to come up with a classification scheme that lists the underlying furniture of reality. Biological science involves all sorts of specialist words with technical meanings. These words are supposed to help us, when we look at biological things (we can call separate things 'particulars'), to divide those things into different groupings, called 'kinds'. We place things together in the same kind when they sh are some properties in common. For example, 'HoxA' refers to a group of genes that are found on chromosome 7 of the human genome, as well as in many other lineages, and which are important in determining the body plan of the developing embryo. We name kinds, in this way, to help us in making inferences about things – in predicting how things are going to behave.

Living stuff can be parcelled up into many different kinds of particulars. Some possible kinds – such as those picked out by terms like 'protein', 'cell', 'liver' and 'gene' - seem more obvious to us than others. But kinds are easy to come up with. Jorge Luis Borges' mock encyclopaedia divided animals into fourteen different kinds, including 'Those that belong to the emperor, embalmed ones, those that are trained, suckling pigs, fabulous ones, stray dogs' and 'Those drawn with a very fine camel hair brush' (Borges 1937). There is a possible kind that contains the top-most half of every human's body. The kind is not empty – people really do have top-most halves. What is doubtful is how useful it could be.

The truth is, we don't want to detail all of the different kind concepts that are possible. But which ones do we want? Sometimes philosophers distinguish silly examples like mine and Borges' from 'natural kinds', where the latter pick out groupings that are discovered in nature, rather than made up by us. The line between the two is difficult to draw, however. It is easier to agree that some kinds are more useful than others. Although usefulness is always relative to a purpose, some kinds are useful across a wider range of different purposes than others. For example, a mushroom hunter might classify a fungus in order to find out if it is edible or not (Dupré 1993). But chemical element classifications – probably the most useful kinds we have ever named – are useful for chefs, and also paint mixers, and fireworks manufacturers and many other groups of people who have divergent purposes in classifying the properties of chemicals. In evaluating definitions of kind concepts, then, I suggest we rank the more useful concepts as more valuable – more worth holding on to, worth teaching – than alternatives that have fewer uses, or are useful across a smaller range of circumstances. This claim applies to kinds in general, but here I focus on applying it to one kind in particular – the biological individual.

I'm going to argue that evolutionary concepts of biological kinds are *more* useful than other concepts, at least in the special case of the kind 'biological individual' and of my 'Levels of selection' account of it. That is, in the particular case of the kind 'biological individual, I'll argue that the Levels of selection definition is the most useful. 'Fundamental' is a daft word really, an indirect way of putting things in caps and little more. It neighbours with 'most important', 'most interesting', perhaps suggests that other things can be reduced to it. I make none of those claims for the evolutionary definition of the biological individual. Yet I will certainly defend the importance and interest of the evolutionary definition. And I will even present some reasons to think that the evolutionary definition has a certain sort of priority over other definitions.

2. Biological Ontology: individuals

O'Malley and I share an interest in arbitrating the usefulness of concepts aimed at picking out biological chunks which are smaller than clades but bigger than organs. Naming the chunk of interest is made complicated by the huge number of distinct concepts (see Table 1.) which have been targeted at these units, none of which quite coincides with the concepts O'Malley and I each endorse.

Term	Used by	To mean	Examples	
Evolutionary individual	Michod 2005; Ereshefsky & Pedroso 2015; Bouchard & Huneman 2012	Unit which exhibits heritable variance in fitness	*Volvox carteri* Bacterial biofilms	1a
Evolutionary individual	Janzen 1977	Genetic individual –all the parts share one unique genome	Dandelion clone, aphid clone	1b
Organism	Kant 1790	Unit which exhibits organisation	Horse	2a
Organism	Pradeu 2010	Physiological individual, delimited by immune system	Human-gut microbes collection, *Botryllus schlosseri*	2b
Organism	Wilson & Sober 1989	Unit which exhibits functional integration	Eusocial insect colonies, Squid-vibrio collection	2c
Organism/biological individual	Godfrey-Smith 2013			
Organism	Pepper & Herron 2008	Evolutionary individual	Mouse, Honeybee colonies, *Buchnera*-aphid collection	1a
	Queller & Strassmann 2009			1c
	Folse & Roughgarden 2010			1d
Superorganism	Gardner & Grafen 2009	Evolutionary individual	Clonal groups Honeybee colonies	1e
Darwinian individual	Gould & Lloyd 1999	Units at *all* levels of compositional hierarchy	Gene, mitochondrion, cell, horse, species	3
Simple	Godfrey-Smith 2009	Evolutionary	Bacterium	1a

reproducer, Darwinian individual		individual		
Scaffolded reproducer, Darwinian individual	Godfrey-Smith 2009	Lineage-forming part of an evolutionary individual	Virus, chromosome	1f
Collective reproducer (higher-level Darwinian individual)	Godfrey-Smith 2009	Unit which exhibits bottleneck, germ separation and integration	Human, Aphid-*Buchnera* collection, colony, buffalo herd	1g
Biological individual	J Wilson 1999	Biological particular	Developmental module, organ, protein, gene regulatory network	4
Unit of selection	Lewontin 1970	Unit which exhibits heritable variance in fitness	Deer, cellular organelles,	1a
Unit of selection	Maynard Smith 1987	Unit which exhibits fitness variance	Somatic cells	5
Unit of selection	Brandon 1999	Developmental module	Neural crest	6
Unit of selection	Lloyd 2005	Interactor	Horse	7
		Replicator	Gene	8
		Manifester of adaptation	Horse	1e
		Beneficiary of adaptation	Gene	9
Unit of evolutionary transition, reproducer	Griesemer 2000	Unit which copies with material overlap and development	Giraffe, *E. coli*	1h
Unit of evolution	Maynard Smith 1987	Unit which exhibits heritable variance in fitness	Horse	1a
Biological individual	Dupré & O'Malley 2009; O'Malley this volume	Unit of metabolic collaboration	Human-gut microbes collection; *Medicago*-Rhizobial bacteria collection	2d
Evolutionary individual	Clarke 2013; In review	Unit with capacity for heritable variance in fitness only at one level, in virtue of individuating mechanisms	Horse, Meiotic driver gene, Tasmanian devil facial cancer, aphid-*Buchnera* collection.	1i

Table 1.

I've used a numbering system to indicate where there is repetition or where different definitions constitute rivals for a single concept. The two concepts with the greatest number of alternative definitions are 1 and 2, which we may think of roughly as 'evolutionary' and 'organisational' concepts respectively. This rough method indicates that there are around nine distinct concepts named in this table. The table exhausts neither possible nor actual concepts in the vicinity. Some concepts – number 6, for example, are obviously distinct and not intended to compete against the others - we might say that its resemblance to the others is only semantic. Yet all of the concepts are united in picking out some thing that is a *biological* thing, and which is supposed to conform to some very general standards of particularity (thingness), such as spatiotemporal location and cohesion[1].

While O'Malley advocates a particular sort of organisational concept – a metabolic concept -of the individual, I advocate instead for a sort of evolutionary concept. These are distinct concepts, rather than rival definitions of a single concept. I think there really are chunks that fit the definition underlying O'Malley's metabolic concept, and they really are different chunks from those picked out by my own definition. Neither will I resist the distinctiveness of the other eight concepts listed (though I might think that some definitions of them are better than others) nor, for that matte r of 'My right leg and my left eyelid plus my hamster's tail'. What I discuss, instead, is the relative *usefulness* of these distinct categories and I will defend my conviction that the concept numbered '1' in my table, and especially that version of it numbered '1i' stands above the other concepts in terms of usefulness: the predictive inferences it supports, the explanatory value it offers, and the range of contexts across which it offers these advantages.

These are not the only reasons we might have for maintaining a concept. Some are valuable because they capture an intuitive or historical idea, rather than for their inherent clarity or empirical applicability. There is always a tension between preserving the traditional meaning of a term, in order to avoid the communicative disruption brought about by revision, and seeking to enhance the work our language does for us by urging revisions. I suspect that the former urge pulls in favour of those organisational concepts numbered '2' above. My agenda here is unashamedly revisionist, however. While I do understand the reassurance offered by maintaining concept '2', I also think that science has made available an enhanced concept: evolutionary theory is able to explain why our ancestors came to use concept '2', as I'll explain in part 6. In a nutshell, I accept O'Malley's claim that her metabolic individuals are distinct from my evolutionary individuals – but I deny that the concept she defines is useful enough to be worth holding onto.

First, note that the definition I advocate is not the same as the ones criticized by O'Malley - what *she* calls the evolutionary individual. O'Malley's targets correspond to the definitions numbered 1b and 1g in my table. What, instead, is the concept '1i' that I advocate?

3. Clarke's Levels-of-selection approach to evolutionary individuality

The concept I define refers to a kind, and the definition allows us to decide whether particular things belong in the kind group or not. The concept functions as a 'sortal' term, so it allows us to answer questions about *how many* members of the kind there are – to count individuals. All concepts work by drawing distinctions, and my concept distinguishes individuals from *parts* of individuals, and from *groups* of individuals (Pepper & Herron 2008). There are concepts which are similar but which define

[1] Although whether all these concepts do in fact meet those standards is open to debate.

a biological individual in contrast to something distinct. For example, we might be concerned to distinguish a biological individual from a *non*-biological individual. Or between living and *non*-living things. Similarly, we might want to distinguish a biological individual from a biological *process* or *property*. These distinctions must be drawn by distinct concepts. Most commentators in the debate regarding biological individuality, sometimes also referred to as a debate about organismality, are concerned with the distinction between individuals, groups and parts, all of which may be assumed to be biological/alive, and all of which may be assumed to be objects as opposed to properties or processes[2].

Evolutionary definitions distinguish biological individuals from biological parts and from biological groups by thinking about which things are treated as objects, rather than as parts or as groups, *by the process of evolution by natural selection*. Several subtly different evolutionary definitions have been proposed (see all concepts labelled number 1 in Table 1). My 'Levels-of-selection account' defines an evolutionary individual in terms of its possession of mechanisms that ground a capacity to participate in a process of evolution by natural selection.

Definition: An evolutionary individual is a collection of living parts which has some *capacity* for responding to selection at the between-collection level, *because of* the action of individuating mechanisms.

The relevant capacity is one that objects can have more or less of, and they can have it at multiple hierarchical levels[3]. *Exclusive* evolutionary individuals have the capacity at only their own hierarchical level. Simplifying a little, an evolutionary individual is the stuff that has the capacity to respond to natural selection. We add more detail to that description by looking to evolutionary theory to tell us what sorts of properties an object needs to have in order to respond to natural selection. Lewontin, building, of course, on Darwin, summarised these properties as reproducing with heritable variance in fitness (Lewontin 1970). And we can add even more by detailing the sorts of mechanisms that can ground the manifestation of those properties[4] (Clarke 2013). As an example, a bottleneck in the individual's life cycle can help to ground heritability across generations of those individuals, by sieving out genetic variation that could otherwise lead to lots of divergence between generations.

If we focus on an object that is too small it won't have the properties necessary for responding to selection – my concept says it's a mere part of an individual. Likewise, if we focus on an object that is too big, it won't have the properties either. Empirical investigation together with evolutionary theory can tell us, of any particular bundle of living matter, whether it does or doesn't have the properties necessary for responding to natural selection. The concept thus generates verdicts about the individuality of any lump of living matter – for example, mitochondria are not individuals, but parts; ecosystems are not individuals but groups; symbiotes in general are proper parts only to the

[2] One implication of this is that my account doesn't deal with viruses. Only *if* we decide to consider them as alive, then I say they are evolutionary individuals.
[3] Note the implication of this that some thing may be an individual as well as being a part, or a group, if the relevant capacity is grounded at different hierarchical levels to intermediate degrees.
[4] There are two types of mechanisms which are together sufficient a) policing mechanisms which prevent the object's parts from undergoing differential selection and b) demarcation mechanisms which enable to object to compete against others of its type. There are many different ways to realise these mechanism types, and they vary across different lineages. See Clarke 2013 for details.

extent that there are mechanisms guaranteeing their common response to selection along with their partners.

My evolutionary concept satisfies the desiderata of a good scientific concept. It supports inferences of a very useful kind. Plugged into the theory of natural selection so that it bears fitness, the evolutionary organism concept supports successful *quantitative* predictions (about the likely spread or decrease of a trait in the population), as well as generating *explanations* of the surprising design and diversity we observe around us (Clarke 2012; In review). It is very general, because it is applicable to objects in every single part of the tree of life, rather than being restricted to particular groups or particular eras (Clarke 2013). So it is highly projectible, which means that it can support a very wide array of inductive inferences, without being limited to particular times or places.

One of the primary functions of this evolutionary definition of the individual is to unify the 'organism', which functions as the bearer of fitness in standard evolutionary models, with the major transitions literature (Margulis 1970; Buss 1987; Wilson & Sober 1989; Maynard Smith & Szathmary 1995). In particular, with those accounts of major transitions which treat a transition as an event in which a new individual is formed, at a new hierarchical level of selection, by merger of pre-existing individuals (Michod 1999; Okasha 2006; Bourke 2011; West et al 2015)[5]. On this view, the unit which bears fitness and the unit which emerges during a process of transition are one and the same.

My concept doesn't mistake genes as the only source of heritability in evolution and certainly does not equate to Janzen's view (concept 1b) which delimits living things by genotype. Genetic homogeneity is not a necessary or sufficient condition of individuality on my account. Population genetics doesn't really settle problems of evolutionary individuality at all. It assumes that diploid organisms will bear two copies of each gene, but it doesn't make any further claims about what qualifies as an organism[6]. We can track the fitness of seeds, leaves, whole trees or even whole clones. We can even track the fitness of somatic cells or mitochondria if we choose to. We just won't generate accurate predictions about the future traits of such units if they are not functioning as levels-of-selection individuals.

4. Legume–rhizobial sets

In her article, O'Malley (this volume) highlights the ancient symbiotic relationship that takes place between between plants of the *Medicago* genus and a set of rhizobial bacteria, as a particularly strong example of a metabolic individual. These bacteria fix nitrogen within specially adapted nodules on the roots of the host plant, which in its turn provides those bacteria with carbon. Any plant may host ten or more rhizobial strains at the same time. Each partner is able to survive independently of the other – the symbiosis is not obligate - but each do much better when enjoying an association (Denison & Kiers 2011).

An evolutionary view treats this case as one in which a multitude of distinct evolutionary individuals interact with one another. The plant is one such individual, and each bacterial cell is another. The

[5] Note that this is not the way O'Malley understands major transitions.

[6] Genes themselves are not evolutionary individuals, on my view, except on those occasions when they are selected separately from the rest of the genome, as in the case of meiotic driver genes.

combined set fails my definition of an evolutionary individual because there is no mechanism for transmission of phenptypes across generations. The bacteria are transferred horizontally, in that they are taken up from the environment early on during the plant's development. Because the bacteria spread through the soil, while the plant seeds travel above ground, the two lineages don't track one another - any plant tends to be infected by different strains of bacteria from those that infected its parent plants. This means that novel plant-bacterium phenotypes will rarely be passed on. Bacterial mutations are passed on to offspring bacteria and might do well if they are successful across a range of different plant hosts. And plant mutations are passed on to offspring plants, where they can do well if they are successful in interaction with a range of different rhizobial strains. But novel traits whose success depends on a particular bacterium-plant pair will be lost. The evolutionary fates of the different partners thus fail to coincide – they do not respond to selection as a unit.

The separation of the distinct evolutionary individuals is essential to explaining various phenomena associated with this symbiosis. For example, horizontally transmitted symbiotes tend not to co-speciate with their partner, or undergo genome reduction, because selection acts in the normal way on each separate species population. The bacteria spend part of their life cycle surviving without a plant's help, and they have to compete with one another for access to the plant hosts. This process sieves out those deleterious mutations that can accumulate in the genomes of vertically transmitted symbiotes (Bright & Bulgheresi 2010).

If I resist the reification of metabolic individuals do I lack resources to explain 'how the plant gets by in the world' (O'Malley, this volume)? Not at all. An evolutionary approach recognises the bacteria as a very important part of the plant's environment, and vice versa, aiming to elucidate the fitness gains each partner gets from the interaction.

One particularly strong example of an evolutionary explanation of these symbioses draws on market theory in economics (Werner et al 2014). This view makes sense of the enduring relationship at the level of the two-species – and the footprints that long relationship has left on the genomes and phenotypes of each species – by taking account of the fact that the metabolic relationship is not fixed across the lifetimes of the partners, but is instead dynamic. The plant is able to modify the quantity of the metabolic resource it provides to the bacteria. This enables it to impose sanctions – providing less carbon and restricting oxygen supply - on those nodules which underperform their nitrogen-fixing duties (Kiers et al 2003), or to preferentially allocate resources to top-performing nodules. This is significant in so far as it helps us to explain how the interaction remains stable against cheaters – the plant can simply withdraw its cooperation from partners that don't pay their way, and so maximise the amount of nitrogen it gets. In fact, some parasitic rhizobial strains are able to cheat this system, by sharing a nodule with a mutualistic strain. Denison & Kiers think the symbiosis survives despite this threat *because* the expected fitness benefits to mutualistic strains depend on their abundance in the local area relative to host plants (Denison & Kiers 2004a). The theory of biological markets predicts that the 'price' demanded for any service will fluctuate according to various factors including the number of hosts as well as competition for hosts, in addition to environmental conditions such as background levels of nitrogen. Note that these models don't rely on being able to circumscribe the markets. It is assumed that the number of players in a given market will be variable, and that buyers/sellers will come and go over time (Wyatt et al 2014).

5. "Nothing makes sense except in the light of evolution"? (Dobzhansky 1973)

There are some old reasons to think that evolutionary explanations take a very general sort of priority over others, as Dobzhansky insisted. For example, many authors have held that ultimate (evolutionary) explanations, which explain a trait by invoking a history of selective success, have priority over proximate explanations, which explain a trait by detailing its more immediate developmental or mechanical causes: *why* is always more important than *how*. However, recent authors have argued convincingly that this distinction between proximate and ultimate causes is, in the end, unsustainable (Laland et al 2011; Calcott 2013; Laland et al 2013). Real evolutionary processes involve ongoing reciprocal causation between populational and mechanical phenomena, such that the status of any particular cause as either proximate or ultimate is perspective-dependent. A metabolic phenomenon occurring as a consequence of mutation or environmental shift may be treated as proximate, and a mechanistic explanation sought for its consequences. But among these consequences may be subsequent selection driven by an effect on fitness, putting the very same phenomenon into an ultimate explanatory role. So complete evolutionary explanations will include many and varied how and why components. In explaining the emergence of a new evolutionary individual during a transition event there are numerous explananda. At each stage, we are interested in accounting for *why* the new individual emerged – ie what was the selective benefit (Calcott 2008)? We want to know *how* it emerged – what was the series of mutations of developmental steps or environmental changes that allowed the benefit to be enjoyed? And we also want to answer a maintenance question – what prevents the interaction from breaking down? Little is served by competing these components against one another.

Brandon and Rosenberg advanced a different argument, that biological kinds have to be understood evolutionarily, because they are inherently functional. *"To call something a wing, a feather, a tissue, a cell, an organelle, a gene, is at least implicitly to describe it in terms of function, ie the purpose it serves in the behavioural economy of some larger system."* (Brandon & Rosenberg 2003, 148). Functional definitions only make sense when justified evolutionarily, by providing a causal-historical explanation in terms of selection *for* functions. So evolution provides *constitutively causal* explanations of biological objects. A definition of an ice crystal need not invoke any historical process of formation. But in defining biological objects, to say what they are we need to say what they do…what they are *for*. To put the point another way, biological stuff has a history, and that history leaves marks that would otherwise be inscrutable. Just as you cannot hope to understand the political affairs of a sovereign state without knowing its history, so biological objects won't make sense unless you know something of the story about how they came to be.

This case can be overstated, since there are surely large areas of biological science, medicine and physiology for example, which have been little changed since the advent of evolutionary theory. A neat way to bring out the relevant point is to ask 'What difference would it make if creationism were true?' – i.e. if it turned out that there had never been any evolution by natural selection. Some fields, such as biochemistry, might proceed largely as before, because they deal in current functions rather than selected effects. Yet there is reason to think that organisms might be a special case. There are certain features of living things that would be inexplicable, if it were the case that creationism were true[7]. One is the hierarchical compositionality that is apparent in many life forms. Why would life

[7] Or would at best require ad hoc explanations.

have a nested structure, with organelles inside cells inside multicellular agglomerations, if it had not emerged out of a piecemeal process which built new organisms out of interactions between existing ones? And, perhaps even more pressingly, why should organisms so often suffer maladies and maladaptations because their parts are struggling to get on or to reconcile their interests? That living things are compositional, and that they exhaust so many resources on complex mechanisms of conflict resolution, demand an evolutionary explanation, for they are stark relics of a particular contingent history.

This is a broad use of the term 'evolutionary' to delimit explanations. I don't limit the category to genetic or population-genetic explanations. Nor do I consider evolutionary explanations to be necessarily focused on optimality. It is important not to assume that all traits are adaptive. Some 'why' questions have developmental answers. Some traits are mere side-effects of selection for other properties. But one question for which no developmental or physical explanation will do is 'Why are there organisms?' ' In other words, why does life come in the form of cohesive packages of different sizes, rather than being some sort of homogeneous soup of living matter? The right answer is evolutionary. Life is packaged up so that it can participate in selection processes at various hierarchical scales.

6. In what sense does a scientific concept have priority over its traditional counterpart?

I don't want to insist on priority in a reductive sense: I don't think we should junk concept '2' and only use concept '1i' from now on, any more than we should replace Eddington's commonplace table with the scientific table (Eddington 1927). What sort of priority do I mean then?

Suppose we consider an organisational definition, which defines the kind 'organism' as containing only those objects which are organised in a special kind of way. There is no mention of 'evolution' in this definition. And yet the organisational definition and the evolutionary definition will pick out roughly similar things – me, you, my dog, that bird. Why should this be? The organisational concept is designed to explain the features of a class of things that is in some sense obvious to human observers. They are things with which we interact, things which have agency. Their parts are connected to each other in obvious ways, so that they die if we sever the connections, for example. We have always noticed these things because it has been useful to us to notice them, much more useful than if we operated with a concept that apprehended an approaching tiger as an unconnected collection of tiger parts. We have used the concept 'organism' since long long before anybody started to formulate a theory of natural selection. it remains unnecessary to understand the theory of natural selection in order to be fairly competent with the use of the kind 'organism'. So what can the two definitions possibly have to do with one another? Why do they often pick out the same things?

The answer is that the theory of evolution by natural selection explains why there are organisms, in other words, why our world is populated with bits of stuff that act in unity, that jump out at us and succumb in their totality to our attacks. Evolution – the *process*, not the theory – created those things that are so numerous and so significant in the human psyche that we made up a special group name to describe them all – organisms. And consideration of the *theory* of natural selection – the theory that explains how evolution works – can tell us things about organisms that cannot be deduced by looking at the examples around us. It can tell us what sorts of properties organisms cannot have, for example – about impossible organisms. It can tell us about organisms that are

possible but non-existent. It can tell us how organisms came into existence, and why. And we can use these sophistications to help us to correct our intuitive, folk concept. To settle cases in respect of which our intuitions are silent. And to help us understand which of the 'other' definitions of 'organism' are good ones. In this sense, I think that concept 1i is able to capture what concept 2 – the notion of one single life, one animal or plant – really is.

7. Worries about a 'metabolic individual'

O'Malley advocates for a concept of the biological individual that is defined in terms of metabolism - the 'biologically structured conversion of energy and carbon' (O'Malley & Powell 2015). A metabolic individual is a collection of diverse parts, which are in engaged in metabolic collaboration – energy exchange - with one another. They range from 'electron trades within and between cells' to *Medicago*-Rhizobia sets up to 'global biogeochemical cycles' (ibid.) I assume, given that viruses are meant to be excluded from the class of metabolic individuals, that some threshold of metabolic autonomy must also be met (O'Malley this volume). The parts must exchange energy with one another in such a way that the sum is self-sustaining, I think.

Metabolic interactions, I assume, are fairly ubiquitous. All living things rely, to a greater or lesser extent, on products or processes performed by other living things, in order to survive and reproduce. For example, humans rely on a mate in order to produce offspring, and they rely on a variety of gut flora to allow them to digest their food and maintain their immune systems. Furthermore, modern humans rely on their families, communities and societies more generally in order to meet their needs. They rely on plants and bacteria to oxygenate the atmosphere so that they can breathe. They rely on various other life forms to act as food sources. Humans exchange energy or carbon with all these other living things. So I wonder about the threshold amount or type of interaction, or sense of autonomy, that would circumscribe a human as a metabolic unit. If anything upon which a living thing depends for survival qualifies as a metabolic part then it seems natural to think that there can only be one metabolic individual in existence – the whole planet.

Even accepting, as I do, a significant, perhaps even starring, role for metabolism as explanatory of evolutionary individuals, is this explanatory role best served by a concept of a metabolic *individual*? Individuals, in whatever domain they occur, are particulars. Unlike classes, particulars are supposed to have spatio-temporal identity. They have births and deaths, rather than existing timelessly. We can expect answers to questions about whether one individual is the same numerical individual as another or not, about what sorts of events the individual cannot survive, about what things are their parts.

Some metabolic interactions will occur within a community in which different members constantly come and go. In a typical ecosystem, or a microbial community, any particular organism or cell may participate for some period of time and then leave. The legume-rhizobia collaboration may be more stable, in so far as one plant might retain the same ten or so strains of bacteria in its root nodules throughout its life. Nonetheless, there will rapid turnover of particular bacteria cells during that time. Furthermore, the boundaries of the set that actively engages in metabolic interaction will vary over time, as different nodules vary their level of cooperation or of sanction.

Where does the metabolic individual begin and end, in these cases? Does any metabolic individual persist across changes to the identity of its parts? Can it survive the death of a single participant?

What if the parts remain but temporarily suspend their active metabolic engagement? Is the plant, but no particular bacterium, a necessary participant in the interaction, and if so, why? Maybe the individual persists so long as a threshold energy transfer is maintained, regardless of the identity of the separate collaborators?

If we are going to make room, in our ontology, for O'Malley's metabolic individual concept, then these questions need to be answered, and the answer needs to be motivated – there needs to be some explanation or generalisation that depends upon the question being answered that way, and not some other way. I suspect that a greater degree of light would be shed, instead, by thinking about metabolism as an extremely important *process* in which biological individuals engage.

A view which treats a whole legume-rhizobia set as a cohesive individual overlooks any conflict between the parts, and the variation across different nodules in levels of metabolic interaction. A view which focuses on the category of metabolic exchange without attention to the identities of the exchangers doesn't take account of the effects of infection by multiple competing strains of bacteria. A metabolic view also obscures the fact that many hosts will interact with multiple mutualists simultaneously, rather than with only one. For example, plants of the genus *Medicago* engage in collaboration with mycorrhizal fungi as well as with rhizobial bacteria. The fungi thus ends up indirectly interacting with the bacteria, in so far as each relies on the other to sustain its partner. This can drive further interesting dynamics such as divisions of labour between different mutualists (Werner et al Forthcoming). These dynamics are not captured by a view which cuts things up according to the particular metabolites transferred.

Conclusions

I have tried to argue that my concept of the evolutionary individual is more useful than O'Malley's concept of the metabolic individual. For example, the evolutionary concept is equipped to meet all the explanatory challenges accomplished by the metabolic view of the legume-rhizobia collaboration, and it supports several further explanations of phenomena about which the metabolic view can say little. Even if there are particular contexts in which a different view of the individual is most useful, we might say that the concept of the evolutionary individual is useful across the biggest range of explanatory contexts.

I don't deny the significance, perhaps the pivotal, significance of metabolism to making evolutionary individuals what they are. I agree that metabolic perspectives can contribute 'additional explanatory resources' for evolutionary theory. Yet, I do aim to cast doubt on the usefulness of focusing particular attention on units delimited by metabolism. I suggest that the explanatory value of thinking about metabolic processes is not best served by postulating metabolic *individuals*. The metabolic interactions, such as those occurring between trees and their mycorrhizal fungi, are fascinating and important. But creating a concept to unify the partners in such an interaction is less useful than, for example, applying biological market theory to explicate the evolutionary forces that sculpt those interactions.

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