The new puzzle of biological groups and individuals

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Essay review

The new puzzle of biological groups and individuals

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From groups to individuals. Evolution and emerging individuality.

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Introduction

The world is in constant change. Much that once individually struggled for survival is now coevolving, cooperating, and entering symbiosis—and the day will come where higher-level individuality emerges out of it, where formerly loose collections become individuals in their own right. For human beings, this day, this evolutionary transition, already lies in the past, and has happened more than once as the integration of mitochondria, the emergence of multicellularity and the functional role of symbiotic gut bacteria for our survival show. We now stand before another possible transition, and only the future will reveal what is awaiting our species. This is our not-yet-written book, open for fascinating speculation.

From groups to individuals—Evolution and emerging individuality offers conceptually precise reconsideration of empirical data on the emergence and maintenance of biological individuality in evolutionary transitions and of the implications for closely

connected issues such as fitness, selection and adaptation at different levels. Careful editing prevents the differences among the eleven thought-provoking individual contributions from hindering the emergence of a coherent whole, aiming at a theoretical framework for the notion of biological individuality. The book is structured around three complementary foci: on organisms and individuality; on adaptation and complex individuals; and on groups and collectives as individuals. Whilst advanced knowledge of key issues in the philosophy of biology may sometimes be required, there are many well-developed considerations and new arguments that invite us to see familiar issues from different angles, so that, taken as an individual whole, the book merits positive selection.

Unavoidably for any review about something so rich in content, my focus neglects many valuable pages of the book. I will follow the structure of the book and retrace the central threads of chapters one to four (the first of the three parts of the book) to introduce and connect some central issues and views. Against this background, I then provide a more general reflection linked only with specific parts of the other, no-less-interesting contributions. The result is a fusion of possible lessons drawn from the individual chapters that, like pieces of a puzzle, fit together such that a particular higher-level whole emerges. The reader is invited to construct his or her own puzzle from the arguments made in this challenging book and debate.

Four visions of the individual

Chapter one, "Darwinian individuals", by Peter Godfrey-Smith, begins with a historical sketch of the notion of biological individuality and its changes due to evolutionary theory on the one hand, and the study of problem cases on the other. For instance, if

"reproduction is making a *new* individual, while growth is making more of the same" (p. 18), then examples such as aspen groves, where apparently distinct "trees" can be united by a common root system from which they all grow, put into question an easy distinction between reproduction and growth, making it unclear what *the* individual exactly is. Matters get worse when it comes to collective entities that seem to be individuals in their own right, like bee colonies or symbiotic associations. Still, even if there might not be *the* individual in biology, Godfrey-Smith highlights two related special kinds of individuals: Darwinian individuals and organisms. In identifying a Darwinian individual, an entity that takes part in evolution by natural selection, "things that matter … are things that can *reproduce*" (p. 20), where reproduction can be simple, scaffolded or collective. By having a closer look at collective reproduction, Godfrey-Smith argues for a quantitative analysis in terms of different degrees to which entities possess three essential features: a bottleneck (a narrowing that divides generations); a germ line (reproductive specialization); and functional integration (mutual dependence of parts). This enables comparison of, for instance, slime moulds, different species of bees and us, where a human-being collection of cells is a reproducer in its own right to a higher degree than the other examples.

By contrast, the notion of organism follows traditionally from a *non-evolutionary* perspective, one that takes a physiological or "*metabolic* view: organisms are systems comprised of diverse parts which work together to maintain the system's structure, despite turnover of material. […] Organisms are essentially persisters, systems that … only contingently … reproduce" (p. 25). Despite this contrast, organismality also comes in degrees, disqualifying similarly any dichotomy of *whether or not* something is an organism. Additionally, just as Darwinian individuals may make up collectives of higher-

level Darwinian individuals that "tend to partly de-Darwinize their constituent parts" (p. 26), collectives of organisms may make up higher-level organisms where "a high degree of organismality at one level in a hierarchy implies lower degrees at others" (p. 26).

Keeping both special kinds of individuals in mind, Godfrey-Smith identifies the degree to which certain entities are both Darwinian individuals and organisms or rather one than the other. Viruses are Darwinian individuals to a very high degree while their organismality appears to be absent, whereas it is the other way round in the case of sterile social insects or sterile animals like mules. Symbiotic associations (mostly plants or animals in association with bacteria) can have a high degree of (multispecies) organismality without forming the sort of parent–offspring lineages that are necessary to being a Darwinian individual, such as in the case of squid–*Vibrio* symbioses. However, there are also cases of stronger metabolic connections among the symbiotic partners, like in the case of aphids and *Buchnera*, which do form parent–offspring lineages. The upshot of chapter one is not only that Darwinian individuality and organismality come in degrees (and should be so understood) but to study further the dynamic linking among both kinds.

Chapter two, "Defining the individual", by Charles J. Goodnight, uses an "intuitive concept of shared evolutionary fate" (p. 37) to guide a formal approach to entities and groups in terms of contextual analysis and multilevel selection. Goodnight offers a detailed discussion of three competing definitions. To the extent that the level at which fitness is assigned follows practical constraints, the "individual" is an "arbitrary construct of the observer" (p. 42), which affects the interpretation of how selection is working. One problem is "that the species selection we see when we assign fitness at the level of the species may be revealed as organismal selection when we assign fitnesses at the level

of organism" (p. 44) such that qualitatively different interpretations of how selection is acting emerge if fitness is assigned above the level at which selection is actually acting. Against this background, Goodnight generates a second definition via the logical move of putting individuality at the *lowest* measurable level. However, as well as practical constraints, difficulties arise for this definition in the context of cells within metazoa, where not only germ line cells but also somatic cells, owing to mutation in mitotic cell division, satisfy classical criteria for evolution by natural selection. Employing the second definition would imply that these "cells within a metazoan are not qualitatively different than, for example individual bees or ants within a colony" (p. 46). To distinguish them, Goodnight introduces quantitative considerations that take into account mechanisms suppressing the potential for evolution of certain entities. For example, germ and somatic cell lines are segregated early in the development of higher animals, which reduces evolution by natural selection among these cells. The consideration of such mechanisms thus leads to a third definition of individuality that is about the lowest level at which a *response* to selection can occur, taking into account the potential for selection to *actually lead* to evolutionary change. This third definition faces even more experimental constraints than the second one since the possibility of seeing a response to selection depends on many parameters that may be very complex and may vary in time.

Chapter three, "Species and organisms: What are the problems?", by Ellen Clarke and Samir Okasha, provides another viewpoint in the debate by considering not only the *sources* of but also revealing *parallels* between the species problem and the problem of individual organisms. A central question in the former problem is whether species are natural kinds that "partition the set of all living things into non-overlapping groups in an

objective way" (p. 56), whereas the latter problem is about how to parcel up certain portions of living things into *individual* organisms that play a "pivotal role in evolutionary biology as the bearer of fitness and as the demographic unit" (p. 58). As a key problem case the authors discuss slime mould, a single-cell amoeba which reproduces clonally but which, in the case of famine, aggregates with thousands of other amoebae into a morphologically differentiated and thus organism-like higher-level structure with quasi-germ line parts.

One parallel between the species problem and problem of individual organisms is that both suffer from the issue of 'vagueness", in that unavoidably there are intermediate and thus vague borderline cases of species and, similarly, organismality comes in degrees and may change in time, as the example of slime mould illustrates. Another parallel issue is that of 'multiple criteria'. Because biologists use multiple criteria for defining species (e.g., reproductive isolation, genetic relatedness and phenetic similarity), different and partly overlapping sets of entities are identified—which is also true in the case of organisms where, for example, bottlenecks, germ soma separation and functional integration are debated criteria.

The relatedness of 'vagueness' and 'multiple criteria' in both the species and the organism problem is further analysed in two crucial contexts of inquiry: diachronic and synchronic contexts. Species seen from a diachronic perspective always face vagueness, which often disappears from a synchronic perspective, where it is rather a question of choosing from multiple defining criteria. Similarly, vagueness of organismality is more a problem from a diachronic perspective, notably in cases "where individuals at one level of hierarchy emerge over time from ancestors at a lower level of hierarchy" (p. 68). Still, to the extent that evolution is gradual, vagueness also affects synchronic contexts of

inquiry since each definition criterion for species and organisms comes, at least for some species and some organisms at some point in time, in degrees.

After discussing possible 'solutions' promoted by punctuated equilibrium theories, the authors consider a distinction between category and taxa questions to clarify where 'vagueness' and 'multiple criteria' are the predominant problems. Category questions, such as "Is *x* a species/organism?" (p. 69), concern the *generality* of the category across all cases; i.e. what it generally means to be a species and not a variety or to be an organism and not only part of it. While for such questions the problem of multiple criteria becomes predominant, taxa questions, such as whether *y* is a member of the considered species *x* or whether *y* is part of the specific organism *x*, are more concerned with the *gradualness* of evolution and organismal transitions, where vagueness is what is more troublesome.

Chapter four, "Immunity and the emergence of individuality", by Thomas Pradeu, analyses further the relation between evolutionary and physiological/metabolic views, where he promotes an immune-system-based *physiological* view of biological individuality and its *complementarity* with evolutionary approaches. Physiologically speaking, the immune system establishes organism boundaries by including some entities while rejecting others, thereby enabling a distinction between what is part or is not part of an organism. Furthermore, from an evolutionary perspective, the immune system is "one of the main "policing" mechanisms in living individuals, … by which a high-level individual … prevents the emergence of variants having a different fitness at a lower-level" (p. 77), by the "elimination of new variants favouring their own fitness" (p. 83) among other mechanisms. In sum, the *complementarity* of evolutionary and physiological/metabolic views can be seen in the central role that the immune system plays in the 'de-

Darwinization' of constituent parts (cf. Godfrey-Smith, p. 26) that is presupposed in the emergence and maintenance of (new) levels of individuality.

In contrast to classical physiological /metabolic views, which may have limited generality, Pradeu argues that *all* studied multicellular organisms (and possibly all organisms) have an immune system in the sense of "biochemically specific interactions leading to the rejection of some living entities" (p. 81). This seems to be a necessary truth in light of the pathogens that any kind of organism has to cope with. Following a discussion of the immune system's role in the prevention and elimination of tumour cells that may arise in any multicellular organism (p. 85), it is shown that immunity is, in addition to being an *extremely general* (possibly universal) property characterizing individuality, the "most important mechanism to explain the evolution of the multicellular organism's individuality" (p. 86). This explanatory role does not only concern the *maintenance* but also the *emergence* of individuality. Importantly, "the criterion for immune elimination of abnormal constituents is not genetic homogeneity" (p. 87), which is anyway both rarely found in multicellular organisms and not necessary from an evolutionary point of view—rather the opposite is the case in, for instance, symbiotic bacteria that increase the host's fitness. The suggestion of using functional integration to identify (degrees of) individuality has often been criticized for lack of generality, but Pradeu here offers a promising solution, insofar as the immune system is *non-contingently* a (quasi) universal property of organismality at any level.

Towards a context-dependent definition

In what follows, I build on my particular reading of this challenging book to suggest a novel understanding of biological individuality and organismality, from the perspective of

a metaphysically suggested and empirically confirmed *context-dependency* of functionally defined biological property types (cf. Esfeld & Sachse 2011).

As highlighted in almost all chapters, biological individuality and organismality *come in degrees*. What remains rather implicit is that the very degree depends on environmental conditions. To see this dependency, one may for instance follow Goodnight (chapter two) in focusing on the potential for evolution, and then arguing that the degree of individuality is context-dependent since the *manifestations* of potentials (or dispositions, in other words) are context-dependent. By taking explicitly into account the role of different environments we can *generalize* what Goodnight says about invoking mechanisms suppressing the potential for evolution, in order to distinguish somatic cells from true individuals (pp. 46–47). My claim is that this is a reference to a *particular* (though important) feature of environmental conditions of cells within metazoa. Taking into account all 'relevant' environmental conditions would allow better comparison of degrees of biological individuality.

Slime mould serves again as a good example: under certain environmental conditions it is the single-cell amoeba that is the individual, while under other environmental conditions, when certain resources are missing, the individual is the formed aggregate of cells with "quasi-germinal and … quasi-somatic" (p. 145) specialized cells, as Philip Huneman also notes in chapter seven (Adaptations in transitions). This means that changes in what the individual is and becomes are triggered by environmental changes. Taking this context-dependency into account hence provides a better understanding of evolutionary transitions that are also "a matter of degree" (Huneman, p. 164).

What might motivate a context-dependent understanding of biological individuality, according to which changes in what the individual is are seen as triggered by

environmental change? My argument is that *a*) two biological individuals may be similar with respect to their potential (e.g. for selection) but differ with respect to the set of environmental conditions under which the potential is manifested and, *b*), taking these differences into account may be crucial for adequate predictions and explanations.

A minimal framework helps to clarify the structure: being to some degree *X* (biological individual/organism) requires having to some degree *Y* (properties suggested by different views, which are of course at the centre of the debate), whose manifestation depends on the context *C* (that may vary and change in time). This framework thus defines biological individuality and organismality not only in terms of a *binary* relation as it is classically done (e.g., something is an individual if it has *Y* to some degree), but in terms of a *ternary* relation taking into account differences and changes in individuality/organismality due to different environmental conditions.

This naturally raises questions about the 'relevant' set of environmental conditions. After all, being to some degree *X* by having to some degree *Y* may remain stable with respect to certain environmental differences. My idea of a ternary (*X*–*Y*–*C*) relation in the definitions does not need to reflect *all* metaphysically *possible* environments but only the actual and common ones. This relaxes the experimental constraints by allowing justified abstractions, where "ultimate justification for any theoretical model rests in its empirical usefulness" (p. 112), as Andy Gardner argues in chapter five. The task of identifying the right balance between precision and abstraction is thereby linked to explanation and prediction, meaning that the 'relevant' environmental conditions are only those that play a role in the explanations of degrees of individuality/organismality.

To illustrate, we can sketch a context-dependent interpretation of Pradeu's immune-system-based view on organismality. In order to define (degrees of) organismality,

Pradeu refers to specific biochemical interactions within organisms that lead to the inclusion of some entities (that are thus part of the organism in question) and to the rejection of other entities, such as pathogens (that are thus not part of the organism in question). Since the existence of pathogens is one of the main arguments for Pradeu's immune-system-based view, let me simplify his approach to imply the following: organismality is (at least partly) defined *with respect to something that is not part of the organism*. Against this background, there are various possible abstractions that can be made when defining (the degree of) organismality. We might ignore different environmental conditions if it is of no scientific use to refer to them, because they *do not differ* with respect to the relevant pathogens. When *comparing* organisms *differing* in their ability to eliminate pathogens, other kinds of abstractions become scientifically useful. Let us think of organisms able to reject only pathogens of type P_1 while other organisms are able to reject pathogens both of type P_1 and P_2. For explanations and predictions concerning environments where only pathogens of type P_1 are present, it would be of no scientific use to consider the *different* capacities to reject pathogens since this difference is *not manifested*.

Similar issues emerge in "Colonies are individuals" (chapter nine), where Matt Haber analyses the superorganism revival and discusses the right balance between precision and abstraction when comparing colonies with organisms (p. 196). He focuses on the "problem" that there are no paradigmatic organisms (p. 201), while I would here like to stress the *dual role* that environmental conditions play. Metaphysically speaking, for any difference in organismality between two entities, there is a possible environment in which this difference is not manifested. If our world would hypothetically *only* contain these two entities and the mentioned environmental conditions were *fixed*, we would

not have any debate about degrees of or differences in organismality. Since our world also contains environmental conditions under which both entities manifest different degrees of organismality, there is a problem, which is amplified by the existence of many more than two living entities and many years of evolution and environmental change (cf. the diachronic view proposed by Clarke & Okasha, chapter three). In this sense, the context-sensitivity of individuality causes problems, because different and gradually changing environments undermine the possibility of arriving at a simple dichotomy of organism or not-organism, and force us to recognise different degrees of individuality and organismality. However, the context-sensitivity of individuality is also helpful, because by quantifying over all 'relevant' environmental conditions we can see that under particular environmental conditions even two biologically different individuals (or organisms) can be similar with respect to their individuality (or organismality).

Many examples that support my perspective can be found within the volume. For instance, viruses are examples of individuals that can reproduce only given particular environmental conditions external to viruses (Godfrey-Smith, p. 20). Natural selection leads to group adaptations (and thus justifies us in taking the group as an individual) only under "very special circumstances" (Gardner, p. 107). Another challenging example is that of tumour cells, discussed by Minus van Baalen (chapter six) in the context of horizontal transmissions and suppression of within-soma diversity. Following his insight that there is no such thing as *the* germ line, but rather "a more or less loose association of a hierarchy of smaller parts, … each having differential options for spreading" (p. 122), we may consider a soma cell that becomes a tumour cell through mutation, which makes it an individual to a higher degree than it was before. My point now is that the degree of *manifested* individuality of the tumour cell depends on the given conditions, for

instance on the kind of immune system and the tumour cell's location in the organism, which affect the possibility of transmission to other organisms and thus the possibility of a genuine lineage (as in the case of Tasmanian devil facial tumour disease; cf. p. 46 and p. 122). A possible transmission, in turn, depends on the possible 'victims' and their behaviour. Thus, whether or to what degree mutations lead to the emergence (or evolutionary regain) of individuality depends clearly on the given conditions.

This conclusion can also be drawn from "Groups, individuals, and the emergence of sociality" (chapter eight) by Andrew Hamilton and Jennifer Fewell, where social organizations and the division of labour, the "sine qua non of sociality" (p. 177), are analysed. They give a clear analysis of "how division of labor can emerge globally from simple local interactions" (p. 179), where the specialisation of, for example, certain kinds of bee queens "is not simply a reflection of intrinsic differences—it is amplified by the social context" (p. 182). Transposed into my general terms, whether or to what degree some disposition (e.g., task specialization) is manifested, leading in the end to the division of labour and thus genuine sociality, depends on the 'relevant' environments, as nicely shown in experiments discussed.

What the 'relevant' environment is thus depends on the individual/organism in question, and thus becomes even more complicated in symbiotic associations. As Scott Turner shows in his discussion of "Superorganisms and superindividuality" (chapter ten), the fact that symbiotic associations generally comprise phylogenetically distant members does not hinder the "manifestation of a metabolically convenient association between two complementary genomes" (p. 222). To the contrary, "nearly all organisms are, to some extent, symbiotic organisms" (p. 235). What matters here is that whether two phylogenetically distant individuals/organisms start a symbiotic association, and thus, an

evolutionary transition depends on the complementarity of their genomes among other factors; it depends on the respective environmental conditions, where one member is a 'relevant' part of the environmental conditions of the other (and *vice versa*).

Let me finish this review by suggesting one more conclusion that might be drawn by combining the insights of different chapters. Frédéric Bouchard, in chapter eleven, promotes Van Valen's ecological definition of species as a way to understand symbiotic superindividuals. He says, "humans belong to the same group, not because they are inter-reproductive or because their genomes are alike, but because the multigenomic communities that are part of (*Homo sapiens* + gut bacteria + etc.) *function* in the same way in similar contexts" (p. 257). In light of the analogies drawn in chapter three (Clarke & Okasha) we might sketch a close parallel to the ecospecies concept, according to which biological individuality and organismality are defined with respect to relevant environmental conditions or niches. Different entities may then have the same degree of biological individuality and organismality in some environments, while not in others, and it would be clear that only particular environments enable the emergence and maintenance of higher-level individuality and organismality.

References

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