Editorial introduction: The many faces of biological individuality

(Special issue of *Biology & Philosophy* on biological individuality)

Final version published in *Biology & Philosophy*, November 2016, 31(6), pp 761–773,
http://link.springer.com/article/10.1007/s10539-016-9553-z

Thomas Pradeu

(ImmunoConcEpT, UMR5164, CNRS & University of Bordeaux, 146 rue Léo Saignat 33076 Bordeaux, France, thomas.pradeu@u-bordeaux.fr)

Abstract
Biological individuality is a major topic of discussion in biology and philosophy of biology. Recently, several objections have been raised against traditional accounts of biological individuality, including the objections of *monism* (the tendency to focus on a single individuality criterion and/or a single biological field), *theory-centrism* (the tendency to discuss only theory-based individuation), *ahistoricity* (the tendency to neglect what biologists of the past and historians of biology have said about biological individuality), *disciplinary isolationism* (the tendency to isolate biological individuality from other scientific and philosophical domains that have investigated individuality), and the *multiplication of conceptual uncertainties* (the lack of a precise definition of "biological individual" and related terms). In this introduction, I will examine the current philosophical landscape about biological individuality, and show how the contributions gathered in this special issue address these five objections. Overall, the aim of this issue is to offer a more diverse, unifying, and scientifically informed conception of what a biological individual is.

1. Introduction: The significance of the problem of biological individuality

The problem of biological individuality has been central for philosophers of biology, both recently (Wilson 2005; Okasha 2006; Clarke 2011; Pradeu 2012; Bouchard and Huneman 2013; Clarke 2013; Godfrey-Smith 2013; Wilson and Barker 2013) and less recently (Hull 1978; Hull 1980; Hull 1992; Wilson 1999). It has also been widely discussed by biologists (e.g., Medawar 1957; Ghiselin 1974; Buss 1987; Maynard Smith and Szathmáry 1995; Michod 1999; Gould and Lloyd 1999; Pepper and Herron 2008; Queller and Strassmann 2009; West and Kiers 2009; Folse and Roughgarden 2010; Minelli 2013; Herron et al. 2013; West et al. 2015). In general, asking what a biological individual is means asking what constitutes a countable, relatively well-delineated, and cohesive unit in the living world (Hull 1992; Wilson and Barker 2013; Chauvier 2016), but of course each component of this definition needs to be explained and justified.

The exploration of the problem of biological individuality in the last two decades has led to several productive results. In particular, a quasi-consensus has emerged on some important claims. Such claims include question-dependence, rejection of anthropocentrism, the need for a hierarchical approach to individuality, and the idea that individuality comes in degrees (See **Table 1**).

This consensus, incidentally, is not always acknowledged. This has sometimes led to the repetition of certain already well-established claims. It is no longer useful to argue that our conception of individuality depends on the question and scientific context under consideration, that the level of the organism is not the only one at which biological individuality can be realized, or that biological individuality is a continuous rather than a discrete property. The careful examination of the literature on biological individuality also shows that other claims – e.g., that philosophers of biology interested in biological individuality have tended to be ignorant of "real" biological examples – are simply misplaced, as illustrated by the scientifically rich contributions of those like David Hull.

Label	**Detailed claim**	**References**
Question-dependence	The answer to the question 'what counts as a biological individual?' will depend to a large extent on the scientific context in which the question is asked.	(Sober 1991; Hull 1992; Wilson 1999; Wilson 2005; Dupré 2012; Godfrey-Smith 2013)
Anti-anthropocentrism	A scientifically fruitful approach to biological individuality should not be based on human intuition, common sense, or perception. It can be very unhelpful to use human beings (or other vertebrates) as the central model for biological individuals.	(Hull 1978; Hull 1980; Hull 1988; Hull 1992; Wilson 1999)
Hierarchization	Biological individuality is nested and hierarchical; it can be realized at several different levels of the living world (for example the level of the cell and that of the organism).	(Weismann 1893; Lewontin 1970; Bernard 1974; Hull 1980; Gould and Lloyd 1999; Gould 2002)
Continuity	Biological individuality comes in degrees; a biological entity can exemplify biological individuality to lesser and greater degrees.	(Child 1915; Conklin 1916; Sober 1991; Santelices 1999; Pepper and Herron 2008; Godfrey-Smith 2009).
Transitions	There have been transitions in individuality; through evolution, new levels of individuality have emerged as a result of the coming together of previously distinct entities	(Buss 1987; Maynard Smith and Szathmáry 1995; Michod 1999; Okasha 2006; Godfrey-Smith 2009).

Table 1. Consensual claims for philosophers and biologists working on biological individuality.

However, the consensus on some major claims should not hide the fact that there are many disagreements among the participants in the debate over biological individuality. In what follows, I will examine recent challenges to philosophical accounts about biological individuality and I will explain how the papers gathered in this special issue of *Biology and Philosophy* posit themselves with regard to those challenges.

2. Recent challenges

Several objections have recently been levelled at established philosophical accounts of biological individuality (see **Box 1**). First, many consider those accounts exceedingly *monistic*. Should we favour monism or pluralism when thinking about biological individuality? The debate has at least two aspects. The first concerns the question of *individuality criteria*. Many different, non-overlapping, individuality criteria co-exist in the scientific and philosophical literature (Santelices 1999; Clarke 2011; Godfrey-Smith 2013). These include genetic homogeneity, germ/soma separation, the possession of a developmental bottleneck, policing mechanisms, etc. Some philosophers are *monists* – either in the sense that they defend one particular criterion, or insofar as they try to find a fundamental and unifying mechanism underlying several (or even all) criteria (Clarke 2013). Other philosophers are *pluralists*, i.e., consider there must be different criteria of individuality, reflecting different scientific questions and contexts (Wilson 1999; Wilson 2005; Pradeu 2012; Wilson and Barker 2013; Godfrey-Smith 2014; Sterner 2015; Love and Brigandt 2017). The second aspect of the debate about monism focuses on the *scientific disciplines* used to establish our concept of a biological individual. In their reflections about biological individuality, philosophers of biology have tended to focus on a single biological field – generally evolution (Hull 1978; Hull 1980; Hull 1992; Okasha 2006; Godfrey-Smith 2009; Clarke 2013). In so doing, they have left aside many biological fields where the problem of biological individuality has also played a central role, including physiology, developmental biology, immunology, ecology, the cognitive sciences, among others (Dupré and O'Malley 2009; Pradeu 2010; Minelli 2011; Godfrey-Smith 2013; Huneman 2014). The two aspects of the debate are related, at least in the sense that taking into account more biological fields is likely to increase the number of possible individuality criteria.

The second objection is that philosophers have unduly privileged a *theoretical* approach to biological individuality – at the expense of more practical and experimental considerations (Kovaka 2015; Chen 2016; Love and Brigandt 2017). The influence of Hull – and, less directly, of Quine – helps explain this situation: in several texts (e.g., Hull 1992), Hull explained that the only way to distance ourselves from intuition-based approaches to individuality was to construct a theory-based perspective (which also explains why he sees the heavily theoretical field of evolutionary biology as the best pathway to defining biological individuality). A greater attention to practices might suggest, for instance, that, in everyday life, biologists "individuate" entities in a flexible and pragmatic way, without any strong ontological commitment (Love and Brigandt 2017). Of course, it remains to be determined whether such pragmatically isolated entities should be considered "individuals" or not, and on which grounds (Chauvier 2016; Guay and Pradeu 2016a).

The third objection is that the majority of philosophers of biology have neglected the studies of the concept of biological individuality made by historians of science (Lidgard and Nyhart 2017). Many of the issues raised today about biological individuality have already been raised, in a different context, in the past. For example, the idea of nested biological individuality was examined by Leibniz in response to work by Swammerdam, Leeuwenhoek

and others (Duchesneau 2010); the concept of the multicellular organism as a society of cells was analysed by Claude Bernard (1974); finally, the question of part–whole relations, complex life cycles and alternation of generations fascinated nineteenth-century biologists (Nyhart and Lidgard 2011; Nyhart and Lidgard 2017). It would be fruitful and inspirational to examine in detail those proposals compare them with contemporary ones. It is also worthwhile noting that historians interested in biological individuality explore various biological domains[1] – instead of focusing on the domain of evolutionary biology only. Philosophers could perhaps be inspired by this comprehensive approach to the problem of biological individuality.

The fourth objection is that these investigations into biological individuality have often been done in relative isolation from other domains which have produced interesting work on individuality (Guay and Pradeu 2016a). These domains include physics (French 2014; French 2016), the social sciences (Paternotte 2016), and metaphysics (Dorato and Morganti 2011; Morganti 2013; French 2014; Chauvier 2016; Lowe 2016). Importantly, several individuality criteria are common to different sciences, but do not play exactly the same role in each science. It could, thus, be useful to compare these different situations to build a better-informed conception of individuality in biology and philosophy of biology.

Metaphysics can also be helpful. It is well known that individuality has been a central question in metaphysics for several centuries (Strawson 1959; Chauvier 2016; Lowe 2016). Metaphysicians have produced precise analyses of individuality and cognate concepts or views – for instance identity, persistence, four-dimensionalism, sortalism, among many others. These contributions could certainly help philosophers of biology produce a more precise conception of a biological individual (Guay and Pradeu 2016b; Haber 2016). From this point of view, recent innovative work at the interface of philosophy of biology and metaphysics might call attention to several benefits philosophers of biology could get from a stronger attention to metaphysical considerations (Ferner 2016; Wiggins 2016a; Wiggins 2016b).

The fifth objection concerns *conceptual uncertainties*. There is considerable confusion over the definition of the notion of a "biological individual", and of related terms such as "organism", "whole" and "parts", "unity", "cohesion", among others (Santelices 1999; Clarke 2011). In the philosophy of biology literature, we find very few attempts to offer precise definitions of those terms, even though they constitute the backbone of the debate over what a biological individual is.

Objection 1: Monism	Tendency to focus on a single individuality criterion and/or a single biological field (generally evolution).
Objection 2: Theory-centrism	Tendency to discuss only theory-based individuation.
Objection 3: Ahistoricity	Tendency to neglect what biologists of the past and historians of biology have said about biological individuality.
Objection 4: Disciplinary isolationism	Tendency to isolate biology from other scientific and philosophical domains that have investigated individuality, including physics, the social sciences, or metaphysics.
Objection 5: Conceptual uncertainties	Lack of definition of "biological individual" and related terms.

Box 1. Recent objections to philosophical accounts of biological individuality

To these five objections, we can add another, more traditional, one. It asks: To which biological entities can the notion of biological individuality be applied? A concept of

[1] These include morphology (Nyhart 1995), developmental biology (Benson 1981; Maienschein 2011) and cell biology (Duchesneau 1987; Canguilhem 1992; Gayon 1998; Bechtel 2006), among other fields.

biological individuality that would be applicable to only a small fraction of the living world – for instance to animals only – would not be satisfying from a biological point of view (unless of course we have strong biological reasons to make such a distinction). As stated, the need to avoid biases towards vertebrates or even metazoans was emphasized in early philosophical discussions about biological individuality (Hull 1978; Hull 1992; Wilson 1999). But philosophers of biology have recently begun discussing certain neglected cases, some of which might prove challenging for traditional criteria of individuality. This includes studies of fungi (Booth 2014a; Molter 2016), stem cells as compared to non-stem cells (Fagan 2016), living things with highly complex life cycles including some plants (Godfrey-Smith 2016; Griesemer 2016) and some eukaryotic microbes (O'Malley 2016), and even perhaps viruses (Forterre 2016).

The challenges above are examined at length in several recent publications. The move from theory-centrism (Objection #2) to a stronger attention to practices and experimental contexts is made in many parts of current philosophy of science (e.g., Waters 2008; Ankeny et al. 2011; Love 2015), and this move is gaining prominence in the debate about biological individuality (Chen 2016; Fagan 2016; Love and Brigandt 2017). The combination of historical and philosophical approaches (in response to Objection #3) is the main topic of a forthcoming volume edited by Scott Lidgard and Lynn Nyhart (Lidgard and Nyhart 2017). Based on an analysis of past and present-day examples, Lidgard and Nyhart propose to divide the problem of biological individuality into four sub-problems: *individuation* (thresholds, boundaries, inside/outside, autonomy); *hierarchy* (levels of organization in complex systems); *horizontality* (interactions among parts in making a whole); and *temporality* (change through time, particularly in part-whole relations). These four categories are useful to locate and compare many contemporary positions within the debate over biological individuality. In parallel, there is an on-going attempt to collate biology with other domains (which constitutes a response to Objection #4), particularly physics and metaphysics (French 2011; French 2014; Ferner 2016; French 2016; Guay and Pradeu 2016b; Mygal et al. 2016).

This special issue of *Biology and Philosophy* mainly addresses Objections #1 and #5. The next section explains how the contributions gathered here can be seen as replies to these objections.

3. Attempts to build a more diversified and more precise conception of biological individuality

Many of the papers gathered in this special issue are interested in the monism–pluralism debate. Should we adopt several individuality criteria, or should we favour one criterion – and if so which one and with which arguments? Should we ground our concept of individuality in several biological domains or in one given domain – and, here again, if we opt for the monistic choice, on what basis should we do so?

Philosophical debates about biological individuality have focused almost exclusively on an evolutionary approach (Hull 1978; Hull 1980; Hull 1992; Okasha 2006; Godfrey-Smith 2009; Clarke 2013). One organising thought that informs this special issue is that a major aim for philosophers of biology should be to account for the numerous biological fields that explore the question of biological individuality. Indeed, the incorporation, confrontation, and combination of different biological perspectives probably constitutes the most generative way of building a unified and biologically informed conception of biological individuality (see **Figure 1**).

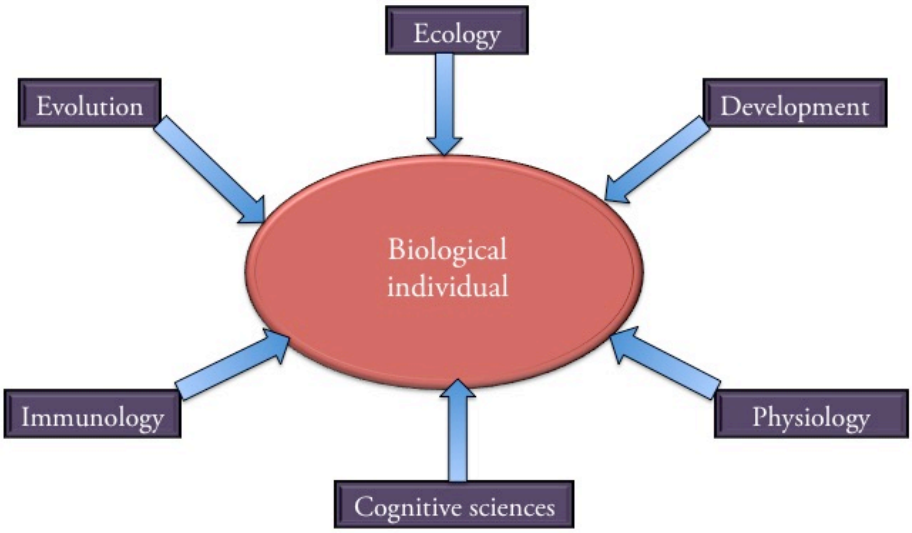

Fig. 1. The concept of a biological individual will be enriched by a confrontation and combination of the perspectives offered by different biological domains. Only six domains are mentioned here, but many others can contribute to debates about biological individuality.

Three papers of this special issue explore the field of *immunology*, in which the notion of individuality has been intensively explored in the last decades (Loeb 1930; Loeb 1945; Medawar 1957; Burnet 1960; Tauber 1991; Pradeu 2012). Lynn Chiu and Gérard Eberl (a world-leading scientist in the field of gut immunology) examine host-microbe associations in light of the recently proposed "equilibrium model of immunity" (Eberl 2016). Scott Gilbert and Alfred Tauber suggest that recent work on symbiosis and so-called "holobionts" (conceived as functionally integrated and cohesive units constituted of a host and the microbes that live within and on it) casts doubt on traditional views on biological individuality, and could potentially re-orient the whole field of immunology. Thomas Pradeu uses immunology to offer a refined conception of the delineation and persistence of physiological individuals, based on the argument that the immune system constitutes, in any living thing, a mechanism of inclusion and exclusion.

Peter Godfrey-Smith examines the relation between biological individuality and the *cognitive sciences*, in light of work on "minimal cognition" and the emergence of early nervous systems (Keijzer et al. 2013). *Developmental biology* plays a central role in the contribution of Gilbert and Tauber, who have long argued for a coming together of the study of development and immunology (Tauber 1991; Gilbert 2002). Furthermore, Pradeu shows that, over more than two centuries, *physiology* has produced very important analyses of biological individuality, which should be combined with evolution-based approaches.

Finally, several contributors pay attention to what the field of *ecology* has to say about biological individuality, including David Queller and Joan Strassmann, Derek Skillings, and, in an "ecological-developmental" perspective, Gilbert and Tauber as well as Chiu and Eberl.

In addition to all these biological domains, the contributors of this special issue explore, at length, studies on *symbiosis*. These studies do not constitute a "biological domain" as such; instead, they are located at the interface of many disciplines, including microbiology, evolutionary biology, ecology, developmental biology, immunology, among several others

(McFall-Ngai 2008; McFall-Ngai et al. 2013). Symbiosis studies have flourished in the last ten years, and they have offered key insights for anyone interested in biological individuality. The fact that virtually every living thing is home to "foreign passengers" – some of which play important functional roles in the host – raises important issues regarding biological boundaries, individuality criteria based on genetic homogeneity, etc. (Gilbert 2002; Bosch and McFall-Ngai 2011; Gilbert and Epel 2015). Building on recent philosophical work on symbiosis (Pradeu and Carosella 2006; Bouchard 2009; Dupré and O'Malley 2009; Pradeu 2011; Godfrey-Smith 2013; Booth 2014b; O'Malley 2016), the contributors of this special issue examine symbiosis from different, yet complementary points of view. One major question concerns what we can call the "holobiont debate", i.e. the question of the degree of unity and cohesion found in a holobiont. This question – particularly animated in some scientific circles (e.g., Zilber-Rosenberg and Rosenberg 2008; Bordenstein and Theis 2015; Bosch and Miller 2016; Douglas and Werren 2016; Theis et al. 2016) – is discussed in all the contributions of this special issue. Queller and Strassmann argue that complex holobionts are generally not organisms because, even when they show some cooperation, they still express levels of internal conflict that are too high to constitute organismic units. Skillings explores the holobiont debate from the point of view of the "founding" example of corals. He holds that most holobionts share more affinities with communities than they do with individual wholes, and that, in general, holobionts do not meet the criteria for being evolutionary individuals, units of selection, or organisms. In contrast, Gilbert and Tauber consider that holobionts are unified communities, acting as units from physiological, developmental, immunological, and evolutionary viewpoints. Pradeu defends the view that, from an immunological point of view, a biological individual is made of all the components that are immunologically tolerated, which include many (but not all) microbes found in or on a host. Chiu and Eberl assert that microorganisms are constitutive of host immunity as external *scaffolds*, varying in degrees of reliability, specificity, and exclusivity. In their view, even if holobionts are not internally integrated enough to qualify as organisms or units of selection, they are still individuals in a different and more general way: the holobiont must be seen as the host plus the microorganisms that scaffold its immunity. Haber sees holobionts as nested individuals, with sometimes distinct, non-overlapping life cycles. Clarke interprets holobionts in light of reproductive synchrony (Frank 1997) and fitness alignment (Friesen 2012) between the symbiotic partners.

By offering this wide range of perspectives, we hope to offer the readers the opportunity to take a better-informed decision in favour of monism or pluralism. For pluralism-oriented people, a further choice is between a "promiscuous" pluralism (where the different perspectives coexist and remain largely autonomous) and a "combining" pluralism (where one major aim is to combine the different perspectives to produce a unified picture) (Guay and Pradeu 2016a).

In addition to examining neglected biological domains, several contributors attempt to clarify certain central concepts in this debate. Queller and Strassmann think that the main debate should be about the notion of an *organism* – which they define as a unit in which all the subunits have evolved to be highly cooperative, with very little conflict (see also Queller and Strassmann 2009). Clarke (2013) defends the view that the notions of *organism* and *biological individual* are synonymous, and in her contribution to this special issue she interprets evolutionary transitions as changes in the extent to which selection acts at one hierarchical level rather than another, a view she grounds in her definition of evolutionary individuality in terms of an object's capacity to undergo selection at its own level. Pradeu insists, on the contrary, on the differences between the notions of *organism* and *biological individual*; he suggests distinguishing at least two categories of a biological individual, namely the *physiological individual* ("unit of functioning") and the *evolutionary individual*

("selective unit"). Godfrey-Smith also distinguishes *organism* from *evolutionary individual*. Complementing previous work in which he defines evolutionary individuals as *Darwinian individuals* (that is, *reproducing* units: Godfrey-Smith 2009; 2013), he focuses on the *organism*, which he defines as a bounded and self-maintaining unit, engaged in traffic with its environment (see also Arnellos and Moreno 2015). Skillings also makes a difference between *evolutionary individuals* (which he defines, following Godfrey-Smith, as *Darwinian individuals*) and *organisms* (which he defines as bounded individuals that are functionally or metabolically integrated, i.e. systems with mutually dependent components that work together to maintain the system's structure or developmental trajectory). Haber offers a different perspective. He shows that, for the individuality thesis, *individuals* (be they organisms, species, etc.) must be understood recursively, meaning that biological individuals are "lineage-generating entities that are both constituted by and constitutive of other biological individuals".

Our hope is that, in exploring new biological fields dealing with biological individuality, and by refining certain conceptual distinctions, this special issue will participate in the on-going project of building a conception of biological individuality that will be more unified, more inspired by historical and metaphysical considerations, and that will better reflect current biological perspectives and practices (Lidgard and Nyhart 2017).

Acknowledgements
I thank all the contributors to this special issue, the many anonymous reviewers, and Adam Ferner for his comments on this introduction.

References

Ankeny R, Chang H, Boumans M, Boon M (2011) Introduction: philosophy of science in practice. Eur J Philos Sci 1:303. doi: 10.1007/s13194-011-0036-4
Arnellos A, Moreno A (2015) Multicellular agency: an organizational view. Biol Philos 30:333–357. doi: 10.1007/s10539-015-9484-0
Bechtel W (2006) Discovering cell mechanisms: the creation of modern cell biology. Cambridge University Press, New York
Benson KR (1981) Problems of Individual Development: Descriptive Embryological Morphology in America at the Turn of the Century. J Hist Biol 14:115–128.
Bernard C (1974) Lectures on the phenomena of life common to animals and plants. Thomas, Springfield, Ill
Booth A (2014a) Populations and Individuals in Heterokaryotic Fungi: A Multilevel Perspective. Philos Sci 81:612–632. doi: 10.1086/677953
Booth A (2014b) Symbiosis, selection, and individuality. Biol Philos 29:657–673. doi: 10.1007/s10539-014-9449-8
Bordenstein SR, Theis KR (2015) Host Biology in Light of the Microbiome: Ten Principles of Holobionts and Hologenomes. PLoS Biol 13:e1002226. doi: 10.1371/journal.pbio.1002226
Bosch TCG, McFall-Ngai MJ (2011) Metaorganisms as the new frontier. Zool Jena Ger 114:185–190. doi: 10.1016/j.zool.2011.04.001
Bosch TCG, Miller DJ (2016) The Holobiont Imperative. Springer Vienna, Vienna
Bouchard F (2009) Understanding Colonial Traits Using Symbiosis Research and Ecosystem Ecology. Biol Theory 4:240–246. doi: 10.1162/biot.2009.4.3.240
Bouchard F, Huneman P (2013) From Groups to Individuals: Perspectives on Biological Associations and Emerging Individuality. MIT Press, Cambridge, MA

Burnet FM (1960) Immunological recognition of self. Nobel Lect Physiol Med 3:689–701.
Buss LW (1987) The Evolution of Individuality. Princeton University Press, Princeton, N.J.
Canguilhem G (1992) La connaissance de la vie, 2. éd. rev. et aug. J. Vrin, Paris
Chauvier S (2016) Why individuality matters. In: Guay A, Pradeu T (eds) Individuals Across the Sciences. Oxford University Press, New York, pp 25–45
Chen R-L (2016) Experimental Realization of Individuality. In: Guay A, Pradeu T (eds) Individuals Across the Sciences. Oxford University Press, pp 348–370
Child CM (1915) Individuality in organisms. The University of Chicago press, Chicago, Ill.
Clarke E (2011) The Problem of Biological Individuality. Biol Theory 5:312–325.
Clarke E (2013) The Multiple Realizability of Biological Individuals. J Philos 413–435.
Conklin EG (1916) The basis of individuality in organisms from the standpoint of cytology and embryology. Science 43:523–527. doi: 10.1126/science.43.1111.523
Dorato M, Morganti M (2011) Grades of individuality. A pluralistic view of identity in quantum mechanics and in the sciences. Philos Stud 163:591–610. doi: 10.1007/s11098-011-9833-z
Douglas AE, Werren JH (2016) Holes in the Hologenome: Why Host-Microbe Symbioses Are Not Holobionts. mBio 7:e02099-15. doi: 10.1128/mBio.02099-15
Duchesneau F (2010) Leibniz: le vivant et l'organisme. J. Vrin, Paris
Duchesneau F (1987) Genèse de la théorie cellulaire. Bellarmin ; Vrin, Montréal : Paris
Dupré J (2012) Processes of Life: Essays in the Philosophy of Biology. Oxford University Press, Oxford & New York
Dupré J, O'Malley M (2009) Varieties of Living Things: Life at the Intersection of Lineage and Metabolism. Philos Theory Biol. doi: http://dx.doi.org/10.3998/ptb.6959004.0001.003
Eberl G (2016) Immunity by equilibrium. Nat Rev Immunol 16:524–532. doi: 10.1038/nri.2016.75
Fagan MB (2016) Cell and Body. In: Guay A, Pradeu T (eds) Individuals Across the Sciences. Oxford University Press, pp 122–143
Ferner AM (2016) Organisms and personal identity: biological individuation and the work of David Wiggins. Routledge, Abingdon, Oxon ; New York, NY
Folse HJ, Roughgarden J (2010) What is an Individual Organism? A Multilevel Selection Perspective. Q Rev Biol 85:447–472.
Forterre P (2016) To be or not to be alive: How recent discoveries challenge the traditional definitions of viruses and life. Stud Hist Philos Sci Part C Stud Hist Philos Biol Biomed Sci 59:100–108. doi: 10.1016/j.shpsc.2016.02.013
Frank SA (1997) Models of symbiosis. Am Nat 150 Suppl 1:S80-99. doi: 10.1086/286051
French S (2014) The structure of the world: metaphysics and representation, 1st ed. Oxford University Press, Oxford ; New York
French S (2016) Eliminating Objects Across the Sciences. In: Guay A, Pradeu T (eds) Individuals Across the Sciences. Oxford University Press, pp 371–394
French S (2011) Shifting to structures in physics and biology: a prophylactic for promiscuous realism. Stud Hist Philos Biol Biomed Sci 42:164–173. doi: 10.1016/j.shpsc.2010.11.023
Friesen ML (2012) Widespread fitness alignment in the legume-rhizobium symbiosis. New Phytol 194:1096–1111. doi: 10.1111/j.1469-8137.2012.04099.x
Gayon J (1998) The Concept of Individuality in Canguilhem's Philosophy of Biology. J Hist Biol 31:305–325.
Ghiselin MT (1974) A Radical Solution to the Species Problem. Syst Biol 23:536–544. doi: 10.1093/sysbio/23.4.536
Gilbert SF (2002) The genome in its ecological context: philosophical perspectives on interspecies epigenesis. Ann N Y Acad Sci 981:202–218.
Gilbert SF, Epel D (2015) Ecological Developmental Biology, 2nd edition. Sinauer

Associates, Inc., Sunderland, Massachusetts, U.S.A
Godfrey-Smith P (2013) Darwinian Individuals. In: Bouchard F, Huneman P (eds) From Groups to Individuals: evolution and emerging individuality. MIT Press, Cambridge, MA, pp 17–36
Godfrey-Smith P (2009) Darwinian populations and natural selection. Oxford University Press, Oxford
Godfrey-Smith P (2014) Philosophy of biology. Princeton University Press, 2014, Princeton
Godfrey-Smith P (2016) Individuality and Life Cycles. In: Guay A, Pradeu T (eds) Individuals Across the Sciences. Oxford University Press, pp 85–102
Gould SJ (2002) The structure of evolutionary theory. Belknap Press of Harvard University Press, Cambridge, Mass
Gould SJ, Lloyd EA (1999) Individuality and adaptation across levels of selection: How shall we name and generalize the unit of Darwinism? Proc Natl Acad Sci 96:11904–11909. doi: 10.1073/pnas.96.21.11904
Griesemer J (2016) Reproduction in complex life cycles: Toward a developmental reaction norms perspective. Philos Sci. doi: 10.1086/687865
Guay A, Pradeu T (2016a) Introduction: Progressive Steps toward a Unified Conception of Individuality Across the Sciences. In: Guay A, Pradeu T (eds) Individuals Across the Sciences. Oxford University Press, pp 1–22
Guay A, Pradeu T (2016b) Individuals Across the Sciences. Oxford University Press, New York
Haber MH (2016) The Biological and the Mereological. In: Guay A, Pradeu T (eds) Individuals Across the Sciences. Oxford University Press, pp 295–316
Herron MD, Rashidi A, Shelton DE, Driscoll WW (2013) Cellular differentiation and individuality in the "minor" multicellular taxa. Biol Rev Camb Philos Soc 88:844–861. doi: 10.1111/brv.12031
Hull D (1980) Individuality and Selection. Annu Rev Ecol Syst 11:311–332. doi: 10.1146/annurev.es.11.110180.001523
Hull D (1992) Individual. In: Keller EF, Lloyd EA (eds) Keywords in Evolutionary Biology. Harvard University Press, Cambridge, MA, pp 181–187
Hull DL (1978) A Matter of Individuality. Philos Sci 45:335–360.
Hull DL (1988) Science as a process: an evolutionary account of the social and conceptual development of science. University of Chicago Press, Chicago
Huneman P (2014) Individuality as a Theoretical Scheme. II. About the Weak Individuality of Organisms and Ecosystems. Biol Theory 9:374–381. doi: 10.1007/s13752-014-0193-8
Keijzer F, Duijn M van, Lyon P (2013) What nervous systems do: early evolution, input–output, and the skin brain thesis. Adapt Behav 21:67–85. doi: 10.1177/1059712312465330
Kovaka K (2015) Biological Individuality and Scientific Practice. Philos Sci 82:1092–1103. doi: 10.1086/683443
Lewontin RC (1970) The Units of Selection. Annu Rev Ecol Syst 1:1–18. doi: 10.1146/annurev.es.01.110170.000245
Lidgard S, Nyhart LK (eds) (2017) Biological Individuality: Integrating Scientific, Philosophical, and Historical Perspectives. The University of Chicago Press, Chicago
Loeb L (1930) Transplantation and Individuality. Physiol Rev 10:547–616.
Loeb L (1945) The Biological Basis of Individuality. Thomas, Springfield
Love AC (2015) Collaborative explanation, explanatory roles, and scientific explaining in practice. Stud Hist Philos Sci Part A 52:88–94. doi: 10.1016/j.shpsa.2015.03.003
Love AC, Brigandt I (2017) Philosophical Dimensions of Individuality. In: Lidgard S, Nyhart LK (eds) Biological Individuality: Integrating Scientific, Philosophical, and Historical Perspectives. University of Chicago Press, Chicago,

Lowe EJ (2016) Non-individuals. In: Guay A, Pradeu T (eds) Individuals Across the Sciences. Oxford University Press, pp 49–60
Maienschein J (2011) "Organization" as Setting Boundaries of Individual Development. Biol Theory 6:73–79. doi: 10.1007/s13752-011-0006-2
Maynard Smith J, Szathmáry E (1995) The major transitions in evolution. WHFreeman Spektrum, Oxford ; New York
McFall-Ngai M (2008) Are biologists in "future shock"? Symbiosis integrates biology across domains. Nat Rev Microbiol 6:789–792. doi: 10.1038/nrmicro1982
McFall-Ngai M, Hadfield MG, Bosch TCG, et al (2013) Animals in a bacterial world, a new imperative for the life sciences. Proc Natl Acad Sci U S A 110:3229–3236. doi: 10.1073/pnas.1218525110
Medawar PB (1957) The Uniqueness of the Individual. Methuen, Londres
Michod RE (1999) Darwinian dynamics : evolutionary transitions in fitness and individuality. Princeton University Press, Princeton, NJ
Minelli A (2013) Individuals, Hierarchies and the Levels of Selection: A Chapter in Stephen J. Gould's Evolutionary Theory. In: Danieli GA, Minelli A, Pievani T (eds) Stephen J. Gould: The Scientific Legacy. Springer Milan, Milano, pp 73–83
Minelli A (2011) Animal Development, an Open-Ended Segment of Life. Biol Theory 6:4–15. doi: 10.1007/s13752-011-0002-6
Molter D (2016) On Mushroom Individuality.
Morganti M (2013) Combining science and metaphysics: contemporary physics, conceptual revision, and common sense. Palgrave Macmillan, Houndmills, Basingstoke, Hampshire
Mygal VP, But AV, Mygal GV, Klimenko IA (2016) An interdisciplinary approach to study individuality in biological and physical systems functioning. Sci Rep. doi: 10.1038/srep29512
Nyhart LK (1995) Biology takes form: animal morphology and the German universities, 1800-1900. University of Chicago Press, Chicago
Nyhart LK, Lidgard S (2011) Individuals at the center of biology: Rudolf Leuckart's Polymorphismus der Individuen and the ongoing narrative of parts and wholes. With an annotated translation. J Hist Biol 44:373–443. doi: 10.1007/s10739-011-9268-6
Nyhart LK, Lidgard S (2017) Alternation of generations and individuality, 1851. In: Lidgard S, Nyhart LK (eds) Biological Individuality: Integrating Scientific, Philosophical, and Historical Perspectives. The University of Chicago Press, Chicago,
Okasha S (2006) Evolution and the Levels of Selection. Clarendon Press; Oxford University Press, Oxford; NY
O'Malley M (2016) Reproduction Expanded: Multigenerational and Multilineal Units of Evolution. Philos Sci. doi: 10.1086/687868
Paternotte C (2016) Collective Individuals: Parallels Between Joint Action and Biological Individuality. In: Guay A, Pradeu T (eds) Individuals Across the Sciences. Oxford University Press, pp 144–164
Pepper JW, Herron MD (2008) Does biology need an organism concept? Biol Rev Camb Philos Soc 83:621–627. doi: 10.1111/j.1469-185X.2008.00057.x
Pradeu T (2012) The Limits of the Self: Immunology and Biological Identity. Oxford University Press, New York
Pradeu T (2010) What is an organism? An immunological answer. Hist Philos Life Sci 32:247–268.
Pradeu T (2011) A Mixed Self: The Role of Symbiosis in Development. Biol Theory 6:80–88. doi: 10.1007/s13752-011-0011-5
Pradeu T, Carosella E (2006) The self model and the conception of biological identity in immunology. Biol Philos 21:235–252.
Queller DC, Strassmann JE (2009) Beyond society: the evolution of organismality. Philos

Trans R Soc Lond B Biol Sci 364:3143–3155. doi: 10.1098/rstb.2009.0095
Santelices null (1999) How many kinds of individual are there? Trends Ecol Evol 14:152–155.
Sober E (1991) Organisms, Individuals, and Units of Selection. In: Tauber AI (ed) Organism and the Origins of Self. Springer Netherlands, Dordrecht, pp 275–296
Sterner B (2015) Pathways to pluralism about biological individuality. Biol Philos 30:609–628. doi: 10.1007/s10539-015-9494-y
Strawson PF (1959) Individuals: an essay in descriptive metaphysics. Methuen, London
Tauber AI (1991) Organism and the Origins of Self. Kluwer, Dordrecht
Theis KR, Dheilly NM, Klassen JL, et al (2016) Getting the Hologenome Concept Right: an Eco-Evolutionary Framework for Hosts and Their Microbiomes. mSystems 1:e00028-16. doi: 10.1128/mSystems.00028-16
Waters CK (2008) How Practical Know-How Contextualizes Theoretical Knowledge: Exporting Causal Knowledge from Laboratory to Nature. Philos Sci 75:707–719. doi: 10.1086/594516
Weismann A (1893) The all-sufficiency of natural selection. Contemp Rev 64:309–338.
West SA, Fisher RM, Gardner A, Kiers ET (2015) Major evolutionary transitions in individuality. Proc Natl Acad Sci 201421402. doi: 10.1073/pnas.1421402112
West SA, Kiers ET (2009) Evolution: what is an organism? Curr Biol CB 19:R1080-1082. doi: 10.1016/j.cub.2009.10.048
Wiggins D (2016a) Continuants: Their Activity, Their Being, and Their Identity. Oxford University Press
Wiggins D (2016b) Activity, Process, Continuant, Substance, Organism. Philosophy 91:269–280. doi: 10.1017/S0031819115000637
Wilson J (1999) Biological individuality : the identity and persistence of living entities. Cambridge University Press, Cambridge & New York
Wilson RA (2005) Genes and the agents of life: The individual in the fragile sciences, biology. Cambridge University Press, Cambridge & New York
Wilson RA, Barker M (2013) The Biological Notion of Individual. In: Zalta EN (ed) The Stanford Encyclopedia of Philosophy, 2016th edn.
Zilber-Rosenberg I, Rosenberg E (2008) Role of microorganisms in the evolution of animals and plants: the hologenome theory of evolution. FEMS Microbiol Rev 32:723–735. doi: 10.1111/j.1574-6976.2008.00123.x