

Darwinian Individuals

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1. Introduction

The theme of "individuality" has become a point of contact between biology and philosophy.¹ The contact began when biologists themselves were often rather philosophical, and at a time when biological evolution was no more than a vague speculation, especially around the beginning of the 19th century. What is the living individual? What is the basic unit of life or living organization? Questions like this were pursued by J.W. Goethe, Erasmus Darwin, Rudolph Leuckart, T.H. Huxley and others. Plants were often the initial spur to discussion, followed by newly described marine organisms with strange life cycles. The discussion was influenced by the rise of the cell theory, but some writers looked for individuals well below the level of the cell. In mid 1850s the botanist Alexander Braun surveyed ideas about "the vegetable individual," and noted speculations about tiny agents present in every living thing, sentient granules inhabiting the "secret halls of the bark-palaces we call plants" where they "silently hold

¹ This paper is based in part on my 2010 Lakatos Award lecture, given at the London School of Economics. I am grateful to everyone present for very useful comments, and also to Austin Booth, David Haig, and Thomas Pradeu.

their dances and celebrate their orgies" – the orgiastic granule as precursor to the selfish gene.²

Darwin, in the *Voyage of the Beagle*, described his interest in "compound" animals in the sea, where "the individuality of each is not completed" (1839, p. 128). He noted the connection between the polyps in these "zoophytes" and buds on a tree, which "must be considered individual plants" (as his grandfather Erasmus had argued).³ Evolutionary theory soon transformed the discussion. In the early 20th century Julian Huxley searched for "the movement of individuality" in the process of evolution. Huxley had a progressivist view, and saw evolution as heading towards "the Perfect Individual" (1911, pp. 2-3). In his final paragraph of his 1911 book he connected biological evolution to the evolution of "the state," which he saw as presently the most "unwieldy" of individuals, but one "huge with possibility" (p. 154). Julian's headlong optimism on these points might have had some influence on his younger brother Aldous Huxley's more pessimistic view of political evolution in *Brave New World* (1932).

These grand-scale discussions are connected to more practical questions. Evolutionary biology makes use of various counting operations. Counts are affected by assumptions about individuality. Much of the quantitative side of evolutionary theory was fashioned while thinking about organisms where individuality poses few difficulties, such as humans and fruit flies. These animals have fairly clear boundaries in space and time. A move to plants is all it takes for things to get more difficult (Harper 1977). One problem encountered there is an uncertain relation between *growth* and *reproduction*. Reproduction is tied to individuality: reproduction is making a *new* individual, while growth is making more of the same. Many plants make what *look*, at least, like new

² "Mayer of Bonn, basing his theory upon molecular motions, considers the smallest granules of the cell-contents as individuals possessing animal life (biospheres) which built up plants for their dwellings. 'Like hamadryads these sensitive monads inhabit the secret halls of the bark-palaces we call plants, and here silently hold their dances and celebrate their orgies.'" The 1850s seem to have been a period of particular interest in these topics, as seen in Leuckart (1851), Braun (1955), T.H. Huxley (1852). For some of the history of thought about these issues, see White (1979) and Nyhart and Lidgard (2011).

³ "A tree is properly speaking a family or swarm of buds, each bud being an individual plant" (Erasmus Darwin's *The Botanic Garden*, 1791, note 14). In a talk at ISHPSSB 2011, Greg Priest (unpublished) argued that these cases had an important role in the development of Darwin's evolutionary thought, as they gave him a new way of thinking about the relations between individuals and species.

plants by growing them directly from the old. Strawberries do so by sending off above-ground runners. In an aspen grove, thousands of apparently distinct "trees" can be united by a root system from which they all grew (Mitton and Grant 1986). Some may have become physically disconnected, while others remain connected. Are these cases of the growth of one continuing individual, or reproduction by a single parent? Can we say whichever we like?

One way to find order is to say that in these cases, asexual "reproduction" is mere growth. A view of this kind was defended in the 19th century by Thomas Huxley, grandfather of Julian and Aldous. A modern version was vividly expressed by Daniel Janzen in his 1977 paper "What are Dandelions and Aphids?" Both dandelions and aphids alternate between sexual and asexual reproduction, where the asexual stage involves making an egg that is a genetic clone of the mother. Janzen argued that from an evolutionary point of view, a single dandelion is a scattered object with many small parts that have each grown from these asexually produced eggs. An individual dandelion may be as big as an oak, though it has a very different shape; a dandelion is "a very large tree with no investment in trunk, major branches, or perennial roots" (p. 587).

Another set of problems about individuality is raised by "collective" entities – groups of living things that are in some ways like organisms or individuals in their own right. Problem cases here include ant and bee colonies, and lichens. Each lichen is a close association between a fungus and a group of algae. Sometimes collective entities can clearly be living individuals in their own right; humans are collectives made of cells. In other cases it seems that the collective does not count as a biological individual, but is just a group of lower-level ones – consider a buffalo herd or a school of fish.

It is possible to try to steer a path through all the cases and constraints here, to find *the* true biological individuals. But it is also possible to take a step back. Perhaps there are many kinds of things that can be called "individuals," relevant for different purposes. Monozygotic human twins deserve two votes in elections, but perhaps they are a single unit in another sense? The message might be to withdraw from the attempt to give a substantial theory. In the 19th century there was a good deal of philosophical baggage travelling with views about individuality, in part because life itself was so poorly understood. The baggage also included a concern with *indivisibility* as a feature of

individuals. Once that historical context is gone, questions about biological individuality can be treated in a more relaxed way. Perhaps a biological individual is just any object that some part of biology recognizes as worth describing. It might be an organism, a part of an organism, or a larger thing like a colony or ecological system. There are no fundamental or most-real individuals in biology.

That is a reasonable attitude in many ways. But it is possible to look for a theory which takes more of an interest in the idea of individuality. One thing that evolution does is create new kinds of objects, things which can be counted and are set apart from their surroundings. Instances of these objects keep recurring, and they persist as matter passes in and out of living systems. Building these things is not the only thing evolution does. Later this paper will look at ways in which it does, in a sense, the opposite. But it does do this some of the time. To understand how this works is to understand the evolution of individuals, in a sense that is not as inflated as some of the old discussions, but goes beyond saying that biological individuals are just whatever biologists find it useful to talk about. When we follow this path, though, we find at least two categories with a special status, two kinds of individuals, with a set of relationships between them.

2. Darwinian Individuals

My starting point is evolution by natural selection. I will use a simple and familiar summary of this process, similar to summaries from Darwin's time and soon after. Perhaps the best known formulations are due to Lewontin (1970, 1985). As Lewontin has it, evolution by natural selection will take place in any collection of entities in which there is *variation, heredity, and differences in reproductive success*.⁴ The presence of these three features is not strictly sufficient for change to occur, and there are other attempts to give a foundational description of how natural selection works, but here I will work within this "classical" framework: variation, heredity, and differences in reproductive success are the features of populations that give rise to Darwinian change.

⁴ For more details on these summaries, see Godfrey-Smith (2007).

Any collection that has these features can be called a *Darwinian population*, and any member of such a collection is a *Darwinian individual*.⁵

A summary like this takes some things for granted. It assumes that we can recognize a population, a collection of distinct things that can be counted, and also that we can recognize these objects as connected by *parent-offspring* relations. This is assumed in the idea of heredity – are parents similar to their offspring? – and the idea of reproductive success – does this individual have more offspring than that one?

For organisms like us, as noted earlier, applying these concepts is easy. Once we extend to other cases, we find problems. But now we know more about what to look for. The kinds of things that matter here are things that can *reproduce*. This, however, is another problematic concept, so I will next look more closely at the idea of reproduction.⁶

A common-sense analysis provides a starting point. Reproduction involves the production of new individuals which are of the same kind as their parents. Reproduction is different from growth, different from the appearance of new individuals with no parents, and different from the production of things of the wrong kind, such as waste and artifacts.

Some kind of reproduction – some kind of multiplication or making-more – is needed for any Darwinian process to occur. But it can be a very rudimentary version, one that does not look much like cases we are familiar with, and one in which reproduction is poorly distinguished from other things. The similarity of "parent" and "offspring" can be low, the boundary between them unclear, and maternity uncertain and diffuse (Blute 2007). From these simple beginnings, forms of reproduction are themselves evolutionary products, and as new kinds of reproduction evolve, different kinds of evolutionary processes become possible.

My next step is to break reproduction down into several distinct modes. I recognize three different kinds of reproducers, *simple*, *scaffolded*, and *collective* reproducers.

The paradigm cases of simple reproducers are cells, especially bacterial cells. A

⁵ Lloyd and Gould (1999) also use the term "Darwinian individual" for an evolutionary unit. Their analysis is a version of the "replicator/interactor" view, and their Darwinian individuals are interactors. This kind of analysis is criticized in Godfrey-Smith (2009).

⁶ See Griesemer (2000) for an alternative analysis of reproduction.

cell can make more things like itself, using machinery internal to it, and it is not made out of smaller parts that can do the same thing – that can make more objects like themselves using their own machinery. If something can reproduce but does contain other things that can reproduce in this sense, then it is a *collective* reproducer. The paradigm there is a large animal such as a human. People reproduce, making more people, but our reproduction is organized cell-level reproduction.

Simple reproducers need not be the smallest reproducers in a hierarchy of parts and wholes. There are also *scaffolded* reproducers. These are objects which *get* reproduced, as part of the reproduction of some larger unit (a simple reproducer), or that are made *by* some other object. They do not contain the machinery of their own reproduction; their reproduction is dependent on "scaffolding" of some kind that is external to them.⁷ Paradigm cases of scaffolded reproducers are viruses, which induce cells to make more of them, and the chromosomes and genes within our cells. Genes in this analysis are understood as material objects handled with the same criteria used in the other cases.⁸

Further analysis is needed for all three of these modes of reproduction, and the problems they raise are distinct. Here I will look more closely at collective reproduction. When is a group of reproducing objects a reproducer in its own right?

Organisms like us, bee colonies, buffalo herds, and lichens all give rise to more of themselves. In a loose sense, it is reasonable to call all of these cases of reproduction. But they are not all on a par, from an evolutionary point of view. It is possible to find features of collectives which distinguish the clear or paradigm cases of reproduction from the more *marginal* ones. Three features can be used to make this distinction. All come in degrees. I symbolize them with capital letters.

The first is *B*, which stands for "bottleneck." A bottleneck is a narrowing that marks the divide between generations. This narrowing is often to a single cell, but is a matter of degree. *B* matches, in an intuitive way, the idea of a "fresh start" at the

⁷ This use of the idea of "scaffolding" here is derived from a related concept used by Sterelny (2004).

⁸ Genes are questionable Darwinian individuals, in fact, because the boundaries separating "one" gene off from others are so indefinite. This problem is becoming more acute as genetics advances. I set that problem aside in this paper (see Godfrey-Smith 2009, Chapter 7).

beginning of life. It is also important from the standpoint of evolutionary theory. Because a bottleneck forces the process of growth and development to begin anew, a small change in the initial stage can have a multitude of downstream effects. When a large organism starts life small and simple, it creates a window of opportunity for reorganization and change (Bonner 1974, Dawkins 1982).

The second parameter is symbolized with G , which stands for *germ line*. G measures the degree of reproductive specialization within a collective. When G is high, many parts of a collective are unable to become the basis for a new collective of the same kind. In mammals like us, for example, only a small proportion of cells can give rise to a new whole organism, those "sequestered" for the production of sex cells. Our other "somatic" cells can reproduce at the cell level, but they cannot (naturally) give rise to a new human.

The role of G is also illustrated by eusocial insects, such as honey bees. In honey bee colonies the queen reproduces (along with the male "drones"), and the female workers do not. In other insects, including other bees, there is no reproductive division of labor. This divide helps mark the distinction between cases where there is a group of insects who happen to live and interact together, and cases where the colony counts as a reproductive unit in its own right.

The third parameter is I , which stands for "integration" of the collective in an overall sense. This involves a general division of labor (aside from that in G), the mutual dependence of parts, and the maintenance of a boundary between a collective and what is outside it.

Clear cases of collective reproduction are associated with "high scores" on all these features. Marginal cases are associated with low scores. There are lots of intermediate and partial cases, though. The situation can be represented with a space, as in Figure 1.

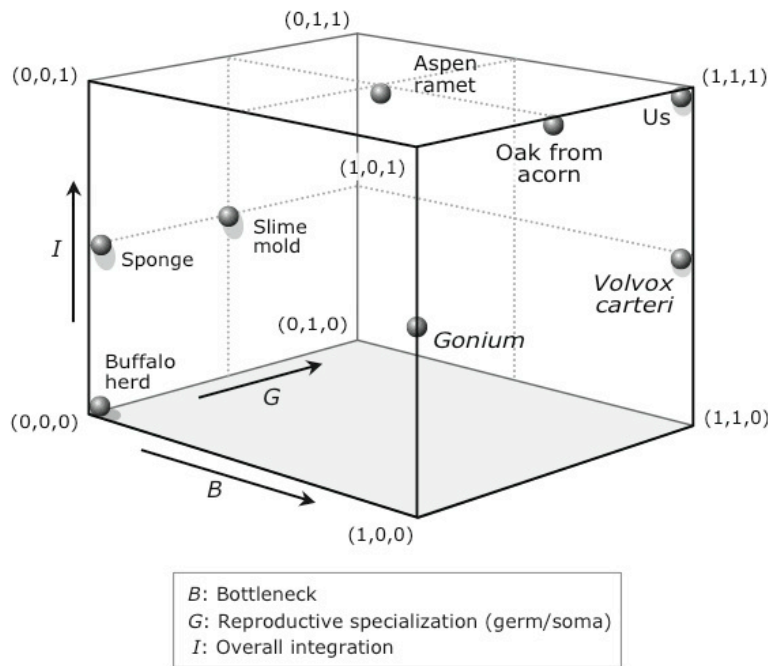


Figure 1: Forms of collective reproduction⁹

Figure 1 makes only three-way distinctions on each dimension, between low, intermediate, and high values. What is represented in each case is a mode of reproduction. In some cases (like the sponge and aspen) an entity can engage in more than one mode. With respect to *B*, the distinction made is between the absence of any bottleneck (low), some significant narrowing (intermediate), and a very small (for example, one-celled) stage marking the start of the life-cycle (high). With respect to *I*, the distinction is between loose aggregations of entities capable of independent living (low), a level of integration seen in colonies and very simple organisms like sponges (intermediate), and the level seen in complex multicellular organisms (high). In the case of *G*, I distinguish cases where all lower-level units are capable (asexually or sexually) of giving rise to a new collective (low), partial reproductive specialization (intermediate),

⁹ Figures 1 and 2, which appear in *Darwinian Populations and Natural Selection*, were drawn by Eliza Jewett-Hall.

and cases where there is a sharp distinction, established early in development, between germ and soma (high). All the categorizations of cases in the figure are made in relation to a lower level in a hierarchy. In most cases the lower level is that of cells, though in the case of the buffalo herd the lower level is that of individual buffalo.

The buffalo herd scores low on all three. A sponge reproducing by fragmentation (not through sex) differs from the herd in *I*. A slime mold fruiting body, making more fruiting bodies, has an intermediate level of *I*, some reproductive specialization, and no bottleneck. *Gonium* and *Volvox carteri* are colonial green algae. In a finer-grained treatment of *I* they might be differentiated, but here they both count as intermediate in *I*, reproducing through a bottleneck, and are distinguished by the fact that the former has no reproductive specialization whereas the latter has a germ/soma distinction (Kirk 1989, Michod et al 2003). We and the oak growing from an acorn are multicellular organisms reproducing through bottlenecks, differing only in *G*.

It is also possible to look at distinctions within a particular group, and consider fewer dimensions. In Figure 2, several kinds of bee colony are compared. The simplest bee social structure is *communal* (Michener 1974). Here a number of females make use of a common nest, each reproducing and provisioning their eggs independently. In *semisocial* bees, colonies contain a number of females of the same generation, who differentiate into a majority who both forage and lay eggs, and a smaller group who do not reproduce. The bees cooperate in the provisioning of offspring. Then, on the right, there are colonies in which a single queen lays the vast majority of eggs, most females are non-reproductive workers, and these "castes" are determined early in each bee's life. At the top right, honey bee colonies contain tens of thousands of individuals, with sharp divisions into castes and elaborate division of labor. Colony members communicate using the "waggle dance" and chemical alarm signals. Bumblebee colonies have smaller numbers, less differentiation between castes, no dances or chemical alarms, and some aggression between individuals (Wilson 1971).

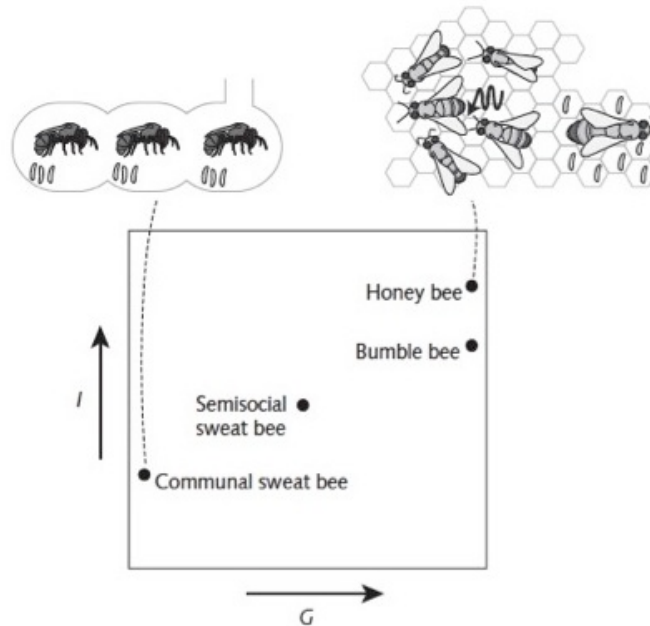


Figure 2: Collective reproduction in bee colonies

Using this analysis, let's look back at some problems discussed earlier. Janzen (1977) argued that in plants and many other organisms, asexual propagation is not reproduction. But *some* asexual reproduction must count – in bacteria, surely? Perhaps he means that for collectives, reproduction must be sexual? But why should that be? Alternatively, the claim might be that in things that *can* have sex, reproduction must be sexual. Then there is a problem coming from the fact that some organisms are only very occasionally sexual. Janzen used the case of aphids. Aphids usually cycle between sexual and asexual reproduction, and the cycle is tied to the seasons. They reject sex when times are good, and use sex when summer ends. In Janzen's interpretation, a big scattered aphid individual grows and grows through the summer, and then finally reproduces by means of sex. But as aphids have moved into warmer climates, they have in some cases reduced the role of sex, perhaps to zero. In Arizona, where it is nearly always summer, aphids go on for generation after generation in an asexual way (Knowles 1998). For Janzen, this is all growth of a few huge organisms. I think it is not. The aphid lines can evolve, can locally adapt. Mutations will arise, and some will do better than others. This is reproduction in the sense that matters to evolution.

This judgment makes sense within the spatial framework. In asexual reproduction by aphids, there are high values of B , G , and I . In asexual reproduction in aspen, also discussed earlier, there is *less* B and *less* G (Figure 1). The production of a new aspen stem is somewhat like the production of a new individual, but somewhat like growth of the old one.

So my treatment of one kind of "individual" comes from a view about how evolution works. Many things have the basic features required to take part in Darwinian change. We do, our cells do, and our genes within our cells do. Various things also *approximate* meeting the requirements. They are partial or marginal cases; they will behave in a way that has *some* connection to the Darwinian pattern. One thing that evolution does is produce new things that enter into the Darwinian pattern of change. As one Darwinian population evolves, it can give rise to new kinds of Darwinian individuals; they gradually come into focus. These new individuals include things like us, which came into focus as the cells that make up animals changed how they behave. Darwinian individuals can also go *out* of focus – lose their Darwinian characteristics. Once organized animals like us exist, our cells do not stop varying, reproducing, and so on. But as collectives like us become Darwinian individuals in their own right, the smaller parts that gave rise to them have their evolutionary activities partly suppressed. The evolution of new individuals partly "de-Darwinizes" the old ones that make them up.¹⁰

I have been discussing how collectives become Darwinian individuals. One way to look at this is to say that they can become *organisms*. A honey bee colony, for example, is often seen as an organism, or as very similar to one (Hölldobler and Wilson 2009). However, the relationships here are not so simple that we can say that becoming a collective reproducer is the same thing as becoming an organism. The connection is more complicated, and organisms have their own role in the story.¹¹

¹⁰ Ellen Clarke (2011) argues that highly integrated collectives sometimes encourage, rather than suppress, evolutionary processes in their parts. So de-Darwinization is not always the fate of old individuals that become parts of new ones. I agree there are cases like this – the human immune system runs on this principle – but suggest that de-Darwinization of parts is the rule.

¹¹ The ideas in the rest of this paper have been influenced by Austin Booth, and developed in collaboration with him. Booth presents his own treatment of the relationship between Darwinian individuals and organisms in Booth (forthcoming).

3. Organisms

In this paper I work within quite a traditional view of organisms, and one not tied to evolutionary theory. This is a *metabolic* view: organisms are systems comprised of diverse parts which work together to maintain the system's structure, despite turnover of material, by making use of sources of energy and other resources from their environment.

These views can be challenged in several ways. Many traditional formulations are too vague to deal with problem cases (Pradeu 2010). They need at least some sharpening up. Here I will treat the metabolic view as a general approach, with variants and unresolved questions, and work within it without settling all the details.

Organisms in this sense can have any history. Even reproduction is optional. An organism might persist indefinitely without making more individuals. Organisms are essentially persisters, systems that use energy to resist the forces of decay, and only contingently things that reproduce.

In the previous section Darwinian individuals were understood in a gradient way. There are clearer and more marginal cases. The same is true of organisms. Human beings and other mammals are clearly organisms. The Portuguese Man o' War (*Physalia physalia*), has often been considered a questionable case – perhaps a colony of attached organisms rather than one organism. But talk of a "degree of organismality" would be better than talk of whether something is or is not an organism (Queller and Strassman 2009). Even thinking in terms of a single scale is probably too simple, as there may be several dimensions of variation. The extent of cooperation between the parts is one, and another is the system's "geometry." Some collaborations do not form units but networks that extend without boundaries, where each member interacts with its neighbors but not with its neighbor's neighbors, and nothing unites a definite set of parts into a single system.

In the case of Darwinian individuals we encountered questions about collectives. There can be Darwinian individuals within Darwinian individuals, making them up, even though collectives tend to partly de-Darwinize their parts. The same sort of question arises here. Can there be organisms that are parts of organisms? Here I do not mean just

that one organism might be found within the boundaries of another, but it might be one of the parts that *makes* the larger system into an organism.

An "exclusion principle" is possible: in a hierarchy of parts and wholes, if an organism is present at one level, then its parts cannot be organisms and it cannot be a mere part of an organism. We can see where a principle would come from. For a collective to be an organism, cooperation and mutual dependence must exist between the parts, with respect to the activity of maintaining the collective's structure. If an object at level n in a part-whole hierarchy is an organism, it has a capacity for self-maintenance *in its own right* that is apparently incompatible with it being a mere part of an organism at level $n+1$.

In a paper that makes major contributions to this area, Queller and Strassman (2009) say at one point that "the organism is the largest unit of near-unanimous design" (p. 3144). "Unanimity" is understood in terms of cooperation. A formulation like this embodies an exclusion principle: if something at level n in a hierarchy of parts and wholes is an organism, due to being the largest object showing near-unanimity of design, then there cannot also be an organism at a higher level. However, elsewhere in the same paper Queller and Strassman say that they *do* think that organisms can contain organisms, and that an organism must merely display "high cooperation and very low conflict" among an organism's parts (p. 3144). This is an example of writers being pulled, I think, both by the appeal of some sort of exclusion principle and by empirical cases (such as honey bee colonies) which suggest that organisms making up organisms are possible.

Queller and Strassman also, in this paper, endorse a gradient treatment of the organism category – there are "degrees of organismality," and these involve two related dimensions (cooperativeness and absence of conflict). A gradient approach provides the best way to handle the question of exclusion. A categorical version of the principle – no organisms making up organisms – can be rejected. But the truth in this idea is that if the parts of a system have a significant amount of metabolic autonomy, and can keep themselves going somewhat independently, this *reduces* the degree to which the larger system counts as an organism. Significant metabolic integration at level n implies a lower

integration of the objects at level $n-1$. More generally, a high degree of organismality at one level in a hierarchy imply lower degrees at others.¹²

In the first section I said that "indivisibility" is one of the associations carried with the idea of individuality that modern biology has moved beyond. But this piece of baggage has tracked us down again, and was not entirely baggage after all. An organism is not literally indivisible. Many organisms can stay alive having been divided. There is also a sense in which an organism can be made up of organisms as parts. But there is also a sense in which this is not true. If a whole system has a highly organismal form of integration, if it is a whole with respect to its metabolic activity, then its parts must, necessarily, be *less* organismal. Those parts must be highly interdependent, less able to function as metabolic wholes themselves.

In the case of Darwinian individuals, there is some of the same phenomenon, but it apparently takes a weaker form. Returning to the case of collective reproducers, one dimension relevant to their status is I , integration. This plays a role in both concepts of the individual discussed here, and in both cases high degrees of integration at one level imply lower degrees at other levels. The status of a collective as a reproducer at all is affected by these relationships. But B and G (bottlenecks and germ lines) are also relevant to whether something is a collective reproducer, and with these features there is no inverse relationship between levels of a part-whole hierarchy. At least in principle, if the parts of a system reproduce with a germ line, a whole that they comprise might do the same. It is also the case, however, that a germ line in a collective will tend to suppress Darwinian evolution in the reproducing parts, as the human germ/soma distinction suppresses Darwinian evolution in human cells.

4. Relations

Next I will look at relations between the two categories discussed so far, Darwinian individuals and organisms. A summary of the view I will defend is given in Figure 3.

¹² See Anderson and McShea (2001) for a relevant discussion of individual-level and colony level properties in ants.

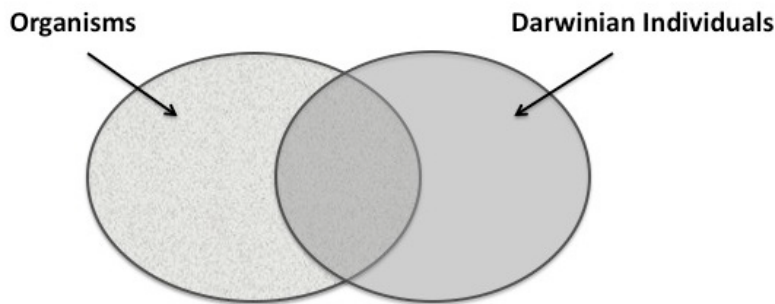


Figure 3: Basic relationships

This diagram puts definite borders back onto categories that I have been arguing have a graded character. This is just for the purposes of summarizing basic relationships, especially the fact that some things are in both categories while others are only in one. It would be more accurate to say that some things have high scores with respect to one feature while having low scores on the other. For parts of the discussion below I will use, for convenience, language which suggests these are more discrete categories than they are. One of my reasons for using this figure is because with its help, we can see a reason why earlier discussions of "individuality" in this area have been so difficult: they have been pulled to and fro by criteria associated with two different roles.¹³

Some systems are both organisms and Darwinism individuals: Many familiar organisms are in this category. Fruit flies are an example. Darwinian processes are what *give rise* to organisms. There is a complication here that we will come to later, but in general, organisms in a world like ours will be embedded in Darwinian populations. They will be able to reproduce. Evolution can also produce organisms that do things that are self-destructive; they might allow their mates or children to eat them. Darwinian processes favor self-maintenance some of the time, but may also favor self-destruction in the course of reproduction.

¹³ Discussions that reflect this to-and-fro include Santelices (1999) and R. Wilson (2007). Bouchard (2010) argues for a different separation of roles: "whereas all organisms are individuals, not all individuals are organisms."

Some Darwinian individuals are not organisms: The most important examples are scaffolded reproducers. These include viruses, which evolve despite having no metabolic capacity of their own, and chromosomes and genes (though again see footnote 8). Reproduction in cells includes the cell copying their chromosomes. As a consequence, chromosomes and genes have their own parent-offspring relations. They are Darwinian individuals, but nothing like organisms. Though chromosomes and genes are dependent on cells and organisms for their reproduction, they can acquire an evolutionary path of their own, which can include the evolution of capacities that are detrimental to the cells and organisms on which they rely. These scaffolded reproducers do not acquire not a *life* of their own, but can have their own evolutionary path. This is because genetic material can be copied and passed on independently of a cell's reproduction, and also because of the invention of sex. Sex scrambles genetic material, and allows one piece of a genome to be passed on while another piece is not.

Some simple reproducers are also in or close to this category: cells within your body that are so dependent on other cells that they are not close to being organisms in their own right. But these are not nearly as far from being organisms as chromosomes, viruses, and genes.

Some organisms are not Darwinian individuals: This is the more surprising category, one that is coming into view with recent work. First, we can note some relatively unimportant cases: sterile castes of social insects, and sterile animals like mules. These are organisms that are close relatives of things that are also Darwinian individuals. Depending on how we think about what the "capacity" to reproduce involves, maybe they are Darwinian individuals as well.

The more important cases are certain kinds of symbiotic associations. It is becoming clear that most or all plants and animals live in close associations with symbionts (Dupré and O'Malley 2009). These symbionts are often bacteria. Sometimes there is a mere association, and sometimes parasitism, but sometimes there is collaboration between the two sides. In a subset of those cases, it can be argued that symbiotic partners are integrated into the metabolic system that comprises the organism. And in a further subset of *those* cases, they are integrated in a way that does not make the whole complex, the combination, into a Darwinian individual in its own right. Then there

is an organism that is not a Darwinian individual.

A good case for thinking about these issues is the squid-Vibrio symbiosis.¹⁴ The Hawaiian bobtail squid (*Euprymna scolopes*) takes in a small number of bacteria of a certain kind (*Vibrio fischeri*) when it is very young. These bacteria grow into colonies within specialized "crypts" inside the squid, which form part of the squid's "light organ." No other bacteria can colonize these crypts. The organ lights up in a way that provides camouflage from predators watching from below, as it prevents the squid from casting a shadow. This shadow would be cast by moonlight – the squid hunts at night. At the dawn of each day, most of the bacteria are expelled, and the colony regrows from the remainder while the squid hides on the sea floor.

It can be argued that the squid-Vibrio *combination* is the organism (perhaps a "squibrio"). I think that the squid-Vibrio is not *highly* organism-like (Queller and Strassman make a similar judgment), and I will say more about this below. But this is a good case for working through the issues, as it illuminates some relationships clearly. Crucially, if we accept that the combination *is* an organism, then we find that the combination does not reproduce in the sense that is relevant to being a Darwinian individual. The combinations do not form parent-offspring lineages.

Uptake of bacteria by the squid occurs not from its parents, but from bacteria in the sea. The parts of the ocean containing the squid have more of the bacteria than other parts of the ocean; there is a sense in which the squid are "seeding" the ocean for other squid, when they expel excess bacteria each day. But if you are a squid, there is no mechanism ensuring that the bacteria in you are the offspring of bacteria in your parents, or any other specific individuals. The bacteria in you might come from many sources, and some might have not been inside squid for many generations. Squid-Vibrio combinations "make more of themselves" in *one* sense, but not in the sense that gives rise to parent-offspring lineages. The parent-offspring lines connect only the parts – they connect bacteria with bacteria and squid with squid.

The squid part of the complex always has two parents. The bacterial colony is started by quite a small number of bacteria. Recent work suggests that the number is just

¹⁴ For a review of this system, see Nyholm and McFall-Ngai (2004). For a more detailed discussion of its relation to debates about individuality, see Bouchard (2010).

6-12, one or two bacteria for each of six "crypts" that initially house them within the squid (Wollenberg and Ruby 2009). Bacterial colonies inside an adult squid do contain several strains; the diversity is not lost as the squid ages. Some of the bacteria that initiate a colony may have an ancestry that can be traced back to other colonies just a few bacterial generations back. Others may have not have ancestors inside squid-Vibrio complexes for a great many generations – perhaps ever. This is not a case where each squid-Vibrio collective has a definite and reasonably small number of parent collectives, even though each squid has exactly two parent squid and each colony-initiating bacterium has one parent bacterium.

So the combinations are not Darwinian individuals, but maybe they are organisms. They are a metabolic knotting of reproductive lineages that remain distinct.

Let's compare this case to another, the aphid-Buchnera symbiosis. Aphids, curse of gardeners and farmers, make yet another appearance in this paper. Many aphids contain bacterial symbionts (*Buchnera aphidicola*) which are carried inside specialized cells in the aphid, and synthesize essential amino acids for the aphid from the aphid's low-quality food supply. The association is as much as 250 million years old, and neither partner can survive without the other. These symbionts are transmitted directly from aphid mother to offspring, carried in the aphid ovary or embryo (Wilkinson et al. 2003).

In this case, if we identify the organism with the combination, aphid-plus-bacteria, then these combinations do stand in parent-offspring relations to each other. The bacteria in an offspring aphid are descendants of the bacteria in the parent aphid. This is a "vertically" transmitted symbiont, while the squid-Vibrio case has a "horizontally" transmitted symbiont. The aphid-Buchnera combination is a collective reproducer.

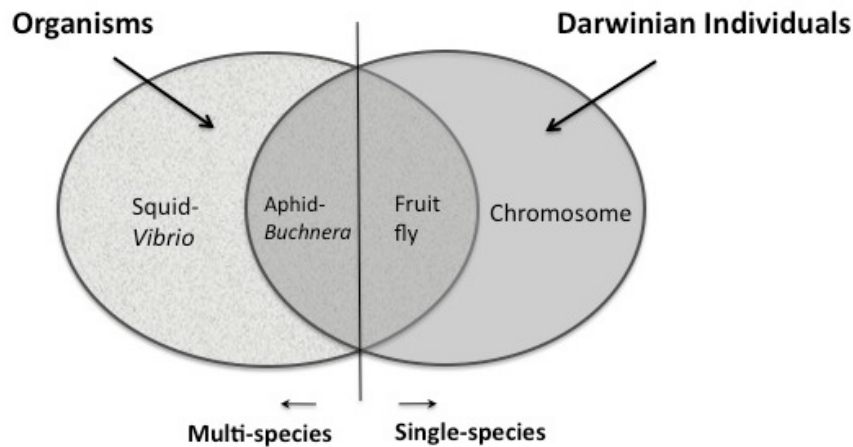


Figure 4: A fuller picture

So if we accept that an organism can comprise a familiar animal part plus its symbionts, then there can be organisms that are multi-species units. They can be multi-*kingdom* units, in fact. In the complete diagram, we have some multi-species organisms which are Darwinian individuals, and some which are not. Not pictured on the diagram are symbiotic associations which are not integrated enough to count as organisms or Darwinian individuals – good examples might be ant-acacia associations (Wheeler 1913). There are also single-species organisms like the fruit fly, and Darwinian individuals that are not organisms at all.¹⁵

The way this diagram organizes the cases may make two simplifications. These involve the line separating single-species from multi-species cases. First, could there be organisms that are not Darwinian individuals where the partners are members of the same species? It is thought that tight symbiotic pairings generally arise because each has partner different biochemical capacities. If this is the general rule, such units are unlikely to arise from single-species collaborations. Second, is there some reason why scaffolded reproducers on the far right could not consist of parts from more than one species? (This

¹⁵ Sterelny (2011) notes that a replicator-interactor view of evolution can handle symbiotic associations differently. Both the squid-Vibrio and the aphid-Buchnera combinations can be seen as *interactors*. It does not matter how the symbionts are acquired by each individual.

question was raised by Katie Steele.) The cases I have in mind for the far-right category are either members of species-like units themselves (viruses) or are parts of organisms, like genes, where each token will exist inside an organism of a single species. But could there be multi-species Darwinian individuals that are not organisms? I don't know of such cases.

With the overall picture laid out, I will spend some more time on problems arising with the cases on the left, organisms that are not Darwinian individuals. Some writers think that this is a huge category and includes ourselves. This is argued, in effect, by Dupré and O'Malley (2009) and Pradeu (2010). We might be in this category because there are vast numbers bacteria on and inside us, especially inside our guts, and some of these are important to the development and the functioning of our digestive system. These bacteria are picked up from many sources. We are influenced by those in our parents, as in the aphids, but pick up some from whatever is around us, as in the squid. Dupré and O'Malley base their argument on the role of the bacteria in metabolic cooperation. Pradeu bases it on the fact that the bacteria are *tolerated* by the organism's own policing mechanisms, its immune system.

These arguments use permissive criteria for inclusion in the organism. The human-carried symbionts are not essential to life, as in the aphid-Buchnera case. And they are not, as far as I know, as physically integrated as they are in the squid-Vibrio case. We might say that we reach a point where there is a free choice of perspective available, a choice whether to use a permissive or a restrictive attitude for inclusion. Or, again, it is better to recognize genuine differences of degree here. There are degrees of physical integration of symbionts into their hosts, and degrees of mutual dependence. When we reach the arguments of Dupré and O'Malley and Pradeu, we reach a point where the use of discrete categories in my Figures 3 and 4 becomes problematic. A full assessment of these arguments subsuming the middle category into the far left depends also on empirical work which is only presently taking shape.¹⁶

¹⁶ In fruit flies, work on the metabolic role of symbionts is at a fairly early stage. See, for example, the project at: <http://flyendo.arl.arizona.edu/index.php>. In the case of *heritable* endosymbionts, Mateos et al (2006, p. 363) say that "[o]nly Wolbachia and Spiroplasma... were confirmed as symbionts. These findings indicate that in contrast to some other insect groups, other heritable symbionts are uncommon in *Drosophila* species, possibly reflecting a robust

Some others would argue that the far left category should be a small one, in principle. If it is important for your offspring to find the right microscopic partner, a mother will make vertical transmission possible if she can. Also, in cooperating systems there is the possibility of free-riding or cheating, which may subvert the collective's efforts. Vertical transmission helps the maintenance of cooperation (Sterelny 2004). If you subvert your host, the host is unable to reproduce, and your reproduction is tied to their reproduction, then your subversion will perish with the subverted host. If you can disperse "horizontally," independently of host reproduction, then you can take advantage of hosts without undermining your own efforts. Cooperation is more easily maintained in symbioses with vertical transmission.

The squid-Vibrio case show that fine-tuned symbioses *can* exist with horizontal transmission. On the other hand, the squid and Vibrio can survive apart from each other. The aphid-Buchnera partners cannot survive apart, so the degree of organismality in the combination is higher in this case. To at least some extent, fusion of reproductive lineages seems to go with tightness of metabolic integration. if this is right, the far left hand side category is put under pressure by a kind of consolidation, in which metabolic collaborations become Darwinian individuals.

6. "The Movement of Individuality"

I started from a discussion of evolution and reached the Darwinian individual as one kind of evolved object. Then we looked at a second, the organism. Evolution includes the origination of individuals of both kinds. Some things fall into both categories, and some are in one but not the other. On the right hand side there are reproducing entities that are not organisms, or organism-like. Aside from viruses these include genes and chromosomes. These might be expected to appear in organic evolution because of the importance of template-based processes for control and inheritance in cells. Once templates are being copied, there are scaffolded reproducers, and by various paths these can acquire an evolutionary role of their own, one not entirely tied to the cells and organisms on which they depend metabolically.

innate immune response that eliminates many bacteria."

On the left are organism-like collectives whose parts are reproductively separate. This left hand category is squeezed by a kind of consolidation, in which metabolic collaborations become Darwinian individuals. But Darwinian individuals are also continually reaching out to form *new* associations and collaborations, making use of the capacities of other Darwinian individuals. Associations are coming into being in the vicinity of the left as well as being pulled into the center. Many of these get no closer than the vague vicinity of the left hand category. Some associations remain loose or part-time. Some are barely collaborations at all. Some are cooperative, but are organized in networks that have no boundaries, such as the "biofilms" formed by many bacteria. Others give rise to systems like the *Vibrio* and the squid. So in the vicinity of the left of the chart there is a to-and-fro, in which we see both the consolidation of systems into Darwinian individuals, and the reaching out of existing individuals to others, forming new associations, and giving up some autonomy in the process.

William Hamilton once referred to the "gavotte of chromosomes" seen in the processes of cell division and in sex (1975). This is a good image – a courtly dance, tuned by evolution, of joining and separating. We can see some of the same thing on a larger scale, in – to adopt Julian Huxley's phrase – "the movement of individuality." The process at this larger scale is not itself an adaptation, a to-and-fro tuned by evolutionary design. Instead it is the recurring upshot of masses of separate evolutionary events. But there is some of the same rhythm of sealing off and opening up, of consolidating and reaching out, in the dynamic linking organisms and Darwinian individuals.

* * *

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