

Is evolution fundamental when it comes to defining biological ontology? No.

Maureen A. O'Malley
University of Bordeaux
maureen.omalley@u-bordeaux.fr

Introduction

There are various sorts of individuals in biology, and the two most obvious are biological and evolutionary. They share some common physical bases, but are not – in the view I advance here – the same thing. Distinguishing them is not some sort of philosophical parlour game: it is central to evolutionary and ecological analysis, as I shall show. Another way of framing the issue is to ask whether evolution has some sort of explanatory privilege over other aspects of individuality. The question motivating my chapter and Ellen Clarke's, is, therefore, phrased as: 'Is evolution fundamental when it comes to defining biological ontology?' or perhaps more aptly, 'Should we give evolution priority when defining biological ontology?' My answer is 'No', whereas Clarke's is 'Yes'. This is not ontology for its own sake, however. As I (and Clarke) will argue, the point of worrying about ontology is because of the epistemic implications of negative or positive answers.

My discussion begins with Peter Godfrey-Smith's (2013) diagram of the relationship between evolutionary (and particularly Darwinian) individuality, and biological individuality. After outlining what each of these categories means, I go on to discuss the epistemic (explanatory and predictive) rationales for this categorization scheme. One area in which the differences between biological and evolutionary individuality can be informative is when identifying and explaining what are known as 'major transitions in evolution'. I outline how keeping distinct these two characterizations of individuals helps understand what evolutionary transitions in individuality are and how they happen.

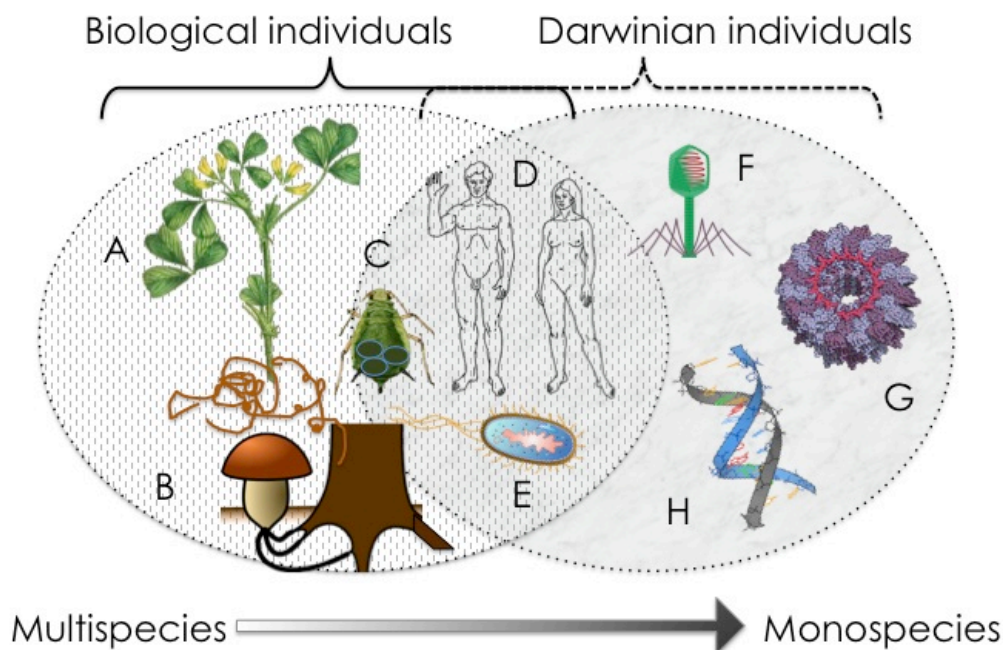
The distinction

Distinguishing biological from evolutionary individuals is fairly standard today, especially amongst philosophers teasing out the individuality captured by any particular biological model (e.g., Pradeu 2012; Booth 2014; Bouchard 2011). Figure One represents this distinction. In the left-hand circle are things that are coherent, metabolizing, interacting entities. Because only some of these entities are thought to warrant the word 'organism', the more general category is often labelled 'biological individuals'. For example, when considering animals such as ourselves (*Homo sapiens*, Fig 1: D), we usually imagine a large group of highly differentiated cells all with the same genome. We do this even though we know there are viruses and other 'foreign' mobile DNA elements in our nuclear genome, as well as remnant bacteria in most of our cells – the mitochondria – plus all manner of functionally important microorganisms in our intestines and elsewhere. For unicellular organisms (Fig 1: E), we tend to consider them similarly, but as one-cell, one-genome arrangements. The biological systems that fall outside these classically 'organismal' biological individuals are of importance for how my argument develops. These are the multispecies entities (i.e., composed of organisms from different evolutionary lineages) that are illustrated in Figure One with different plant-symbiont arrangements (Fig. 1: A and B).

In the right circle are evolutionary individuals, which Godfrey-Smith (2013; 2009) has rebranded as 'Darwinian individuals'. On the far right are entities that form lineages, and on which selection operates, but which do not in most accounts have organismal status. There is notable overlap in the middle, and this is where anything that is a biological individual is also a Darwinian individual. I discuss all these distinctions in more detail in the following section; for now, note that my chapter ranges across Figure One, whereas Clarke's chapter and her other work (e.g., Clarke 2015) refer only to entities that fit in the overlapping category.¹ The final dimension of this figure to bear in mind is the continuum of multispecies-monospecies running from left to right. All the boundaries in this figure are rather fuzzy.

Figure 1: A revisualized version of Godfrey-Smith's (2013) diagram of the two kinds of individual and their relationship. A: *Medicago* and rhizobia; B: tree and mycorrhizal fungi;² C: aphid and *Buchnera*; D: *Homo sapiens*; E: *E. coli*; F: bacteriophage; G: tobacco mosaic virus; H: DNA (representing entities such as mobile genetic elements).

All images from Wikimedia Commons. Credits: A: Saint-Hilaire/Ninjatacoshell; B: Natr; C: Snodgrass; D: Carl Sagan/NASA; E: Database Center for Life Sciences; F: Nossedotti (Anderson Brito); G: Zlir'a. H: Dcrjsr.



¹ Clarke (this volume) thinks that viruses and mobile DNA elements need not be considered, because in most accounts they are not alive. Those same accounts, however, would agree that viruses are evolving and subject to selection.

² Mycorrhizal fungi do not have the fruiting body shown in the image. The mushroom shape is just there to indicate this is a fungal arrangement.

Elaborating the distinction

What are some of the implications of this diagram? The case of viruses helps illustrate what is at stake in distinguishing biological and Darwinian individuals. Viruses and bacteriophage (Fig. 1: G and F respectively; the latter are the viruses that infect bacteria), plus mobile and non-mobile genetic elements³ (e.g., plasmids and transposable elements) are examples of the former; Fig 1: H) can form evolutionary lineages and be objects of selection. But they are not organisms, except in the most revisionary characterizations of organismality. Some of these revisions have been inspired lately by discoveries of giant viruses that have genomes larger than those of many reduced parasitic microorganisms (Raoult et al. 2004). These reconceptualizations suggest that the virus is the actively replicating entity that takes over a cell, thus making that cell a 'virus factory' (Claverie and Abergel 2010; Forterre 2010). The viral-factory cell in the act of cellular co-option is thus 'alive' in a sense the free-floating virus particle is not. I am not working with this redefinition in my discussion, but if it were to be used would conceivably place viruses on the other side of the diagram (the 'multispecies' end) when and only when in the process of being reproduced by cells.

Looking on the far left-hand side of the diagram, we can consider closely connected groups of organisms that are often mutualistic, persistent and regularly regenerated metabolic wholes without a common inheritance. In other words, these entities are composed of sub-entities that have separable biological and evolutionary individuality. Figure One illustrates this sort of entity with two partnerships often used as model systems: a legume (illustrated by *Medicago*) and the endosymbiotic rhizobial bacteria that enter legume roots (Fig. 1: A), and a wider range of plants with endosymbiont fungi in and around their roots (Fig. 1: B). Other well-known symbioses of this sort are the collectives forming corals, or hydrothermal vent tubeworms, or lichens, or dependently co-metabolizing consortia of microorganisms.⁴ Liaisons such as these co-produce the main properties of the biological individual, including nutritional mode and means of generating energy, waste disposal, invader protection, and capacities for a range of interactions with other organisms and the environment. The tightest liaisons are mostly metabolic (an empirical fact, not a philosophical argument). However, as Godfrey-Smith has often pointed out, these co-produced entities – despite co-creating and sharing properties that form the collective entity – often reproduce separately. He calls the repeated co-production of such entities, generation after generation, 'reconstruction' – a process that does not generate a single fused lineage (Godfrey-Smith 2015, p. 10122). A biological individual such as either of the examples in Figure One is thus 'a metabolic knotting of reproductive lineages that remain distinct' (Godfrey-Smith 2013, p. 30).

This view fits with a general understanding of 'organism', which is of entities that are self-maintaining, self-perpetuating lineage-formers that are units of selection in their own right (e.g., Queller and Strassmann 2009; Pepper and Herron 2008; Santilices 1999). These are the entities captured by the overlapping categories in the middle of Figure One. As

³ 'Genes' are examples of the latter in Godfrey-Smith's original diagram, and I will only mention in passing their problems as an exemplar for this discussion. Mitochondria and chloroplasts (plus other plastids) might be considered additional examples, but because their evolutionary fates appear controlled by the evolutionary fates of their hosts, they would not normally be given any stand-alone status in such a diagram. For further discussion of such entities, see the main text.

⁴ For some less well-known but just as fascinating systems of this sort, see Herron et al. (2013).

well as the expected organisms fitting there – from humans to bacteria – ‘organisms’ such as aphids and their endosymbionts (*Buchnera*) can be found (Fig. 1: C; also Godfrey-Smith 2013).⁵ Why are they seen as the same unit and not placed to the left-hand side along with other multispecies entities? Because *Buchnera* are inherited vertically (parent to offspring) from the mother aphid, and not horizontally (from the environment) as happens for the entities farther to the left and outside the overlap. This is an important distinction that for many evolutionary theorists (including Clarke) demarcates the equivalent of a distinction in kind: between composite biological individuals that reproduce vertically, and composite biological individuals for which some constituents are repeatedly acquired horizontally.⁶ The former are biological *and* Darwinian individuals; the latter at best biological (Godfrey-Smith 2013).

Why does it matter if entities do not reproduce as one unit but rather as multiple units that contribute to a larger collective entity? It matters for evolutionary Darwinizing purposes because evolution is defined on the basis of reproductive success. The counting procedures that make up the machinery of population genetics are established on that basis. Although I think a simple definition of reproduction is tremendously problematic, and that there might in fact be a broader category of evolutionary individuals that are not necessarily Darwinian individuals but composed of them and aligned fitness-wise (see O'Malley 2016), my qualms are not germane for the moment. We can simply acknowledge the fact that many collective entities, no matter how close and intimate their lives, still carry out localized reproduction (i.e., *not* across the whole system simultaneously, via some sort of bottleneck). This means that from a population-genetic perspective – the gold standard of evolutionary analysis – the fitness of the participants contributing to that collective must be considered separately (Mushegian and Ebert 2015). As Godfrey-Smith puts it, ‘counts are affected by assumptions about individuals’ (2013, p. 17-18), and population genetics for better or worse does its explanatory work with the separated individuals and not the collective ones. If population genetics does count the aggregated biological individuals, it can only be when they have reached the host-controlled reproducer stage (however, see below for how population genetics can decompose even these arrangements). We see, therefore, a decoupling of biological individuality (the lives lived) and Darwinian evolutionary individuality (turning on a reproductive fulcrum).

Any claim that biological individuals are ‘less explanatory’ than evolutionary Darwinian individuals (e.g., Clarke) would be focused exclusively on the overlapping section of Figure One (entities that are both biological and Darwinian). This can be a perfectly legitimate thing to do for certain epistemic purposes, as long as it is clear to everyone that the systems on the far left have been excluded (likewise those on the far right, because of not being ‘alive’). The multispecies systems can indeed be broken down and analysed as separate Darwinian individuals (e.g., the legume without its root endosymbionts; the rhizobia without their plant host). This is exactly how population genetics would treat them. But population genetics can also treat the mitochondrion in eukaryotes (e.g., animals, fungi, plants, protists) separately because it has experienced a different evolutionary history from that of the host cell's nuclear genome. Is that sort of

⁵ Haber (2013) would also place eusocial insect colonies (‘superorganisms’) here, even if he does not want to call them organisms.

⁶ I will ignore for the purposes of this paper just how very mixed (vertical and horizontal) most transmission systems are (Ebert 2013; see O'Malley 2016 for further discussion).

separation what we want to do all the time? I suggest not. A case has been made along these lines against regarding 'selfish genes' as appropriate units of analysis (see Huneman 2010). We need not think this strategy is wrong through and through, however. There are explanatory and descriptive aims that can only be achieved when the constituent entities of multispecies biological individuals are separated, and other aims that rule out such separation. These explanatory differences rest on the distinction between biological and evolutionary (i.e., Darwinian) individuals, and an acknowledgement that *neither* has out-and-out priority free of explanatory context. This is my more exact answer to the motivating question, plus a rejection of any suggestion that I am 'criticizing' the idea of Darwinian individuality.

Explanatory implications

From what I have said so far, it should be clear that biological individuals are the units of ecological interaction and survival, achieved most basically by their metabolic capabilities. The explanatory focus for such entities is their persistence in and impact on the world. A Darwinian individual, on the other hand, is a unit of selection regardless of whether it can maintain itself metabolically. The explanatory focus for these entities is fitness measured as multiplication of the entities. To put the distinction very crudely, we explain biological individuals by viability, and Darwinian individuals by fecundity.⁷ How does this work?

Take the legume, illustrated in Figure One with *Medicago* (a clover-like genus that includes alfalfa). This plant enters into a close relationship with rhizobial bacteria early in the plant's lifecycle. The bacteria become endosymbionts in the root hairs of the plant, and both roots and bacteria co-develop to achieve a nutrient exchange system. Without the bacteria, the plant has no access to nitrogen, essential for growth and the eventual maturity and reproduction of the plant. The bacteria can survive without the plant, but do less well. But although this is an intimate relationship that has evolved for 70 million years, the bacteria are reacquired horizontally for each generation of the plant (Denison and Kiers 2011). The bacterial lineages that 'infect' the roots of the mother plant may be genetically different from but functionally identical to the lineages that inhabit the roots of the offspring plants. Because of these separable reproductive and evolutionary trajectories, the system – plant and bacteria – can be understood as the unit of *viability*: the entity that interfaces with the world, and has an impact on the reproductive capacities of the constituents. Nevertheless, the units of *fecundity* are the separate lineages, despite the fact that the plant is unlikely to reach reproductive maturity without the rhizobia. It is simply this distinction that the biological and Darwinian individuality concepts are carving up.

We can explain how the plant gets by in the world because it is part of a collective that also includes rhizobia. But the rhizobia become mere environmental conditions when the fitness chips for the plant are counted: the success of the plant is measured by how many more plants there are. Even though I think this kind of calculation has limitations (see O'Malley 2016; also Bouchard 2014), this is how standard evolutionary analyses are done. It is the Darwinian individual that is the focus of the counting, not necessarily the biological individual. Obviously, as Figure One shows, there is often enough overlap, but

⁷ Michod (2005), who also uses the terminology of 'viability' and 'fecundity', sees these units as mutually overlapping, thus also answering 'yes' to the motivating question for this chapter.

as far as population genetics goes, it is too bad for any multispecies collaborative as a unit when there is separation for counting purposes. If we want to explain more, and particularly to predict the viability of, let's say, hypothetically rhizobia-free legumes, then we return to the biological individual – the ecological entity that interacts as a unit. We may also think there is something evolutionarily interesting about how such collectives persist and change the world over evolutionary time (see below), but we cannot expect population-genetic counts to say very much about them as combined systems. If we want to predict what will happen to the Darwinian individual in the future, there are limitations to what can be said without returning to the biological individual, unless factors such as population size or selection co-efficients are known in advance. However, retrospectively, there are some very interesting explanations of Darwinian individuals that account for major turning points in the history of life on Earth.

Evolutionary transitions in individuality (ETIs)

ETIs occur when previously independent reproducers become a single reproducer and unit of selection (Szathmáry and Maynard Smith 1995; Okasha 2005; Clarke 2014). What were once separate evolutionary individuals become single higher-level evolutionary individuals through 'deDarwinizing' processes (Godfrey-Smith 2009). Sometimes this can happen to a group of closely related entities, such as when single related cells become a multicellular entity and a new higher-level unit of selection (Michod 2005). Other times, multispecies collectives fuse their reproductive and evolutionary fates to become a single unit (e.g., cells with mitochondria). Serial achievements of ETIs are postulated to have formed the main or at least most theoretically interesting complexification trend in evolutionary history (Szathmáry and Maynard Smith 1995; Sterelny 1999). ETIs bring about hierarchical complexification rather than the more everyday 'horizontal' complexity (mere differentiation of structure – see McShea 2015). However, even though this discussion refers primarily to Darwinian individuality, there are explanatory moments when biological individuality warrants consideration too.

The origin of the eukaryote cell (an event known as eukaryogenesis) is an example of where this distinction plays a role. Eukaryotic cells, which are large and filled with functionally specialized compartments (e.g., mitochondria, nucleus), arose from prokaryotic cells,⁸ which are smaller cells that have less internal structure but more diverse metabolisms. The prokaryotic progenitor cell was very probably a member of the group of non-bacterial prokaryotes called Archaea (Bacteria and Archaea being the two ways to be a prokaryote). The exact first step of eukaryogenesis is unknown, but at some 'pre-eukaryotic' point an archaeal cell took in a bacterial cell and did not digest or otherwise destroy it. After quite a period of evolutionary adjustment in which the distinctive eukaryotic cell gradually emerged, the engulfed bacterium became the mitochondrion by giving up lots of its genes and functions to the host cell nucleus. It began carrying out basic metabolic and biosynthesizing processes for the host cell (although it stopped doing those activities in some lineages later on). The precise moment at which this archaeal cell carrying a bacterial cell became one unit of selection cannot be identified, but it indisputably happened: a cell with an endosymbiont – each with separate evolutionary fates for a long time – merged reproductive efforts, evolutionary trajectories and 'achieved' another level of evolutionary (Darwinian)

⁸ There are some radical eukaryote-first speculations we can safely ignore here.

individuality. In fact, the fate of the mitochondrion, as I noted in a footnote above, is controlled by the host cell as the cell responds selectively to environmental pressures. We can see evidence of this in the different anaerobic and aerobic capacities of mitochondria-derived organelles in hosts adapted to anoxic, very low-oxygen and oxic regimes (Stairs et al. 2015; Müller et al. 2012).

However, the first point to note for eukaryogenesis is what I mentioned above: that even though such an ETI is universally deemed to have occurred, population genetics can still be applied to the mitochondrion on its own (ditto the chloroplast in plants, which is a similar case of an ETI – see O'Malley and Powell 2016). In such analyses, theorists discuss the effects of mutational biases and population structure on organelle genome architecture and the efficacy of selection (e.g., Lynch et al. 2006; Birky et al. 1983). Nobody at any point, however, is suggesting that mitochondria are viable in their own right and could go out into the world beyond the cell and survive.⁹ Similar analyses are carried out with *Buchnera*, the endosymbionts of aphids. They have lived inside specialized aphid cells (bacteriocytes) for 200 million years, and have lost large numbers of functional genes (Mira and Moran 2001). Despite *Buchnera*'s deep dependence on the aphids, population genetics is often carried out on them to explain the forces behind their genomic and functional reduction (e.g., Moran 1996; Woolfit and Bromham 2003). But again, there is not the minutest possibility that these endosymbionts could be removed from the bacteriocytes and 'set free' to interface directly with the environment outside aphids. This is what their close but unreduced relatives, *Escherichia coli*, are able to do. In other words, *Buchnera* (and mitochondria and chloroplasts) are not expected to be biological individuals although they are expected to conform to the characteristics of Darwinian individuals, when being explained population-genetically. Although *Buchnera* are still regarded as quasi-organismal and not organelles (which is what mitochondria and chloroplasts are), they have a similar status in where they fall with respect to Figure One.

But there is also a more radical way in which separating biological and evolutionary individuality affects the centrality of ETIs in explaining major transitions. When Darwinian individuals are the focus of such macroevolutionary explanations, they invoke primarily a genetic account of those individuals (just as microevolutionary ones do). Why? Because the main way in which to decide what has continuity and cohesion reproductively (and is thus reproducing and forming lineages of the right sort) is by tracking genes. This way, different lineages bearing the appropriate genetic material are the individuals of interest (this is exactly why mitochondria, chloroplasts and *Buchnera*, which have their own genomes, can be analysed population-genetically, and also the reason why Godfrey-Smith's exemplar in this category is 'genes' or 'chromosomes'). A great deal of ETI work has been focused on genes and genomes as the informational bearers of individuality, and on ETIs as the resolution of genetic conflict (e.g., Szathmáry and Maynard Smith 1995). However, we can also think about evolutionary transitions more metabolically, and ultimately explain these turning points by properties associated with biological individuality.

⁹ As a curious aside, this is what an evolution-of-endosymbiosis theorist, Ivan Wallin (1883-1969) argued he'd done in the 1920s. He believed mitochondria were autonomous bacteria – i.e., both Darwinian and biological individuals – and that he had cultured them outside the cell (Wallin 1928). Sadly for his career he was not much believed, although his more general ideas linger on in discussions of endosymbiosis today.

Recently Russell Powell and I have pushed this line, arguing that major transitions in evolution can also be identified and explained metabolically (O'Malley and Powell 2016). We noted several overlooked candidates for major transitions: the divergence of Bacteria and Archaea (probably the most fundamental divergence in the history of life on Earth),¹⁰ and the Great Oxidation Event in which the metabolism of cyanobacteria irrevocably changed planetary ecology and thus the evolutionary trajectory of all lifeforms and their future possibilities. While both these turning points are of the utmost evolutionary importance for understanding why life is the way it is now, these events cannot be accounted for in a major transitions framework focused on ETIs. A metabolic focus, however, immediately homes in on them (e.g., Sojo et al. 2014; Falkowski and Godfrey 2008). In such instances, features of biological individuality play an explanatory role that is not just proximate (how) but also ultimate (why). Making that argument requires some elaboration on the points I made with Powell.

Our paper suggests that some major evolutionary transitions are very likely about genetic (Darwinian) individuals *and* metabolic (biological) individuals (e.g., the origin of cells, the origins of multicellularity). Some transitions, however, might be better explained by Darwinian individuality alone (e.g., eusociality). And quite a few of either a short traditional list (i.e., Szathmáry and Maynard Smith 1995) or a longer revised list might really best be seen as major transitions explained ultimately by metabolism and biological individuality, rather than Darwinian individuality as tracked by genes. To understand why certain evolutionary transitions in individuality occurred, such as the acquisition of the mitochondrion, or the many acquisitions of plastids (photosynthesizing organelles such as chloroplasts, that were once independent organisms), Powell and I suggest that metabolism is not mere background to the ultimate (genetic) explanations, but is a driver of the events in which the resolution of genetic conflict (the prime explanandum in ETI accounts) is in fact secondary.

Eukaryogenesis may well be one of those transitions because metabolic explanations of this event are able to account for the details of why and how this 'fusion' progressed – in a way that tracking genetic individuals cannot (Lane and Martin 2010; O'Malley and Powell 2016).¹¹ Metabolic regulation is a plausible explanation of how conflict was resolved between the two cells that fused into the novel eukaryote; metabolic regulation may also have ongoing explanatory implications for the evolution of various forms of eukaryote multicellularity (Blackstone 2013). The oxygenation of the Earth – an event brought about initially by the combination of two previously disconnected photosynthetic pathways in one organism – is another transition explained metabolically (Hohmann-Mariott and Blankenship 2011; O'Malley and Powell 2016). This world-changing biological event is necessarily left out of ETI-oriented major transition models because of not being explicable in terms of new levels of evolutionary individuality. Metabolism duly identifies and explains this major ecological and evolutionary transformation. Thus, even at a macroevolutionary level of explanation, metabolic (biological) individuals continue to be worth distinguishing epistemically from standard genetic Darwinian individuals. By all means, keep both involved explanatorily, but they should not be conflated.

¹⁰ This is especially the case if, as now seems likely, eukaryotes are just a specialized sort of Archaea.

¹¹ This point obtains regardless of exactly when the mitochondrion was acquired – a topic that is a matter of considerable contestation at the moment.

The bottom line

There are good reasons to keep biological and evolutionary (Darwinian) individuality conceptually distinct, in particular to understand their different implications for ecological and evolutionary explanations. In the process, we may gain some interesting insights into biological individuals and their roles in ultimate and not just proximate explanation.

References

Birky CW Jr, Maruyama T, Fuerst P (1983) An approach to population and evolutionary genetic theory for genes in mitochondria and chloroplasts, and some results. *Genetics* 103: 513-527

Blackstone NW (2013) Why did eukaryotes evolve only once: genetic and energetic aspects of conflict and conflict mediation. *Philosophical Transactions of the Royal Society London B* 368: DOI: 10.1098/rstb.2012.0266

Booth A (2014) Populations and individuals in heterokaryotic fungi: a multilevel perspective. *Philosophy of Science* 81: 612-632

Bouchard F (2011) Darwinism without populations: a more inclusive understanding of 'survival of the fittest'. *Studies in History and Philosophy of Biological and Biomedical Sciences* 42: 106-114

Bouchard F (2014) Ecosystem evolution is about variation and persistence, not populations and reproduction. *Biological Theory* 9: 382-391

Clarke E (2013) The multiple realizability of biological individuals. *Journal of Philosophy* 110: 413-435

Clarke E (2014) Origins of evolutionary transitions. *Journal of Biosciences* 39: 303-317

Claverie J-M, Abergel C (2010) Mimivirus: the emerging paradox of quasi-autonomous viruses. *Trends in Genetics* 26: 431-437

Denison RF, Kiers ET (2011) Life histories of symbiotic rhizobia and mycorrhizal fungi. *Current Biology* 21: R775-R785

Ebert D (2013) The epidemiology and evolution of symbionts with mixed-mode transmission. *Annual Review of Ecology, Evolution and Systematics* 44: 623-643

Falkowski PG, Godfrey LV (2008) Electrons, life and the evolution of Earth's oxygen cycle. *Philosophical Transactions of the Royal Society London B* 363: doi:10.1098/rstb.2008.0054

Forterre P (2010) Defining life: the virus viewpoint. *Origins of Life and Evolution of the Biosphere* 40: 151-160

Godfrey-Smith P (2009) *Darwinian Populations and Natural Selection*. Oxford University Press

Godfrey-Smith P (2013) Darwinian individuals. In Bouchard F, Huneman P (eds), *From Groups to Individuals: Perspectives on Biological Associations and Emerging Individuality* (pp. 17-36). MIT Press

Godfrey-Smith P (2015) Reproduction, symbiosis, and the eukaryotic cell. *Proceedings of the National Academy of Sciences USA* 112: 10120-10125

Haber M (2013) Colonies are individuals: revisiting the superorganism revival. In Bouchard F, Huneman P (eds), *From Groups to Individuals: Perspectives on Biological Associations and Emerging Individuality* (pp. 195-217). MIT Press

Herron MD, Rashidi A, Shelton DE, Driscoll WW (2013) Cellular differentiation and individuality in the 'minor' multicellular taxa. *Biological Reviews* 88: 844-861

Hohmann-Mariott MF, Blankenship RE (2011) Evolution of photosynthesis. *Annual Review of Plant Biology* 62: 515-548

Huneman P (2010) Assessing the prospects for a return of organisms in evolutionary biology. *History and Philosophy of the Life Sciences* 32: 341-372

Lane N, Martin W (2010) The energetics of genome complexity. *Nature* 467: 929-934

Lynch M, Koskella B, Schaack S (2006) Mutation pressure and the evolution of organelle genome architecture. *Science* 311: 1727-1730

McShea, D.W. (2015) Three trends in the history of life: an evolutionary syndrome. *Evolutionary Biology* 10.1007/s11692-015-9323-x

Michod RE (2005) On the transfer of fitness from the cell to the multicellular organism. *Biology and Philosophy* 20: 967-987

Moran NA (1996) Accelerated evolution and Muller's ratchet in endosymbiotic bacteria. *Proceedings of the National Academy of Sciences USA* 93: 2873-2878

Moran NA, Mira A (2001) The process of genome shrinkage in the obligate symbiont *Buchnera aphidicola*. *Genome Biology* 2(12): research0054.1-0054.12

Müller M, Mentel M, van Hellemond JJ, Henze K, Woehle C, Gould SB, Yu R-Y, van der Giezen M, Tielens AGM, Martin WF (2012) Biochemistry and evolution of anaerobic energy metabolism in eukaryotes. *Microbiology and Molecular Biology Reviews* 76: 444-495

Mushegian AA, Ebert E (2015) Rethinking 'mutualism' in diverse host-symbiont communities. *Bioessays* 38: 100-108

Okasha S (2005) Multilevel selection and the major transitions in evolution. *Philosophy of Science* 72: 1013-1025

O'Malley MA, Powell R (2016) Major problems in evolutionary transitions: how a metabolic perspective can enrich our understanding of macroevolution. *Biology and Philosophy* 31: 159-189.

O'Malley MA (2016) Reproduction expanded: multigenerational and multilineal units of evolution. *Philosophy of Science* forthcoming

Pepper JW, Herron MD (2008) Does biology need an organism concept? *Biological Reviews* 83: 621-627

Pradeu T (2012) *The Limits of the Self: Immunology and Biological Identity*. Oxford University Press

Queller DC, Strassmann JE (2009) Beyond society: the evolution of organismality. *Philosophical Transactions of the Royal Society London B* 364: 3143-3155

Raoult D, Audic S, Robert C, Abergel C, Renesto P, Ogata H, La Scola B, Suzan M, Claverie J-M (2004) The 1.2 megabase genome sequence of Mimivirus. *Science* 306: 1344-1350

Santilices B (1999) How many kinds of individual are there? *Trends in Evolution and Ecology* 14: 152-155

Sojo V, Pomiankowski A, Lane N (2014) A bioenergetics basis for membrane divergence in Archaea and Bacteria. *PLOS Biology* 13(3): e1002102

Stairs CW, Leger MM, Roger AJ (2015) Diversity and origins of anaerobic metabolism in mitochondria and related organelles. *Philosophical Transactions of the Royal Society London B* 370: 20140326

Sterelny K (1999) Bacteria at the high table. *Biology and Philosophy* 14: 459-470

Szathmáry E, Maynard Smith J (1995) The major evolutionary transitions. *Nature* 374: 227-232

Wallin E (1927) *Symbiogenesis and the Origin of Species*. Baltimore: Williams & Wilkins

Woolfit M, Bromham L (2003) Increased rates of sequence evolution in endosymbiotic bacteria and fungi with small effective population sizes. *Molecular Biology and Evolution* 20: 1545-1555