

Chapter 7

Organisms: Between a Kantian Approach and a Liberal Approach



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Abstract The concept of “organism” has been central to modern biology, with its definition and philosophical implications evolving since the nineteenth century. In contemporary biology, the divide between developmental and physiological approaches and evolutionary approaches has influenced the definition of organism. The convergence between molecular biology and evolutionary biology has led to the term “suborganismal biology,” while the return to the organism has been characterized by animal behavior studies and Evo-devo. The philosophical approach to the concept of individual is divided between a Kantian understanding of organism, which defines necessary and sufficient conditions for any X to be a “natural purpose,” and an evolutionary approach, which considers what a biological individual is and confers natural selection a key role in this definition. While the former aims to find necessary and sufficient conditions for an organism, the latter thinks in terms of conceptual spaces, being much more liberal in pointing out organisms in the world. The paper examines possible connections between these two approaches and assesses the prospects of a reconciliation between them.

The notion of organism stands between self-evidence and inscrutability: self-evidence, because someone outside of theoretical biology would easily agree that most of the living things are organisms or, in other words, that whatever life is, it comes under the form of “organisms;” and inscrutability, because when one wants to make sense of organisms, difficulties are innumerable: What do make them different from other complex systems? Should they be principally understood as products of evolution, as, according to Huxley’s phrase, “bundles of adaptation?” Are they just an instance of *an organization* or something specific that requires more than “organization” to be understood?

In current days, this difficulty appears even more pressing, for at least two reasons. Borrowing the usual distinction between functional biology and evolutionary biology that Ernst Mayr has drawn based on a difference between proximate and

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ultimate causation (Mayr, 1961), let's survey these reasons. In molecular biology, the pervasiveness of network thinking (e.g., Barabasi, 2018, Newman, 2010) challenges the idea that biological systems should be investigated mechanically or in a reductionist way (i.e., starting from the parts – cells or molecules – and their dispositions). Thus, it contributed to the rise of systems biology (Kitano, 2002, Green, 2013), an approach designed to address organisms as wholes irreducible to the effects of their parts, that is, as a set of instructions given by the genes. While the hope of elaborating the basic explanatory repertoire of biology at the suborganismal level of macromolecules vanishes, the notion of the organism itself, engaged by systems biology, requires a novel theoretical framework.

On the other hand, it has been repeatedly said that the Modern Synthesis in evolutionary biology tended to confer organisms an ancillary status because the basic evolutionary processes stand at the levels of genes and populations. Organisms were something to be explained, as Dawkins (1976) suggests by wondering why genes tend to coalesce into organisms instead of living by themselves; or they were an instance supposedly left aside by evolutionary biology, whereas developmental biology or Evo-devo rightly take organisms as a structuring concept: this omission of organisms was the target of the famous “spandrel paper” by Gould and Lewontin, whose major claim is the inability of the current evolutionary biology to soundly handle organisms. Walsh (2017) sees evolutionary theory as a “suborganismal” account (opposed to a potential organismal one). But for more than a decade, evolutionary theory has been undergoing major controversies about the necessity to revise or expand (Gould, 2002) the modern synthesis framework, and one important issue arising here concerns the status of organisms (Bateson, 2005, Huneman, 2010). Several dimensions of the claim of a return of the organism coexist:

- The idea that organisms contribute to causing their environment (named *niche construction*, Odling-Smee et al., 2003).
- The idea that some variation can be heritable and directed toward adaptation, for instance, based on *phenotypic plasticity* (West-Eberhard, 2003; Sultan, 2015, Walsh, 2015).
- The relevance of organismal development to evolution, while it has been separated from evolution on the ground of various concurring conceptual distinctions, such as development vs inheritance, somatic vs germinal lineages, or even lately theso-called “central dogma of molecular biology”.

Evo-devo has been built around this call to reintegrate developing organisms in evolution (e.g., Raff, 1996; Gilbert et al., 1996), and the developmental systems theory (Griffiths & Gray, 1994; Oyama et al., 2001) is a general account intending to replace genes by developmental cycles as units of selection or evolution.

All these critiques were noticeably led by philosophers (e.g., Walsh, Stotz, Griffiths, Oyama) and biologists alike.

Granted, claims that organisms have been neglected from evolutionary biology seem unfair, to the extent that behavioral ecology is the science of the traits of organisms as adaptations and in general conceives of evolution at the level of organismal phenotypes – named “strategies” (see Grodwohl, 2019). However, what's left out from

behavioral ecology is the sense of the integration of all the strategies within one organism – hence, the specific sense of the organization of the organism, which was precisely the target of Gould and Lewontin (1978) under the name of *Bauplan*, a term borrowed from the German tradition of transcendental morphology in the late nineteenth century.

From the viewpoint of either functional or evolutionary biology, this organismal organization should therefore be the object of a theorizing effort. This is not to say that such an effort does not exist. On the contrary, most of what labels itself “theoretical biology,” from Rashevsky on, thought intensively about what the organization of an organism is, using ideas forged by some inaugural figures of this tradition (Rashevsky, D’Arcy Thompson, Rosen, Ganti, to name a few). In this paper, I will consider that two threads of thought about organisms coexist in biology and will leave out this tradition of theoretical biology; the question of explicitly articulating these two trends to such tradition should be the object of another paper. One of these threads is mostly found in the circles of developmental biology or Evo-devo and philosophically owes a lot to Kant; the other is mostly elaborated by evolutionary biologists and I will argue that it is much more liberal than the former one. They give room to two general ways of thinking about how the two notions of biological *individual* and *organism* are connected. After having presented these two accounts of what organisms are – and their highly different methodologies – I will say a word about their respective conditions of validity.

7.1 Making Sense of Organisms: The Kantian View

7.1.1 Purposiveness

Among philosophers who addressed biology before the Darwinian turn, Immanuel Kant cannot be overlooked. His *Critique of Judgment* provides an “analytic of teleological judgment” that has often been interpreted as an inquiry into the conditions of possibility of biology.¹ And his key claim that “organisms” (or organized being, *Organisierte Wesens*) are the “natural purposes” (*Naturzwecke*) directly connects with the idea that ‘organism’ became a crucial concept for biology at the times of Kant’s philosophy. Developmental biology or embryology developed after Caspar Wolff’s seminal *Theorie der Generation* (1764) into a science of the developing organisms whose key figures in the nineteenth century have been exposed to Kantian thinking, as had been made clear by several historians of biology (e.g., Lenoir, 1982; Richards, 2001; Sloan, 2002). Among these biologists, Blumenbach was in epistolary contact with Kant, and major names such as Pander or Von Baer belonged to the same tradition (Von Baer authored the *Entwicklungsgeschichte den Thieren* (1828), arguably the most important nineteenth-century biology book, as Darwin himself acknowledged).

¹For this claim, Lenoir (1982), Zumbach (1984), McLaughlin (2000), Huneman (2008), and Ginsborg (2004) against Zammito (2018) and Richards (2001).

Comparative anatomy built itself on two key principles, the “principle of the conditions of existence” and the “principle of the connections,” leading to the “principle of unity of type.” The former was advocated by George Cuvier, whose *Leçons sur l’anatomie comparée* (1805) were a milestone in this science; the latter is developed by Geoffroy Saint-Hilaire, who was a young colleague of the former. Even though they are often contrasted as two divergent ways of making biology, the former focusing on *function* and the latter on *form* – and this is the influential reading by Russell (1911) that Amundson (2005) endorsed later on – both their principles target the structured organism.

The fact that Kant’s analytics of biology centers on the notion of organisms – which I will explicate quickly – therefore matches with the new role of organisms in the nineteenth-century biology.² Thus, it sounds natural that those who vindicate a return of the organisms in evolutionary biology through the evolutionary theory of development (or Evo-devo) trace back their key concept to Kant’s view of organisms (e.g., Gilbert & Sarkar, 2000).

When Gould and Lewontin (1978) use the German term “*Bauplan*” to label what – in an organism – resists the adaptationism proper to the Modern Synthesis, in a paper that has been heavily quoted by Evo-devo people when arguing against the treatment of organisms by this Modern Synthesis, the connection between developmental thinking in evolution and a Kantian tradition in biology becomes obvious. It is thus natural that I sketchily expose this Kantian view now. Since this is not a piece of Kantian scholarship, I’ will be fast in reconstructing Kant’s reasoning, citing materials likely to back up my claims (including my work).

Let’s start with this key notion of purposiveness since Kant’s main object is the judgment that ascribes finality to natural systems. Such a judgment explains something by invoking a preexisting concept of this thing – a concept standing “at the root of the production of the object,” as Kant says. This is the most general concept of purposiveness. When Kant adds “*natural* purposiveness,” he means such things that are judged purposive but that are at the same time naturally produced, in contrast with artificial and technical items.

It is often reminded that Kant contrasts mechanisms and teleology – those are his two terms, and a section in the *Critique of Judgement*, the “Antinomy of the teleological judgment,” intends to articulate them. *Mechanism* is about explaining a whole from the parts, and *teleology* is therefore the opposite, explaining the parts from the whole. This latter characterization of purposiveness instantiates the most general definition I gave above (in terms of a kind of causality of a presupposed concept). Saying that I explain the part based on a knowledge of the whole is to say that the part needs the idea of the whole to be understood, and this constitutes the presupposition of a concept at the root of the item to be explained.

Regarding biology, this becomes clear when we turn to a classical example also considered by Kant: the eye. In the eye coexist lots of distinct parts – retina, cones, rods, crystalline, cornea, etc. Each of them follows its proper, distinct “laws”, as he

²A claim defended at length in Huneman (2008, forth).

argued in the First Introduction to the *Critique of Judgement*. If they were arranged differently, for instance, the retina slightly more to the left, then we would see nothing. To explain why all the parts are where and as they are, one has to posit something: the notion of a seeing device, at the root of the production of this organ. Otherwise, it seems that pure chance distributed all these elements in such a way; whereas if the concept of vision is the ground for the construction of the eye, this harmony between the proper laws of each organ becomes necessary. That is a teleological judgment.

This allows us to understand a decisive phrase Kant uses to explicate what is purposiveness: it is the “lawlikeness of the contingent as such” (*First Introduction to the CJ*). What is *necessary* cannot be otherwise, it follows the laws of nature. Whatever *X* is *contingent* on could be otherwise – *X* is contingent upon the antecedent state of the universe, in the sense that, had this state been different, *X* would be different. But some systems are such that to understand them one needs to consider that the contingency of their states (as contingent upon other antecedent states) can be bracketed in favor of a sort of necessity of their features. The “concept” alluded to by a teleological judgment is an instantiation of this necessity, a sort of rule for behavior proper to such systems. This pattern holds for biology: even if contingent on the laws of physics, as contingent, living entities have some lawlikeness of their own when taken as living entities. For instance, it is merely physically contingent that the development of a chick embryo ends up in a chicken or a monster, yet from the viewpoint of a biologist, these two states are not at all on a par. We call this difference viability vs. teratology. *Viability is a norm*. While physics knows no norms, biology does; for instance, besides the norms of development, any *function* in biology states a norm – “functioning vs malfunction” is normative: a kidney that does not eliminate toxins is abnormal even though (or rather: because) its function is to eliminate toxins.³ These norms constitute a “lawlikeness for the contingent as such”; and the “concept” assumed in any teleological judgment instantiates such a norm.

7.1.2 *Regulative Principle?*

Purposiveness, that is, normativity as a lawlikeness of the contingent as such, assumption of a concept at the root of production, and epistemic precedence of the whole over the parts: those are the main elements of Kant’s idea of teleological judgment. And for this reason, an organism, an organized being, is a natural purpose: a purpose, because it has parts that are only understandable based on the whole, hence on the concept of the whole. Thus, from the viewpoint of science, a concept stands at the roots of their production, hence the contingency of the agreement of the parts shows, as such, a lawlikeness – and this lawlikeness is not in the things themselves; it is in the eye of the beholder. This latter point is the other major

³For the normative interpretation of Kant, see Ginsborg (2004, 2014) and Huneman (2014a, b, c).

aspect of this view of organisms as natural purposes – namely, such lawlikeness stems from our project of understanding life as such: it is a “regulative” principle for our cognition. Kant writes: “This principle does not pertain to how such things are possible themselves through this kind of production (things considered themselves as phenomena) but pertains only to the way our understanding can judge them” (CJ § 77, 408). This regulative character makes perfect sense with the requirement that the “concept” at the root of their production is posited by the teleological judgment to the aim of guaranteeing this lawlikeness at the biological level, which will then constitute the object of inquiry for the biologist.

Three things must be written now:

- (a) The “concept” of vision, used to allow an investigation of the eye, and more generally any of these concepts that take the role of norms in biological inquiry behave like *attractors*. What does it mean?

Suppose a complex system in phase space. If the system, when faced with a small range of initial conditions, lightly changes its final state, we have a classic case of predictable determinism. But if in the same situation the system hugely changes its dynamics and final state, it is unpredictable, since the error margin on measuring the initial conditions is mapped onto a very large margin of error regarding the final result. The range of final states now is too large to predict anything from the knowledge of an initial state.

But in addition to these two situations, we can consider a third pattern where, whatever the initial conditions, the system will always end up in the same final state. Such a state is called an *attractor*; an example turned into a metaphor is a valley at the bottom of a mountain: whatever place one lets a stone roll down from the top, it will end up at the same location – down in the valley.

The concept of vision somehow turns a pattern of the type “sensitivity to initial condition” into the pattern of the type “attractor.” Physical conditions of the embryogenesis of the chick can vary a lot, but then one can (most of the time) safely assume that the chick will develop an eye, since the whole development for the biologist is supposed to produce an eye. There are many different obstacles in embryogenesis but in the end the animal mostly sees. Embryologists have a concept to name the way the developmental process almost always reaches the adult type as a target, even when the initial genes are mutated: “canalization,” a term famously coined by Conrad Waddington. Canalization is a form of attractor thinking.

- (b) The “concept” (supposed at the root of the purposive system) being a concept of the whole, one has to emphasize Kant’s shift between the concept pair “means-ends” (which involves references to utility and intentionality) and “whole-parts” in the very meaning of purposiveness (see Huneman, 2007, 2017). Arguably, Kant detached the notion of purposiveness from the notion of utility and intentionality – while it intends to remain scientific.⁴

⁴Notice that this idea of design is quite different from the English tradition: hence, Kant tends to detach organism design from natural theology.

- (c) Philosophically, Kant's analysis puts the difference between things that are likely to be explained by pure physics and things that can't – namely, physics and organisms, to say it bluntly – in epistemology rather than in ontology. Physical systems not organized should be explained starting from the parts; in organisms the direction of explanation is inverted, or at least, an "ideal" causation, from the whole to the part, is articulated to a real mechanical causation (i.e., from the parts to the whole). This difference is obviously epistemic, not metaphysical. It's about what is required for an explanation to be possible.

The concept at the root of the production of the purposive thing is part of the teleological judgment rather than "within" the thing. Many philosophers and scientists in the early nineteenth century, while interested in Kant's account of the whole-parts relationship, will give up on this notion of regulative principle: Blumenbach to begin with, and then Kielmayer or Meckel. Historical epistemology is cleaved about that question: Lenoir, who initially considered what he called the "vital-materialists," namely Kant, Blumenbach, and other German biologists, lumped all of them in a sort of Kantian tradition in which teleology constitutes a regulative framework to search for mechanisms (what he called "teleomechanists"). Larson (1979), Richards (2001), and later Zammito (2018) on the contrary argued that Kant was alone in his view of regulativeness and that biologists will consider that purposiveness as described by Kant (including this focus on whole-parts relationship) is objective; with Zammito, they often also see this disconnection with Kant as a source of the fruitfulness of the attitude. This stance is also a feature of current views of organisms, such as the ones defended by researchers in the wake of Varela, Rosen, or Maturana, who start with the notion of self-organization understood as *autopoiesis* – e.g. Moreno and Mossio (2015), Montévil and Mossio (2015), or Saborido et al. (2011): there is something objective in organisms' being purposive. Yet for Kant, the concept of purposiveness, because of its constitution – namely, positing, within the judgment, a concept at the source of the production of the object – is necessarily regulative, in the sense that it concerns the modalities of the judgment rather than the thing about which one judges.

7.1.3 *Natural Purposes and Self-Organization*

Up to now, I unpacked the notion of purposiveness; but organisms are "natural purposes." What does natural stand for here? Purposes can be artificial – in this case, the "concept" at the root of the production of the thing is simply the idea that the maker, the craftsman, or the artist has when she makes the product. The antecedence of wholes over parts is clearly here taking place. But natural items are such that they have no makers; they seem to be produced by themselves. In this case, when a natural purpose is found, the parts are what exist, so they create themselves in accordance with an idea of the whole – which, says Kant, is merely a "principle of cognition" and not a "principle of production" (CJ §65). This idea of the whole is

not the principle of their *making* but the condition of our understanding of organs and traits as parts of an organism, i.e., as involved in the development and functioning of a living entity.

Kant precisely says:

In such a product of nature each part, at the same time as it exists throughout all the others, is thought as existing with respect to [*um...willen*] the other parts and the whole, namely as instrument (organ). [1] That is nevertheless not enough (because it could be merely an instrument of art, and represented as possible only as a purpose in general); the part is thought of as an organ *producing* the other parts (and consequently each part as producing the others reciprocally). [2] (CJ §65).

Condition [1] for being a natural purpose characterizes a purpose in general, as I explicated it until now. It is not proper to organisms, and it is where arise functions and functionality (as playing a role in a whole). I call it (Huneman, 2014c, 2017) the *design* criterion, since it fits any system that is designed and/or has a design. And criterion [2] specifies what makes a *natural* purpose. Kant then develops his view of what a “part producing another part” means: “Thus, concerning a body that has to be judged as a natural purpose in itself and according to its internal possibility, it is required that the parts of it produce themselves [*hervorbringen*] together, one from the other, in their form as much as in their binding, reciprocally, and from this causation on, produce a whole.” I call this criterion [2] the *epigeneticism* criterion (see also Huneman (2017)). It distinguishes organisms from artifacts because their design, in the sense of an arrangement of the parts according to an idea of the whole, is not achieved by some external agent considering precisely such idea of the whole as a building plan – the process of building organisms is rather done by the parts themselves; hence, they produce themselves: as a consequence says Kant, “organized beings are self-organized beings” (ib.). This essential character of such systems accounts for the sort of triadic phenomenology of organized beings proposed by Kant just before (CJ §64), namely, its self-production as individuals, when the tree grows; as a set of parts, when it grows leaves; and as a species, when it disperses seeds that grow.

This original occurrence of the word self-organizing will be quoted later by Kauffman (1993), who sees Kant as a father of the theories of self-organization, even though we now have a galaxy of “self-X” terms, such as self-assembly, self-maintenance, self-building, etc., within which “self-organization” stands rather on the side of physics. Even though Kant would not acknowledge the formal apparatus of Kauffmann or Santa Fe style theories, he indeed held this strong thesis that living organization is self-organization. But his claim was rather tied to nascent embryology theory, namely, Wolff’s epigeneticism, than to the mathematics of nonlinear differential equations, fractals, and Boolean networks, as it is now (see Ruelle, 1989).

More generally, I don’t refer (with my labels) to the current notion of “epigenetics” (namely, whatever touches on the regulation of gene expression) but only to the notion opposed to preformism, namely, the capacity of living systems to build themselves through all the interactions with their external environment, without a preexisting template, and based on the activity of their parts producing other parts

(for instance, we would now talk about cells). This criterion (2) provides us with a grasp between a general account of organization and the specificity of biological organization, which can't rely on an extant template – a difference being addressed in the introduction of this volume.

7.2 Making Sense of Organisms? From Kant to the Modern Synthesis

For Kant, the design criterion (1) and the epigeneticism criterion (2) are two criteria for ultimately capturing the instantiations of one concept: they are unified through the unity of the concept of purposiveness as a transcendental presupposition, a concept of which they are the two facets. Both refer to an “idea of the whole” as “principle of cognition”; and it is the *same whole* in each case, and Kant analyzes at length the justifications for this claim in his “transcendental deduction” of the concept of purposiveness, undertaken in the Dialectics of the third *Critique*. But does this have any relevance for anyone now interested in the concept of organism? I will argue for the affirmative since, as indicated above, Kant's views of organization in general (criterion 1 above) and of *biological* organization (criterion 2 above) are mentioned as a philosophical foundation for thinking of organisms by Evo-devo people (e.g., Raff, 1996; Carroll, 2005), or theoretical biologists interested in self-organization, or, indirectly, by critiques such as Gould and Lewontin in their *spanrels* paper.

Thus, I will quickly consider what are these two criteria in the context of current evolutionary biology and developmental biology.

7.2.1 Design Criterion

The design criterion consists in presupposing that organisms are wholes in which parts fit the needs and demands of the persistence of these wholes. It is easy to see that such a criterion suits well the practice of behavioral ecology, namely, the sub-discipline of evolutionary biology that studies traits of organisms as adaptations or equilibrium strategies. Clearly, “traits” are more general than parts, but we can consider behavior as something of the organism, and then behavioral traits as parts of this dimension of the organism.

Methodologically, behavioral ecology is generally adaptationist as made clear by Reeve and Sherman (1993) or Krebs and Davies (1995), namely, it starts by assuming that a trait results from natural selection, either by maximizing fitness, or inclusive fitness, or (in the case where fitness payoffs depend upon the frequencies of traits) by realizing an “evolutionary stable strategy,” which is a kind of equilibrium in evolutionary contexts (Maynard-Smith, 1982).

Behavioral ecology asks questions such as the following: “Why do passerines or great tits lay four or five eggs by nest?”; “Why do gorillas of this region change mate every three years?”; and “Why are the leaves of the cypress of this size?”. Behavioral ecologists center on traits, hence on phenotypes; they demand that traits are somehow *heritable*, which means that some alleles make a difference in the value of the trait. Such heritability is assumed; it may be very low but, in most cases, the precise genetic makeup involved in traits under focus is unknown. More than a hundred genes are involved in a phenotype as seemingly simple as the size of mammals, so one should not expect that traits such as foraging behavior, studied in behavioral ecology, rely on a knowable genetic circuitry.

In this approach, parts – traits – are assumed to fulfill environmental demands. One often uses here the method labeled “reverse engineering” – namely, assuming that a part is an adaptation, and trying to reconstitute the environmental demands it was designed to fulfill. For instance, the horn of the *Parasaurolophus* has been intensively studied, and many hypotheses about the environmental demands it addressed have been emitted until one reached a consensus on the idea that it was used as a communication tool in sea or river shores (Turner, 2000) (Fig. 7.1).

To this aim, the structure of the horn, and especially its hollowness, has been taken into account, to deduce what the effect of such a horn could be – emitting recognizable sounds has been declared a much more probable selected effect than fighting competitors with the head.

Assuming that in a given system the conditions for natural selection that population genetics can unravel are met, then the traits we see are adaptations, which means that they fulfill environmental demands. By examining them, we

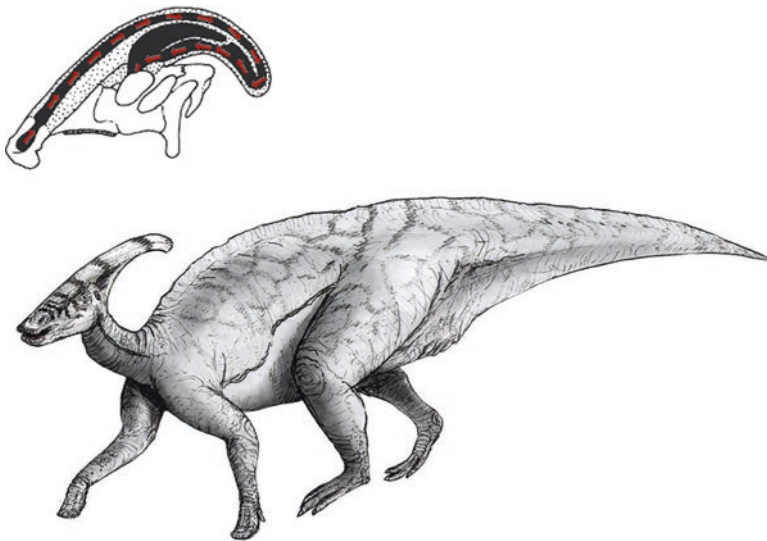


Fig. 7.1 *Parasaurolophus* and its hollow horn

may reconstitute these environmental demands. Such reverse engineering is thereby a legitimate method. This justifies that the design criterion is still nowadays legitimate since we've seen that reverse engineering is a clear instance of this criterion.

But the process of adaptive evolution involves a process of allele frequency change. Population genetics models such a change. In this approach, evolution is due to forces that act on populations modeled as gene pools⁵; those forces are migration, mutation, natural selection, and random genetic drift (which is, to say it quickly, a sort of error sampling, whose intensity – by definition – decreases with population size⁶). Among them, natural selection is the only one that creates adaptation, hence its epistemic primacy for evolutionary biologists. But nothing guarantees that in a given population, natural selection will overcome the other forces: if it is a very small population, or if migration is too strong, natural selection will be superseded by other forces and evolution will not yield adaptation.⁷

More precisely, natural selection understood as the “survival of the fittest” means that it tends to increase fitness, understood as the expected number of offspring. This maximization generally produces an adjustment between organisms and the environment, since meeting environmental demands allows one to survive and reproduce optimally.⁸ The general idea is that being more adapted than others involves surviving more and reproducing more so that the organisms or the traits that maximize their fitness tend to be optimized regarding environmental demands. In a given environment, for instance, the leaves of the cypress will have a size that allows them to maximally photosynthesize, and produce more trees, and more seeds, than if it were having smaller leaves; otherwise, genetic variants with other leaf sizes would thrive against the resident trees and would invade the population. It is such a process, at the level of gene dynamics, which justifies the reverse engineering, hence grounds the design criterion.

However, things are more complicated. Is it really the case that natural selection in principle optimizes and then creates the environmental fit with organisms? Or at least that it tends to optimize⁹? Birch (2015) and Okasha (2018) have indeed shown that there is no satisfying a priori proof that selection by itself and alone always optimizes fitness or inclusive fitness and that equating selection with optimization and adaptation can only be locally legitimate and often waits for empirical corroboration.

⁵See Sober (1984) for a canonical formulation of this account.

⁶On drift see Plutynski (2007), Abrams (2007).

⁷Of course, this is the simplest case and I bypass here issues regarding social evolution and then kin selection and inclusive fitness, (Hamilton, 1964) as well as population structure or maternal effects. Suffices to say that natural selection tends to produce adaptation because maximizing fitness entails optimizing traits with regard to environmental demands.

⁸Fitness is as we know a much-discussed and controversial concept; but this is not my point here.

⁹As to the prospects of this optimization, see also Huneman (2014a, b, 2019b).

To this extent, the design criterion cannot be seen as what should any organism satisfy on the grounds of the fact that a population fulfills the classical conditions of heritability, variation, and fitness that Lewontin (1970) famously formulated as conditions for potential evolution by natural selection (or any other version of the characterization of the conditions of evolution by natural selection).

7.2.2 *Epigeneticism Criterion*

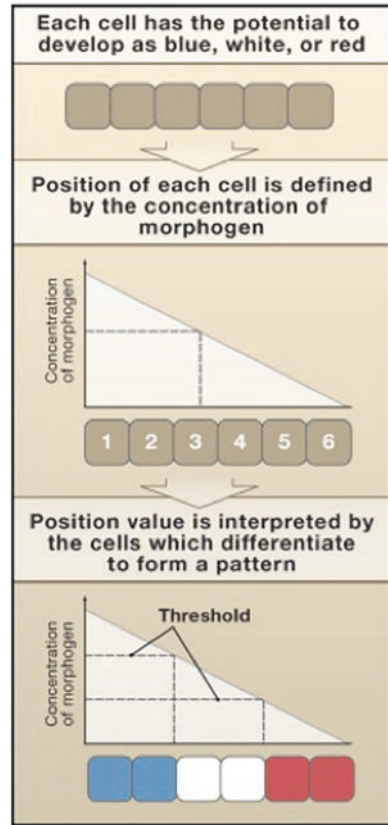
Cell theory, which is, along with molecular biology and evolutionary theory, the third major global theory of life underpinning modern biology (Gayon & Petit, 2019), provides us with a clear instance of this criterion (as explicated in Sect. 7.1.3): cells are producing cells, and this production leads to the organism. But this is also happening in accordance with an “idea of the whole,” as Kant required. Why? Early molecular biology, in the enthusiasm of the discovery of DNA and the genetic code, would easily consider that this idea of the whole is the genotype and therefore exists rather “in” the cell than within the epistemic activity of the researcher. This is a kind of preformationism (as made clear by Müller and Hallgrímsson (2003)), but recent developmental biology has increasingly shown that development is more complex than the unfolding of a program.

Granted, cells differentiate according to what Kant calls an “idea of the whole”; yet unlike what I just said, it’s not the genetic program that differentiates each cell since all carry the same genotype – in most metazoan and plants; on the contrary, differentiation is an epigenetic process involving the environment of each cell, the activation states of the genome in neighboring cells, and for each gene, the gene regulatory network that regulates its expression according to the states of all elements (other genes, transcripts, etc.; see Davidson, 1986; Oliveri et al., 2008).¹⁰ Thus, we seem to move away from the gene-based preformationism toward a more epigeneticist account of development in which cells produce cells in accordance with a general “idea of the whole” that is less located “in” the genotype than instantiated in a distributed way across genotypes, cell environments, and multiplicity of gene regulatory networks (GRN).

To make this kind of production clearer, remember, in developmental biology, the classical French flag model (Fig. 7.2) (due to Wolpert, 1969). In this account, cell differentiation as the response to a gradient of morphogenetic substance turns a continuous proportion of morphogen into a discrete series of expression states (the “flag”). It realizes an instance of this self-organization conceived of by Kant, to the extent that the organism is created on the basis of cells that respond individually to an overall state of the whole that they locally encounter, as represented by the state of the gradient in a flag.

¹⁰ Such process during embryogenesis also involves “programmed cell death” or apoptosis (Kerr et al., 1972), a major dimension of development that I studied in Huneman (2023).

Fig. 7.2 A representation of the French flag model of cell differentiation (Wolpert)



In turn, the GRNs are also, and maybe even more, an instance of this epigeneticism criterion. Developmentalists nowadays think of them as explaining the French flag model among other things (Davidson et al., 2003). They determine the expression of a gene based on the states of hundreds or thousands of other genes or genetic elements in the cell. GRNs react to the state of the organism – which is, for the cell, its environment – and determine in response to the contribution of the focal cell (Fig. 7.3). This corresponds to the self-organizing logic of the epigeneticism criterion.

Moreover, GRNs are implied in both the development of the organism and its functioning, since their dynamics in each case determines what a gene – and then all genes – do, and therefore, what does a cell of such and such genotype within the organism, at each stage of the life cycle. Given that GRNs instantiate the epigeneticist criterion, the fact of their involvement in cell physiology can be interpreted as acknowledging the epigenetic character of organism functioning, which would clearly correspond to the Kantian view of organisms. In any case, we see here a neat intertwining between development and functioning: genetic regulatory networks are involved both in cell specification and pattern formation – and within the regular activity of the cell.

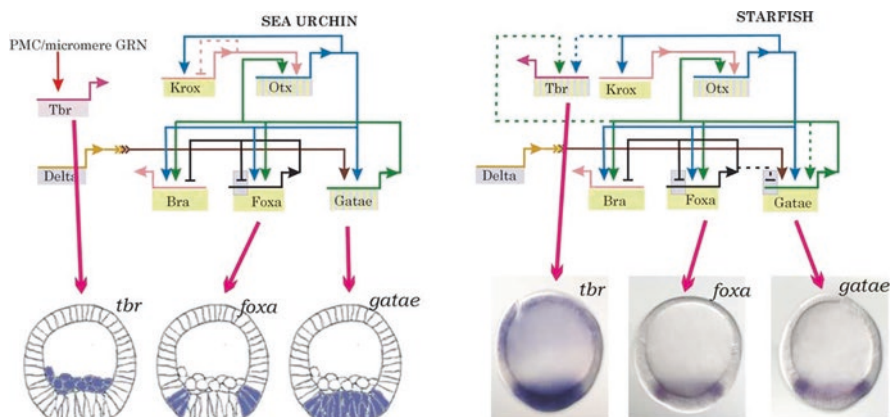


Fig. 7.3 Gene regulatory networks in starfish and sea urchin

While the two criteria for purposiveness were unified by Kant since there was one single “idea of the whole” involved in the teleological judgment and expressed in each of these criteria, my analysis emphasizes differences in the way these criteria can make sense of purposiveness today and possibly reassert the claim that organisms are natural purposes.

The design criterion and the epigeneticism criterion appear indeed not only distinct, as in Kant, but also wholly separated. Emphasizing the design criterion means focusing on the way the whole organism is designed, namely, the way that parts are contrived; these contrivances are the effect and the sign of natural selection. Contrived wholes are adapted, and adaptation results from natural selection, according to the Modern Synthesis. On the other hand, emphasizing the epigeneticism criterion means focusing on development as the proper epigenetic process, and then, more generally, on self-organization of the whole. When authors in the tradition of self-organization as an account of organisms refer to Kant’s idea of self-organization, they commit to Kant’s idea of parts that create other parts and themselves according to the an “idea of the whole”, even though of course they rely on a much richer empirical work, and sometimes they use types of mathematical tools unknown by Kant – Kauffman’s Boolean networks or, on another side, Rosen’s algebra.

But for Kant, the two criteria were unified as two aspects of the same “idea of the whole” which is involved in the notion of “natural purpose” as a transcendental principle for reflective judgment. This transcendental or criticist dimension of Kant’s thinking - visible in the notion of ‘regulative principle’ - is not adopted by the thinkers interested in self-organization, nor is it related to the modern avatar of the design criterion, namely, the various brands of adaptationism (reverse engineering, etc.; see Lewens (2004)). Hence, the two criteria are divided. They can’t be understood as the two criteria of “organisms” (themselves being instantiations of “natural purposiveness”).

Through these reflections, I put in a Kantian light the conflict between adaptationism and developmentalism as it is considered by supporters of Evo-devo, and

sometimes deemed unsurpassable (e.g., by Amundson, 2005). It is not the only possible reading of such analyses of the two criteria of purposiveness, but it helps put them in the context of current theoretical cleavages.

And as it is, it shows that there is a major issue with any attempt to now use the Kantian analysis of organisms – which is one of the major philosophical analyses of this concept – as a way to make sense of organisms in current biological thought. Maybe that leads to a final verdict of unsurpassable cleavage: focusing on the epigeneticism criterion leads to viewing self-organization while focusing on the design criterion sketches of the whole organism as a set of responses to environmental demands, and the two views of the “whole” that emerges on its side remain separated.

With these words, I turn to a wholly different approach, which is the way an ontological theorizing based on Darwinian principles intends to make sense of organisms understood as a major kind of “biological individuality.”

7.3 Evolutionary Individuals: A Liberal Approach Based on Conceptual Spaces

7.3.1 *Transitions in Individuality*

Biological individuality has been the object of many conceptualizing attempts from philosophers and biologists relying on the Modern Synthesis. I’m not trying to review these accounts or systematize them here since this would require a full paper or a book. But I think that the underlying idea grounding these sometimes conflicting accounts is the connection made by David Hull in his seminal paper “A matter of individuality” (1980) – namely, a connection between individuality and natural selection. In a nutshell, to be an individual is to be a target of selection. Since this latter notion is controversial and not well defined, approaches to the individuality/selection connection are numerous. Yet all share the idea that to see what are individuals in the world, one has to identify what is the object of some selection. Some accounts intend to specify what exact concept of a unit of selection is required to single out individuals (e.g., Folse III & Roughgarden, 2010; Clarke, 2014; Bouchard, 2008), while others are more pluralist, allowing for several types of individuality according to the aspect of selection considered (e.g., Goodnight, 2013). Yet in Sect. 7.2, I will argue that these accounts yield views more liberal than the Kantian-based view of organisms because they don’t commit to the idea that something could be either an individual or not an individual, but most of the cases of individuality are graded stages of individuality.

Granted, organisms are individuals; but of course other things can be biological individuals, and this intuition is backed by selection-based accounts of individuality: bacteria (which are unicellular and may not be organisms strictly speaking); genes, given that there exists a selection at the level of genes, for instance, in the case of segregation distorters (Burt & Trivers, 2006); possibly colonies of

hymenopteran insects; and perhaps species, if one follows Ghiselin and Hull who famously argued that species are not classes but individuals whose conspecific organisms are genuine parts (Hull, 1980, Ghiselin, 1974). The Darwinian approach intends to make sense of all individuals based on natural selection. But among them, multicellular organisms enjoy a paradigmatic status: first, they constitute most usually our favorite example of individuals, since they fit our intuition more than species or genes; second, they display spatial contiguity and often genetic homogeneity – in the case of most metazoans – which makes easy to talk of the self-containment and indivisibility implicit in the word “individual.” If, following Aristotle, “individuality” means the logical inseparability (a horse and a horseman can be separated into two concepts of particulars, but a horse cannot), the genetic homogeneity of something that was born a zygote and then developed based on clonal cell division makes it into something apparently logically indivisible.

Hence, “organisms” as understood by the Kantian approach that I exposed, namely, multicellular organisms, are a paradigmatic but not exclusive kind of biological individual. The question of “organisms” may therefore be summarized by the question raised by Dawkins (1976), namely, why does life on Earth comes mostly under the form of organisms rather than by a total mess of genes as the only individuals? The start of an answer is given by the program called “evolutionary transitions,” initiated by Buss (1988) and then Maynard-Smith and Szathmáry (1995) and Michod (1999). The main idea is that throughout evolution, distinct forms of individuality understood as entities that reproduce by themselves and thereby can be targets of selection came into existence. For instance, cells appeared on the basis of macromolecules possibly replicating because of them being autocatalytic and templates; cells that made up life on Earth from 3,5 By ago to 1 By ago evolved into multicellular organisms. And then some of them evolved into forms of individuality that can be composed of individuals and show the division of labor between reproduction and survival/development that is characteristic of multicellular organisms: namely, hymenopteran insects form colonies where a cast reproduces and a cast does defense, territoriality, and foraging without reproducing.

This research program, most generally understood, intends to capture the generic processes leading from groups to individuals made up of a collection of entities. The process of going from prokaryotes or unicellular eukaryotes to multicellularity is one crucial transition. But the same general rules should govern all processes, even though local differences are investigated. As to themselves, multicellular organisms *develop*; the development possibly (and most often) starts with a genetic bottleneck; those individuals contain differentiated cells with identical genomes, hence the need for epigenetic gene expression mechanisms; many recent clades feature sequestration of germ-line paralleling the division of labor in hymenopteran insects (Buss, 1988).

The main process involved in the evolution of forms of individuality is “multi-level selection” (MLS) (Michod, 1999, 2005). It means that selection operates in opposite ways at two levels: the one constituted of entities and the one constituted of groups of these entities – for instance, cells and groups of cells. Among cells, those that reproduce faster or more than the average have better evolutionary

success. But at the level of groups, having too many cells that work “for themselves” may distort the group, and then such a group eventually fares less well than groups where cells are more coordinated. Hence, selfishness – in the sense of reproducing more than others – wins *among cells*, but altruism, in the sense of reproducing less than others, or, more formally, having a lesser fitness, wins *among groups*. This is multilevel selection, a concept considering selection as the result of combining intragroup competition and intergroup competition (Sober & Wilson, 1998).

The researchers interested in evolutionary transitions emphasize not only the fact that multilevel selection may foster altruism (while at the intragroup level, altruism always loses); but also that this process may ultimately lead to groups that are likely to reproduce as a single entity. This is exactly what plausibly happened with multicellular organisms. Briefly said, altruism among cells is maintained because of group benefits, and in some cases, the group starts reproducing as one, and then emerging policing devices ensure the persistence of this reproduction.

This process can be understood in several ways. Appealing to the useful distinction made by Damuth and Heisler (1988) between two kinds of MLS defined by two kinds of group fitness, labeled MLS1 and MLS2, Okasha (2006) and Michod (1999) argued that a transition is a transition between these two kinds of fitness. In MLS1, fitness is defined by counting the total number of offspring of all the individuals of a given group; in MLS2, it's defined by counting daughter groups of a group. This intuitively fits the transition toward multicellularity: a fitness of a group of cells is the amount of cells after one generation; but the fitness of a multicellular organism is the number of daughter organisms, not the total number of cells at the next generation. The transition toward multicellularity is therefore a transition from one to the other type of MLS, from MLS 1 to MLS2. And formally, what makes this possible is the decoupling between these two kinds of fitness, and it often happens because the trade-off between fecundity and viability in cells becomes a convex function when the group size increases (Michod, 2005).

This explanatory scheme is supposed to account for all kinds of transitions. However, multicellular organisms constitute a paradigmatic transition. For this reason, researchers such as Michod and his team extensively investigated a clade in which unicellular and multicellular species coexist – namely, the order *Volvocales* (or *Chlamydomonadales*), within which *Chlamydomonas* is a unicellular species, *Gonium* is a colonial species undifferentiated, and *Vovox* is a colonial differentiated species (the transition took 35 My to occur). But the key role of multicellular organisms for the question of individuality is not only due to the intuitive appeal they have for us, and then our familiarity with metazoan. Within evolutionary theorizing, this is also a salient feature. Take the hierarchy of individuality. What scholars are interested in evolutionary transition research is the generative process that accounts for steps in individuality, as I said. But while individuality is hierarchical, through a hierarchy based on compositionality (chromosomes → cells → multicellular organisms → colonies, as Michod (1999) shows), the nature of this hierarchy is complex. Paleobiologist Niles Eldredge argued in the late 1980s that there are at least two hierarchies, one genealogical and one ecological (Eldredge, 1985).

The genealogical hierarchy consists of levels of increasing complexity in reproduction: each level consists of entities that include entities of the previous level but reproduce by themselves. They have a direct genealogical link. The ecological hierarchy consists of levels of ecological interaction: chromosomes assemble through meiosis; cells interact in microbial ecology; organisms interact within ecological settings; and groups of organisms may compete and cooperate in competitive contexts. Interestingly, “organism” is the level that belongs to the two hierarchies: it is a main agent in ecological interactions, and it is also a crucial step in genealogy.

For this reason, the multicellular organism is crucial for the notion of individuality in Darwinian contexts even though, as Godfrey-Smith (2009) forcefully claimed, not all organisms are Darwinian individuals – since some of them don’t reproduce by themselves – and not all Darwinian individuals are organisms.

7.3.2 *Conceptual Spaces: Being Liberal*

These considerations indicate that such an approach to individuality may not provide a complete account of organisms, even though organisms are individuals. But a closer look at the evolutionary transition programs reveals that this approach is quite different in its spirit from the Kantian approach.

The parallel between bee colonies and organisms, grounded on the division of reproductive labor, comes with a few lessons. Colonies are individuals, in the sense that they can be seen as units of selection under some perspectives, for instance, MLS; but they lack the self-contained character of organisms as well as their capacity to reproduce for themselves. Everything happens as if the transition from MLS1 to MLS2, through which the groups have daughter groups that can be counted, did not come to terms. In Huneman (2013), I proposed to distinguish two kinds of transition, depending on whether they come to an achievement (like multicellular organisms) or not (like bee colonies). Pandas realize exemplarily complete transitions; bee colonies realize component transitions.

But this is less a binary distinction than two poles of a continuum. There are degrees in “component transition” and inversely some organisms may lack or lose features of complete transition – e.g., cancer as disruption of organisms (see Featherston & Durand, 2012), failure of policing devices in the case of immunity disease, etc.

That gives us a flavor of the liberality proper to the Darwinian approach: systems can be more or less individuals, to the extent that they can come from more or less complete transitions. Organisms are a result of the former, but for the same reason, “being an organism” will come by degrees.

However, this continuum of biological individuality has been even more expanded. In a series of papers, Joan Strassmann and David Queller (Strassmann & Queller, 2010; Queller & Strassmann, 2009) have suggested a view of individuality that is less a gradient than a two-dimensional hyperspace (Fig. 7.4). They argue that individuals require cooperation – in the sense of altruism, as indicated in the context

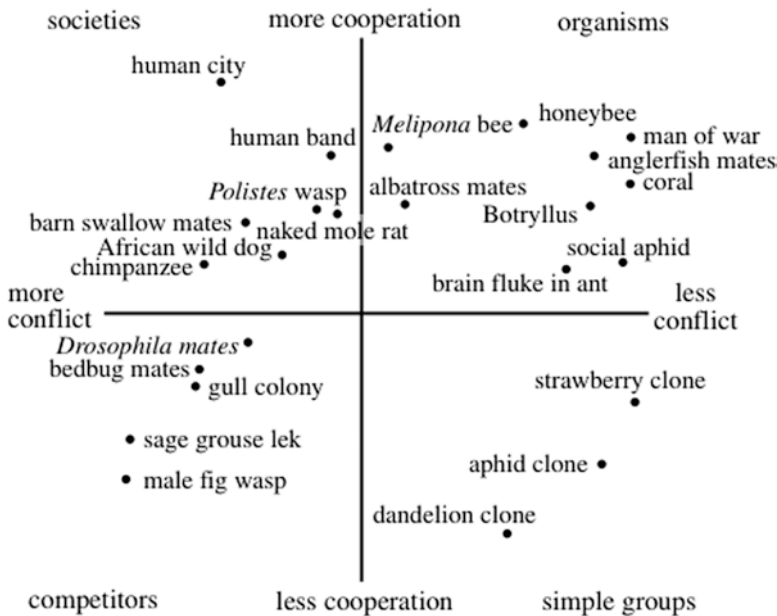


Fig. 7.4 The space of biological individuality, according to Queller and Strassmann (2009)

of multilevel selection – but also a loss of potentiality for conflict. They claim that these are two different things, even though both of them are defined in relation to natural selection, which characterizes this account as a Darwinian account of individuality. Therefore, systems should be situated within a general conceptual hyper-space of organismality – but I would say “individuality” – whose dimensions are the degree of cooperation and the degree of absence of conflict. In honey bees, for instance, there is lots of cooperation, as in corals, but the system of repressing possible alternative queens in bee colonies allows them to have far less conflict than in corals. This means that it is not always possible to say that a system is more an individual than another one – everything depends upon the dimension (decreasing conflict/degree of cooperation) that one favors.

For this reason, I consider the Darwinian approach as the most liberal: not only “being an individual” and then “being an organism” is not a question for which necessary and sufficient conditions (NSC) should be given; but even in the space of individuality, there is some liberality in the dimension supposed to be the most relevant. I call it the conceptual space approach and it philosophically differs from the Kantian approach consisting in building the concept of the organism, thereby setting criteria for being an organism.

Additionally, in this view, there is no requirement for genetic homogeneity or species homogeneity – associations between different species such as aphid and *Buchnera*, or in general host with symbionts, but also ant-plants or kinds of multicellular organisms made up of distinct species can form individual in evolutionary time.

I proposed that the component vs complete transition should be supplemented with another distinction due to Queller (1997) in order to make complete sense of the space of individuality. In effect, most of the transitions in individuality that I talked about are what Queller called “fraternal transitions”: the entities that tend to coalesce into a higher-level individual are genetically similar or close or highly related. But many of the individuals in the space of individuality are made up of genetically heterogeneous entities: think of the lichens made up of fungi and algae. And most deeply in evolutionary history, we have the ancestor of eukaryotic cells, supposed to be the result of encapsulation of an archaea into a bacterium (Margulis, 1970). A story similar to this story of the emergence of the nucleus of a eukaryotic cell has also been told (also by Margulis) about the mitochondria, which is the result of the integration within a eukaryote of a smaller prokaryote, through endosymbiosis. In these transitions, the result is an autonomous individual; the components lose their individuality, not only because they don’t reproduce by themselves but also because they lose many of their genes since the functions supported by these genes can be done through genes of the host individual, and reciprocally.

There is no definite criterion for being a biological individual, but mostly dimensions in an abstract space, and then the characterization of elements of this space according to Table 7.1. Given that transitions can be egalitarian or fraternal and then can be ranged across a gradient that goes from poorly component transition to complete transition, we have four extreme cases for transitions, summarized in Table 7.1. Importantly, given that most organisms are made of cells but also of many symbionts that constitute their microbiota, the egalitarian transitions are all over the place. As a result, an element in the space of individuality can be understood according to the following:

- How it scores on each of the two dimensions (lack of conflicts, cooperation).
- How much complete it is – and here, the measure of the “completeness” is given by the norm of the vector (**OA**) where point A is the putative individual with measures x and y on each axis of the space, and O is the origin (the norm U is computed in the ordinary scalar way, $U^2 = x^2 + y^2$): the largest is this norm, the more complete is the transition.
- To what extent it is egalitarian or fraternal.

Table 7.1 Four types of transition (a quadripartition that structures the space of biological individuality)

The four kinds of transitions		
	Complete transition	Component transition
Fruternal	Transition toward multicellular organisms	Colony of <i>Melipona</i> bees (high level of potential conflict makes them different from organisms; see Queller & Strassmann, 2009); <i>Bacillus subtilis</i> bacteria
Egularitarian	Transition toward eukaryotic cells (mitochondria as symbionts); Termite mounds by <i>Macrotermes</i> (Turner, 2000); Lichens	Some fig-pollinator wasp mutualisms

This conceptual space approach is clearly much more liberal than the Kantian approach; it requires one to be pluralist regarding the sense of individuality and therefore to give up the hope to capture what an organism is. Granted, organisms are in the space of individuality; one can require that they have a high degree of completeness in transition, but this leaves lots of room for many possibilities for organismal structures, features, and functions, as I will consider in the next section.

7.3.3 *Ecosystems, Individuals, and Organisms*

Additionally, taking into account egalitarian transitions raises a complex issue, namely, the individuality of ecosystems. Ecosystems are made up of many individuals of many species and include the overall abiotic element. They are generally not seen as units of selection, given that they don't display (obvious) heritability; thus, they would hardly respond to selection. To this extent, they could not pretend to be individuals in the Darwinian liberal view.

However, ecologists still often think that some ecosystems are more individual than others. The intuition behind this idea is that while some ecosystems are a loose assortment of species, whose unity is in the eye of the beholder, others are quite cohesive sets of entities likely to persist in time.¹¹ As Evelyn Hutchinson – a key figure in modern ecology – tended to say, these communities or ecosystems show much stronger interactions within themselves than with others, and that's why they are ontologically more robust.¹²

I gave a formal characterization of the individuality that such ecosystems feature, called “weak individuality.”¹³^d But my only point here is to show that these ecosystem individuals may enter the space of individuality, even though they are not obviously part of them since concerning them selection cannot be appealed to. I suggest that we have here a local instance of ecological individuals that appears as a limit of evolutionary biological individuals when the degree of egalitarianism of the transition is extremely higher than the coefficient of “fraternity.”

But following the indications I gave while discussing “weak individuality” (Huneman, 2020), one can sketch another conceptual space, proper to ecological individuality. The axes then would be the relative strength of the major interactions

¹¹ This view was held by the very influential treatise *Principles of Animal Ecology*, published in 1949 by prominent ecologists Clyde Allee, Thomas Park, Orlando Park, Alfred Emerson, and Karl Schmidt. They thought that a selection at the level of the group of species fosters the unity of an ecological community exactly as natural selection fosters the unity and individuality of organisms. This view faded away in the 1950s with the emergence of behavioral ecology, which mostly relies on natural selection, (for instance Lack, 1954) and then with the devastating critique of group selection by George Williams (1966).

¹² See Hutchinson (1957). On the problematic ontological character of ecological communities, see Sterelny (2006).

¹³^d I developed a conception of weak individuality to make sense of these accounts of individuality (Huneman, 2014b, c, 2020).

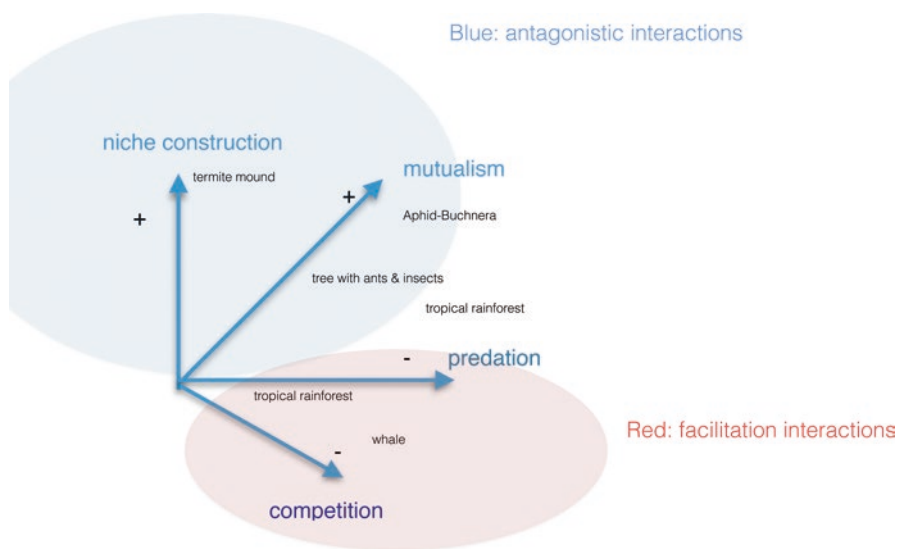


Fig. 7.5 The space of ecosystemic individuality. Each axis represents a structuring interaction. The situation of a given ecosystem depends upon the relative strengths of the interactions. (After Huneman, 2020)

that hold together an ecosystem: competition, mutualism, parasitism, predation, and niche construction.

This “space of ecosystemality,” so to say, pertains to the same conceptual space approach as the space of individuality. It is not wholly orthogonal to it, since ecological interactions are the ground of the selective pressures, which in turn make up the selective force, which drives the constitution of evolutionary individuals. In Fig. 7.5, I present a version of this space of ecosystemality. My only concern here is in showing that the conceptual space approach *generaliter* allows one to conceptualize quite extensively issues related to individuality.

7.4 Confronting the Approaches

Is it possible to go further in confronting these two approaches?

To summarize, we have two distinct approaches toward organisms and individuals in general:

- (a) In the wake of Kant’s *Critique of Judgment*, the necessary and sufficient conditions (NCS) approach provides *the two criteria for organisms*: design and epigeneticism.

In a non-Kantian context, the issue is are they unified? What could be the unification principle? Especially, what happened if only one criterion is fulfilled? As I

wrote, the transcendental perspective implied that the idea of “natural purpose” instantiated by organisms is unified. But outside this perspective, things change. Especially, the two criteria can be fulfilled independently; whereas in the Kantian view, once something satisfies the epigeneticism criterion, an “idea of the whole” is presupposed by the biologist as what guides the epigenetic process, and therefore this idea of the whole is also the design of the system. But independently of Kant, one may find things that satisfy the design criterion – design with no self-production (artifacts) – and things that satisfy only the epigeneticism criterion, especially many of the systems investigated by the so-called science of complex systems, starting with the iconic Bénard convection cells, which are not at all alive and don’t include functional parts.¹⁴

- (b) On the other hand, we have a liberal attitude: the conceptual space approach (CSA). Here, *organisms inhabit a space of individuality*. The axes are defined by cooperation and by lack of conflict, and the transitions feature several degrees of completeness.

This approach meets its proper issues: first, *how to define “degrees” of individuality in the absence of total order*, assuming that the scalar norm is a too-rough measure? Another issue concerns the axes: are they the only ones? And what is the relation with the space of ecosystematicity addressed in Sect. 7.3.3? And finally, given that some modeling of organisms appeal to ecological concepts, by seeing processes in terms of predation and competition rather than execution of a genetic program (e.g., Costello et al., 2012), or sometimes reintroducing ecological concepts such as niche (Scadden, 2006), would it be possible to think of the organism as ecosystems first, before being something else (I investigated the plausibility of this proposition in Huneman (2020))?

One may be dissatisfied with having two accounts of organisms, distinct but with obvious overlaps. Granted, an option could consist in saying the following: organisms are one thing; they pertain to several biological investigations often lumped under the label “functional biology” (*sensu* Mayr); and they are integrated, develop, and feature adaptations, but may not necessarily be under natural selection. On the other hand, evolutionary biology handles entities that could be counted, so that the concept of fitness can be instantiated, since fitness is a mathematical construct based on a probability distribution over offspring numbers.

Thus, a reasonable pluralism could say that there are two concepts of organisms: the direct concept in functional biology and the evolutionary concept according to which organisms represent an important kind of individuals, and then individuals are thought of in evolutionary terms.

¹⁴ Trying to recover from within the set of self-organizing system such as Bénard cells, candle flames or whirlpool, the subset of things that are alive and therefore that feature functions, and then would be in Kantian terms fulfilling the design criterion: this endeavor has been undertaken by Mossio, Moreno and Saborido in a set of papers and by Mossio and Moreno (2015) Their notion of “closure of constraints” would play the role of what unifies the two criteria, in the present perspective.

This reasonably pluralist option is not dismissing the major claim I want to make in this paper, namely, the difference between an NSC approach and an approach via conceptual space (CSA), as I have exposed them. There is a principled distinction between these two approaches, and I tried to show their respective justifications. And the NSC and the CSA approach could be let as it is: they would coexist as two distinct approaches, each favored by one theoretical school, evolutionists being massively interested in the CSA. This strategy fits the view of Godfrey-Smith (2013), who tends to see organisms and individuals as two conceptual elements proper to two distinct explanatory projects, which can sometimes overlap. But the two approaches do not exactly match with, respectively, a developmentalist concept of the organism used in functional biology and an evolutionary-based concept of individual, according to the reasonable pluralism just sketched. Why? Because the Kantian concept is in itself divided between a developmentalist and an adaptationist understanding.¹⁵

Thus, how can we articulate the NCS approach of the organism and the CSA liberal evolutionary approach to individuality? I will sketch two strategies successively. I label the first one the threshold strategy and the second one the pragmatic strategy.

7.4.1 *Threshold Strategy*

According to the threshold strategy, one has to specify a boundary (in terms of a scalar norm) above which X in the space of individuality is a genuine organism. This gives way to articulate individuals and organisms, organisms being a proper subspace of the space of individuality (Fig. 7.5). But how to justify the values of the thresholds? That is the main issue with this otherwise attractive approach. It is hard to do it without some arbitrariness, for instance, by saying that this individual (quaking aspen) is an individual but this other one (ant colony? Dandelion field?) is not an organism. Or, if one wants to avoid being arbitrary, one should provide a concept of organism – which implies an obvious case of circularity, since the whole point here is about determining organisms within the space of individuality (and not extrinsically) in order to make it correspond to the NSC approach to the organism.

But even though we accept arbitrariness or circularity, there is a more pressing issue with this approach. Consider the epigeneticism criterion, which characterizes organisms as natural purpose (*qua* natural) according to the Kantian approach: “Thus, concerning a body that has to be judged as a natural purpose in itself and according to its internal possibility, it is required that the parts of it produce themselves [*hervorbringen*] together” (CJ § 65). We said that this criterion easily fits the development of multicellular organisms. However, in the CSA liberal approach, we

¹⁵ See Jaeger, (this volume), which suggests another route toward this problem.

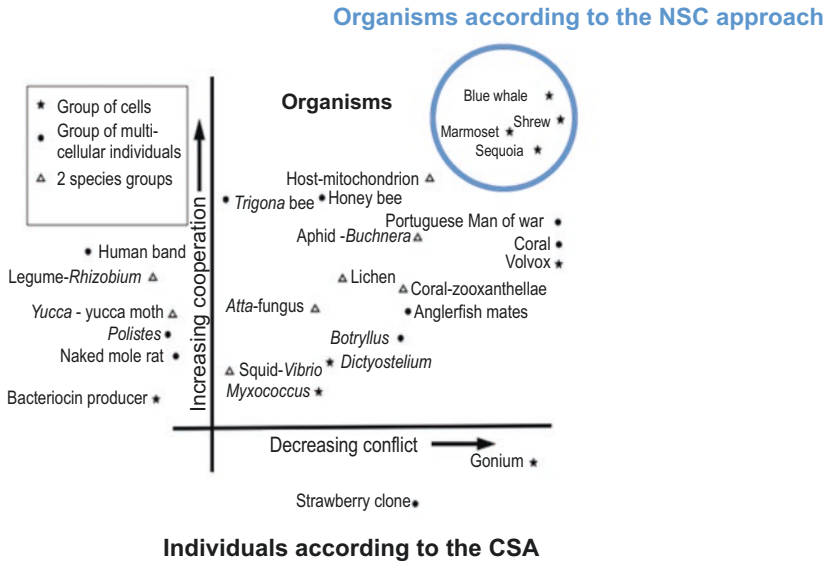


Fig. 7.6 The threshold strategy: organisms according to NCS approach correspond to a subspace in the CSA approach, delimited by a threshold

included products of the “egalitarian” transitions: here, there are heterospecific individuals; along evolution, different species coevolved and concurred in producing such individuals; and along development, a given individual accepts and recruits bacteria (see Nyholm and McFall-Ngai (2004) on the *Vibrio fischeri* bobtail squid with its luminescent bacteria). But this recruitment is not production, at least in the way cells produce new cells. Thus, even within a “zone” of the space of individuality supposed to fit “organisms,” the epigeneticism criterion fails, so the two approaches don’t match (Fig. 7.6).

An answer to the objection would consist in deflating the sense of “production” in the criterion. Hence, any kind of causation, for instance, counterfactual causation, would suffice – and since bacteria recruited in an organism, for instance, in the bobtail squid, are counterfactually cause of the form of the squid – in the sense that if the bacteria were different (its species being different from the set of species recruited by the squid), they wouldn’t end up in the squid –, this case fulfills the epigeneticism criterion.

Ecologists talk of “facilitation” when species A increasing in abundance makes another species B increase in abundance, for instance, by eating more of the predators of B (Bruno et al., 2003). Thus, if causation means something like facilitation, heterospecific individuals could fulfill the epigeneticism criterion. But the drawback is significant: one loses the distinction between the two criteria of organism in Kant’s sense since both of them are now about “causing” (in a nonproductive sense) the form of the parts! Therefore, the design criterion and epigeneticism criterion collapse, and the whole approach loses its benefits.

Thus, whether one accepts or rejects this conceptual alternative, namely, weakening the epigeneticism criterion, the threshold strategy raises massive issues.

7.4.2 *Pragmatic Strategy*

If now we turn to the pragmatic strategy, what are the prospects?

As a strategy, pragmatism means that individuals and organisms are two distinct concepts, whose extensions overlap, and this overlap is determined by the respective uses of these concepts in models and theories. So, “organism” is used in some disciplines and allows to ask questions such as “what is the mechanism of this life-sustaining function?”, but not in others: for instance, when there is a specific process of natural selection at play, one will count individuals, and in case of multilevel selection, models will include two kinds of individuals (e.g., cells/organisms or organisms/herds) rather than two kinds of organisms. Some philosophers came to contest the legitimacy of “organisms” in individuality biology, arguing that it is enough to talk about “individuals” (Haber, 2013; Bouchard, 2008); pragmatists will reject this option and keep the duality of concepts while accepting that in many contexts, “individuals” is the only useful and legitimate concept.

This strategy accounts for the differences between individuals and organisms; it makes sense of the fact that there is no point in inferring from “organisms” traits likely to define individuals in general, or that “organisms” cannot be a subclass of “individuals” since what matters is the context of use of these concepts rather than their purported rigid reference.

However, one major issue is the lack of complete separation between these two concepts: as I said, the evolutionary models account for some aspects of the design criterion (see also Huneman, 2017). Thus, the specificity of organisms with respect to biological entities is to some extent acknowledged within the concept of individuality, defined from the liberal viewpoint of evolution.

A pragmatist strategy assumes that the concepts are independent, in terms of their meaning. It happens that they coincide, in the sense that one concept picks out in some contexts the same thing as the other concept employed in other contexts – even though they are different. The strength of a pragmatist strategy is that the two concepts, as I tried to show, are very different, to the extent that one is defined in terms of NSC and the other comes from a liberal CSA approach.

But since there is an overlap in their signification, to the extent that the design criterion belongs to the organism concept but can be accounted for in the CSA in the context of a discourse about biological individuality, the pragmatist’s strategy may not be perfectly legitimate. One may discuss whether the conditions of applying a pragmatist strategy are met in general. Yet, if the two frameworks, NSC and NCA, are not independent, then they are competing when it comes to accounting for several classes of biological realities; and therefore, they cannot be handled through a pragmatist strategy.

7.5 Conclusion

In this paper, I have reviewed two approaches to the concept of organisms. In the former one, organisms are understood through a “necessary and sufficient conditions” approach, via two criteria inherited from the Kantian approach as an early investigation in the ontology of organization (itself embedded in the birth of descriptive embryology (Lenoir, 1982, Huneman, 2007; forth)), an investigation that the present volume continues. The latter derives from an ontology grounded on evolutionary models and ideas. I insisted on the difference in the logical structure of the two approaches. A conceptual space allows for much more liberality, while the NCS approach is precise in the sense that it supposedly picks up the “organisms” and nothing else. The conceptual space approach does not provide us with an idea of what are organisms and therefore cannot provide identity conditions or truth-makers of the sentence “X is an organism.” It is therefore much more deceptive from an ontological or metaphysical viewpoint. But it may fit some scientific practices, within which sharp boundaries between extensions of concepts and the rest are often hard to find, given the model-relativity of many of the propositions uttered by scientists. Its liberality may be appreciable in other cases; therefore, the distinction I found here between Kantian and evolutionary approaches, namely, a distinction between NCS and CSA, may be relevant for metaphilosophy and helps address other, unrelated, issues.

Clearly, organisms are at the crossroads of several hierarchies of individuals and ways to talk about individuals in biology; Eldredge’s two hierarchies here are indicative of the multiplicity of takes on organisms and, therefore, of the sense in which “organism” can be seen as a crossroad concept. “Design” as a concept making sense of this organization proper to organisms is torn between a selectionist understanding in terms of bundles of adaptations and ultimately natural selection and functions in an etiological sense (Millikan, 1984, Neander, 1991) – and a concept of an organization that anchors organization in self-organizing processes rather than external selective pressures.

As a consequence, the plurality of conceptual schemes to make sense of organisms will probably cohabit in biology, and the duality between functional biology and evolutionary biology is not enough to distinguish these schemes – given that design is an idea proper to both approaches.

In the last step, I tried to propose some ways the two approaches – the NCS Kantian one and the evolutionary liberal one – can mutually relate. The result is a rather mild skepticism (to be aptly contrasted with Jaeger’s chapter, in this volume). I don’t think the concept of the organism, given its uses in biology, can be the place where a pacific coexistence between accounts can take place. The skepticism of this paper tends toward an acceptance of the conflictual and fractured essence of the concept of the organism in biology.

References

- Abrams, M. (2007). How do natural selection and random drift interact? *Philosophy of Science*, 74(5), 666–679.
- Allee, W. C., Park, O., Emerson, A. E., Park, T., & Schmidt, K. P. (1949). *Principles of animal ecology*. W. B. Saunders Company.
- Amundson, R. (2005). *The changing role of the embryo in evolutionary thought*. Cambridge University Press.
- Barabasi, A. L. (2018). *Network science*. Cambridge University Press.
- Bateson, P. (2005). The return of the whole organism. *Journal of Biosciences*, 30, 31–39.
- Birch, J. (2015). Natural selection and the maximization of fitness. *Biological Reviews*, 91(3), 712–727.
- Bouchard, F. (2008). Causal processes, fitness, and the differential persistence of lineages. *Philosophy of Science*, 75(5), 560–570.
- Bruno, J., Stachowicz, J., & Bertness, M. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, 18, 119–125.
- Burt, A., & Trivers, R. (2006). *Genes in conflict the biology of selfish genetic elements*. Harvard University Press.
- Buss, L. W. (1988). *The evolution of individuality*. Princeton University Press.
- Caroll, S. (2005). *Endless forms most beautiful: The new science of evo devo and the making of the animal kingdom*. Norton.
- Clarke, E. (2014). The multiple realizability of biological individuals. *Journal of Philosophy*, 110(8), 413–435.
- Costello, E., Stagaman, K., Dethlefsen, L., Bohannan, B. J., & Relman, D. A. (2012). The application of ecological theory toward an understanding of the human microbiome. *Science*, 336, 1255–1262.
- Damuth, J., & Heisler, L. (1988). Alternative formulations of multi-level selection. *Biology and Philosophy*, 3, 407–430.
- Davidson, E. H. (1986). *Gene activity in early development*. Academic.
- Davidson, E., McClay, D., & Hood, L. (2003). Regulatory gene networks and the properties of the developmental process. *PNAS*, 100, 1475–1480.
- Dawkins, R. (1976). *The selfish gene*. Oxford University Press.
- Eldredge, N. (1985). *Unfinished synthesis: Biological hierarchies and modern evolutionary thought*. Oxford University Press.
- Featherston, J., & Durand, P. M. (2012). Cooperation and conflict in cancer: An evolutionary perspective. *South African Journal Science*, 108(9/10), 1–5.
- Folse, H. J., III, & Roughgarden, J. (2010). What is an individual organism? A multilevel selection perspective. *Quarterly Review of Biology*, 85, 447–472.
- Gayon, J., & Petit, V. (2019). *The knowledge of life today*. ISTES.
- Ghiselin, M. T. (1974). A radical solution to the species problem. *Systematic Zoology*, 23, 536–544.
- Gilbert, S. F., & Sarkar, S. (2000). Embracing complexity: Organicism for the 21st century. *Developmental Dynamics*, 219(1), 1–9.
- Gilbert, S., Opitz, G., & Raff, R. (1996). Resynthesizing evolutionary and developmental biology. *Development and Evolution*, 173, 357–372.
- Ginsborg, H. (2004). Two kinds of mechanical inexplicability in Kant and Aristotle. *Journal of the History of Philosophy*, 42(1), 33–65.
- Ginsborg, H. (2014). Oughts without intentions: A Kantian approach to biological functions. In E. Watkins & I. Goy (Eds.), *Kant's theory of biology* (pp. 259–274). De Gruyter.
- Godfrey-Smith, P. (2009). *Darwinian populations and natural selection*. Oxford University Press.
- Godfrey-Smith, P. (2013). Organisms and individuals. In F. Bouchard & P. Huneman (Eds.), *From groups to individuals*. MIT Press.
- Goodnight, C. J. (2013). Defining the individual. In F. Bouchard & P. Huneman (Eds.), *From groups to individuals* (pp. 37–54). MIT Press.

- Gould, S. J. (2002). *The structure of the evolutionary*. Belknap Press.
- Gould, S. J., & Lewontin, R. (1978). The spandrels of San Marco and the pangloss-ian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London, B205*(1161), 581–598.
- Green, S. (2013). When one model is not enough: Combining epistemic tools in systems biology. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 44(2), 170–180.
- Griffiths, P., & Gray, R. (1994). Developmental systems and evolutionary explanation. *Journal of Philosophy*, 91, 277–304.
- Grodwohl, J-B. (2019). Animal behavior, population biology and the modern synthesis. *Journal of the History of Biology* 52 (4):597–633.
- Haber, M. (2013). Colonies are individuals: Revisiting the superorganism revival. In F. Bouchard & P. Huneman (Eds.), *From groups to individuals* (pp. 196–217). MIT Press.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour I and II. *Journal of Theoretical Biology*, 7(1), 1–52.
- Hull, D. L. (1980). Individuality and selection. *Annual Review of Ecology and Systematics*, 11, 311–332.
- Huneman, P. (2007). Reflexive judgement and wolffian embryology : Kant's shift between the first and the third critique. In P. Huneman (Ed.), *Understanding purpose? Kant and the philosophy of biology* (Vol. 2007, pp. 75–100). University of Rochester Press.
- Huneman, P. (2008). *Métaphysique et biologie*. Kimé.
- Huneman, P. (2010). Assessing the prospects for a return of organisms in evolutionary biology. *History and Philosophy of the Life Sciences*, 32, 341–372.
- Huneman, P. (2013). Adaptation in transitions. In F. Bouchard & P. Huneman (Eds.), *From groups to individuals* (pp. 141–172). MIT Press.
- Huneman, P. (2014a). Individuality as a theoretical scheme 1. Formal and material concepts of individuality. *Biological Theory*, 9(4), 361–337.
- Huneman, P. (2014b). Individuality as a theoretical scheme 2. About the weak individuality of organisms and ecosystems. *Biological Theory*, 9(4), 374–381.
- Huneman, P. (2014c). A pluralist framework to address challenges to the modern synthesis in evolutionary theory. *Biological Theory*, 9(2), 163–177.
- Huneman, P. (2017). Kant's concept of organism revisited: A framework for a possible synthesis between developmentalism and adaptationism? *The Monist*, 100(3), 373–390.
- Huneman, P. (2019a). How the modern synthesis came to ecology. *Journal of the History of Biology*, 52, 635–686.
- Huneman, P. (2019b). Revisiting darwinian teleology: A case for inclusive fitness as design explanation. *Dies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 76, 101188.
- Huneman, P. (2020). Biological individuality as weak individuality: A tentative study in the metaphysics of science. In A. S. Meincke & J. Dupré (Eds.), *Biological identity* (pp. 40–62). Routledge.
- Huneman, P. (2023). *Death: Perspectives from the philosophy of the biology*. Palgrave-McMillan.
- Hutchinson, G. E. (1957). Concluding remarks. Cold Spring Harbor symposium. *Quantitative Biology*, 22, 415–427.
- Jaeger, J. (this volume). The fourth perspective: Evolution and organismal agency. In M. Mossio (Ed.), *Organization in biology*. Springer.
- Kauffman, S. (1993). *The origins of order: Self-organization and selection in evolution*. Oxford University Press.
- Kerr, J. F., Wyllie, A. H., & Currie, A. R. (1972). Apoptosis: A basic biological phenomenon with wide-ranging implications in tissue kinetics. *British Journal of Cancer*, 26(4): 239–257.
- Kitano, M. (2002). *Foundations of systems biology*. MIT Press.
- Krebs, J. R., & Davies, N. (1995). *Behavioral ecology: An evolutionary approach*. Blackwell.
- Lack, D. (1954). *The natural regulation of animal numbers*. Oxford University Press.

- Larson, J. L. (1979). Vital forces: Regulative principles or constitutive agents? A strategy in German physiology, 1786–1802. *Isis*, 70, 235–249.
- Lenoir, T. (1982). *The strategy of life. Teleology and mechanism in nineteenth century German biology*. Reidel.
- Lewens, T. (2004). *Organisms and artifacts: Design in Nature and Elsewhere*. MIT Press.
- Lewontin, R. C. (1970). The units of selection. *Annual Review of Ecology and Systematics*, 1, 1–18.
- Margulis, L. (1970). *Origin of eukaryotic cells*. Yale University Press.
- Maynard-Smith, J. (1982). *Evolution and the theory of games*. Oxford University Press.
- Maynard-Smith, J., & Szathmáry, E. (1995). *The major transitions in evolution*. Oxford University Press.
- Mayr, E. (1961). Cause and effect in biology. *Science*, 134, 1501–1506.
- McLaughlin, P. (2000). *What functions explain: Functional explanation and self-reproducing systems*. Cambridge University Press.
- Michod, R. (1999). *Darwinian dynamics*. Oxford University Press.
- Michod, R. E. (2005). On the transfer of fitness from the cell to the multicellular organism. *Biology and Philosophy*, 20, 967–987.
- Millikan, R. G. (1984). *Language, thought, and other biological categories*. MIT Press.
- Montévil, M., & Mossio, M. (2015). Biological organisation as closure of constraints. *Journal of Theoretical Biology*, 372, 179–191.
- Mossio, M., & Moreno, A. (2015). *Biological Autonomy*. Springer.
- Müller, M., & Hallgrímsson, E. (2003). Preformationism. In O. Müller (Ed.), *Keywords and concepts in evolutionary developmental biology*. MIT Press.
- Neander, K. (1991). The teleological notion of function. *Australasian Journal of Philosophy*, 69, 454–468.
- Newman, M. (2010). *Networks: An introduction*. Oxford University Press.
- Nyholm, S. V., & McFall-Ngai, M. J. (2004). The winnowing: Establishing the squid-vibrio symbiosis. *Nature Reviews. Microbiology*, 2, 632–642.
- Odling-Smee, J., Laland, K., & Feldman, M. (2003). *Niche construction: The neglected process in evolution*. Princeton University Press.
- Okasha, S. (2006). *Evolution and the levels of selection*. Oxford University Press.
- Okasha, S. (2018). *Agents and goals in evolution*. Oxford University Press.
- Oliveri, P., Tu, Q., & Davidson, E. (2008). Global regulatory logic for specification of an embryonic cell lineage. *Proceedings of the National Academy of Sciences*, 105(16), 5955–5962.
- Oyama, S., Griffiths, P., & Gray, R. (Eds.). (2001). *Cycles of contingency: Developmental systems and evolution*. MIT Press.
- Plutynski, A. (2007). Drift: A historical and conceptual overview. *Biological Theory*, 2(2), 156–167.
- Queller, D. C. (1997). Cooperators since life began. *The Quarterly Review of Biology*, 72, 184–188.
- Queller, D. C., & Strassmann, J. E. (2009). Beyond society: The evolution of organismality. *Philosophical Transactions of the Royal Society London Biological Sciences*, 364, 3143–3155.
- Raff, R. (1996). *The shape of life*. University of Chicago Press.
- Reeve, H. K., & Sherman, P. W. (1993). Adaptation and the Goals of Evolutionary Research. *The Quarterly Review of Biology*, 68(1), 1–32.
- Richards, R. (2001). *The romantic conception of life*. University of Chicago Press.
- Ruelle, D. (1989). *Chance and chaos*.
- Russell, E. S. (1911). *Form and function*. Cambridge University Press.
- Saborido, C., Mossio, M., & Moreno, A. (2011). Biological organization and cross-generation functions. *British Journal for the Philosophy of Science*, 62(3), 583–606.
- Scadden, D. (2006). The stem-cell niche as an entity of action. *Nature*, 441(7097), 1075–1079.
- Sloan, P. R. (2002). Performing the categories: Eighteenth-century generation theory and the biological roots of Kant's a priori. *Journal of the History of Philosophy*, 40(2): 229–253.
- Sober, E. (1984). *The nature of selection*. MIT Press.
- Sober, E., & Wilson, D. S. (1998). *Unto others. The evolution and psychology of unselfish behavior*. Harvard University Press.
- Sterelny, K. (2006). Local ecological communities. *Philosophy of Science*, 73(2): 215–231.

- Strassmann, J. E., & Queller, D. C. (2010). The social organism: Congresses, parties, and committees. *Evolution*, 64, 605–616.
- Sultan, S. (2015). *Organism and environment: Ecological development, niche construction, and adaptation*. Oxford University Press.
- Turner, D. (2000). The functions of fossils: Inference and explanation in functional morphology. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 31(1), 193–212.
- Walsh, D. M. (2015). *Organisms, agency, and evolution*. Cambridge University Press.
- Walsh, D. (2017). Chance caught on a wing. In P. Huneman & D. Walsh (Eds.), *Challenging the modern synthesis: Adaptation, development and inheritance*. Oxford University Press.
- West-Eberhard, M.-J. (2003). *Developmental plasticity and evolution*. Oxford University Press.
- Williams, G. C. (1966). *Adaptation and natural selection*. Princeton University Press.
- Wolpert, L. (1969). Positional information and the spatial pattern of cellular differentiation. *Journal of Theoretical Biology*, 25, 1–47.
- Zammito, J. (2018). *The gestation of German biology*. University of Chicago Press.
- Zumbach, C. (1984). *The transcendent science: Kant's conception of biological methodology*. Martinus Nijhoff.

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