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CHAPTER 3

Biological Organization from a Hierarchical Perspective

Articulation of Concepts and Interlevel Relation

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1. Introduction

Introductory biology books often refer to what Ahl and Allen (1996) call the "conventional levels of organization": a sequence from the cell to the biosphere through intermediate levels of organism, population, community, and ecosystem (p. 77, fig. 4.1). This scheme is frequently supplemented with additional subcellular or molecular levels. Even without the reference to social hierarchies, it is also common to represent the hierarchical levels of natural systems as lower or higher (bottom or top), denoting their position with the use of a scale or rank of some sort.

The contrast between reductionist and nonreductionist approaches regarding the understanding of the specificity of biological systems, along with their constitution and dynamics, has several lines of contention in the philosophical literature. One such key issue is the different appreciation of the hierarchical arrangement of biological systems into levels of organization and the corresponding interpretation of the nature of such levels and, particularly, about the relationships established among them.

When the relation among levels is considered in its bottom-up form, it does not usually become controversial in discussions about reductionism. On the contrary, some variants of hierarchical representation are commonly proposed to be more fitting for a reductionist view of biological systems, despite their variety and complexity (Oppenheim and Putnam 1958).

In contrast, when the relation among levels is considered in its top-down form, it is frequently criticized or even dismissed entirely. This is exemplified in the widespread opposition to the concept of downward causation (Campbell 1974), even in approaches that are not strictly reductionist. In very general terms, the occurrence of downward causation implies that higher-level entities or processes have a genuine causal influence on those at lower levels—that is, that higher-level events are the cause of identifiable effects on events at a lower level.[1]

Until recently, in the philosophy of science, the subject of levels and their relation has been discussed mainly in the areas of the philosophy of mind and of cognitive sciences, where corollaries of the so-called mind-body problem figure centrally in the debates, that aim to understand the relation, if any, between physical properties and mental phenomena. In the philosophy of biology, the subject has been more directly addressed in the debate over levels of selection and macroevolution (see from Brandon and Burian 1984 to Okasha 2006). Even in this context, the nature of the relationship among levels is an unsettled issue (beyond the more direct debates about whether to accept multiple loci of selection or on reaching a consensus regarding which ones to admit and under which conditions). As attested by Samir Okasha, the problem stems from a philosophers' concern: "In a multi-level scenario matters are less simple. Presumably, multi-level selection involves causality at more than one level of the hierarchy. But this raises a number of questions. Are the higher- and lower-level causal processes autonomous, or are they interdependent? Might selection at one level ever be 'reduced' to selection at a lower level? If higher-level selection has an impact on lower-level phenomena, does this mean that 'downward causation' is occurring? (The significance of this question is that some philosophers regard downward causation as a suspect notion)" (Okasha 2006, 77).

Recently, the philosophy of biology has seen a renewed interest in levels of organization. Some of those perspectives aspire to break the very dichotomy between reductionism and antireductionism by focusing on the specific dynamics of the component parts and their relations in order to explain the behavior of complex systems. They also accept the relevance of higher levels in natural systems and the explanatory need to take them into account. Among these views, the most representative are the various neo-mechanistic views (see, for instance, Bechtel and Richardson 1993; Machamer et al. 2000; Bechtel 2008; Craver 2007; Craver and Darden 2013).

However, a more detailed analysis of the concept of level generated within that approach (i.e., Craver and Bechtel 2007) brought into question the basic intuitions regarding the causally specific significance of interlevel relations held by current hierarchical approaches in biology, claiming that "things at different levels of organization . . . do not causally interact" (Craver 2015, 23) and, therefore, leave no room for genuine interlevel relation.

This line of thinking has been followed by discussions that have led to even more deflationary accounts of levels and hierarchies,[2] "where levels of organization give way to more well-defined and fundamental notions, such as scale and composition" (Eronen 2015, 39), or even to eliminativism about levels:[3] "I argue that no distinct notion of levels is needed for analyzing explanations and causal issues in neuroscience: it is better to rely on more well-defined notions such as composition and scale. One outcome of this is that apparent cases of downward causation can be analyzed away" (Eronen 2013, 1,042).

There are, of course, exceptions to this trend, and we can find other philosophical approaches (for instance, Dupré 2012 or Mitchell 2009) that endorse multiple causal interactions among levels of organization in biological systems. It could therefore be worthwhile to speculate about the reasons for this widespread suspicion in the philosophical literature regarding the legitimacy of considering interlevel relations.

One reason for the different acceptance of those two kinds of relations among levels derives from the natural and standard characterization of levels of organization in the context of "nested compositional hierarchies" (Tëmkin and Eldredge 2015). However, explicitly hierarchical approaches in ecology, evolutionary biology, or biological complexity do customarily clarify and develop, in each case, the precise meaning of that general description in terms of nested composition.[4] The compositional aspect in these hierarchical perspectives involves a complex, rich set of more specific relations among the levels that extends beyond mere spatial inclusion (being part of) or material constitution (being made of) (see section 3).

But such a nuanced view of nested compositional hierarchies is not equally acknowledged by nonexplicitly hierarchical perspectives that regard the hierarchical ordering as a given, resulting from the bottom-up direction of composition. Proponents of the hierarchical approach in ecology had already stated a similar concern: "Most biologists are already familiar with the general idea of hierarchy through the concept of 'levels of organization' (cell, organism, population, community). However, even our informal discussion should make it clear that the term hierarchy is not restricted to this simple sense. . . . It is clear that ecological organizations show hierarchical structure, but it should also be clear that the simple series is unlikely to be useful across the range of observation sets and spatiotemporal scales involved in ecosystem analysis" (O'Neill et al. 1986, 60–61).

The questioning of interlevel relations stems also from the apparent disregard or lack of awareness, in mainstream biology and philosophy, about the contributions made by scholars working in the explicitly hierarchical framework. Evidence for this may be found by observing the bibliographical references mentioned in the literature, and the repeated complaint about the alleged lack of a detailed, precise, and articulated conceptual framework regarding the concepts of hierarchy or level of organization (see section 2).

The purpose of this chapter is not to respond to these particular accounts (mechanistic or other). Rather, they are mentioned as a symptom or a testimony of an odd imbalance between those areas of science where explicitly hierarchical approaches have been developed making use of interlevel causal relations and those philosophical perspectives so distrustful of the conceptual soundness of such kinds of relations. It is my claim that an oversight of the very relevant scientific approaches and a restricted rendition of the concept of levels of organization are two motives that help in our understanding the underlying rationale of that symptom.

This chapter is instead an attempt to clarify the concept of level of organization, to make it applicable across different conceptual schemes, and to establish a basis for coherent discussion and commensurability among varied and even alternative views on biological systems. In this sense, the goal is not to provide a technical definition or a precise and definitive taxonomy but, first, to assume a general and intuitive notion of levels and then furnish it with more specific content, attempting an articulation among different kinds and degrees of (interlevel) relation. According to the view advocated here, hierarchy is primarily understood as meaning "interlevel relation," and the concept of level of organization makes sense within such an explicit hierarchical framework.

2. Definitions and Classifications. Charge of Ambiguity and Plurality of Meanings

It is often stated that the concept of level is insufficiently developed and has acquired a plurality of meanings and uses in scientific literature, making it difficult to apply in practice. This is one of the reasons why many authors propose and develop their own concepts for explanatory purposes.

The recently emerged neomechanistic perspective on the levels of organization raised similar concerns: "The notion of *levels* is ubiquitous in discussions of science. Yet . . . it is unclear" (Bechtel 2008, 143); "Despite the ubiquity of levels talk in contemporary science and philosophy, very little has been done to clarify the notion" (Craver 2015, 23); "The term level is notoriously ambiguous" (Eronen 2015, 39).

This complaint about the ambiguity, lack of precision, and alleged resulting confusion of the term *level* seems to always accompany any critical discussion about the concept that such term denotes. Should we then admit that the current state of affairs is the same as more than fifty-five years ago, when the philosopher Mario Bunge voiced a similar concern: "As used in contemporary science and ontology, the term *level* is highly ambiguous. . . . The aim of the present paper is to list the usual and some possible meanings . . . of the word 'level,' to specify them briefly, to illustrate them and to propose some problems in which those concepts are involved" (Bunge 1960, 396)? Or that we are in the same situation as more than thirty-five years ago, when, despite his previous efforts, Bunge continued to lament the lack of "consensus on the significance of the terms 'level' and 'hierarchy,' which are used in a variety of ways and seldom if ever defined" and, again, set out to "remedy this situation" (Bunge 1979, 13)?

But the claims of vagueness of the notion of levels of organization appear to be unjustified and, in fact, quite far from the truth if we consider the rich literature devoted to the subject. Undoubtedly, there are many different versions of the term "level of organization" according to different theoretical perspectives (see note 4). This does invite some degree of ambiguity, especially if one disregards the specific theoretical contexts in which the concept of level plays an explanatory or modeling role. Further, there are indeed ambiguous formulations of the concept that steer away from epistemological precision. Nevertheless, a declaration of a general lack of clarity and precision leading to overall confusion as the trigger for generating additional definitions is certainly an overstatement. Moreover, such criticisms are hardly necessary, because having precise and theoretically sound concepts should not preclude the development of new or elaborated versions to answer specific theoretical demands in a particular field or area of research (or their more recent empirical findings or theoretical advances). This necessity is precisely what prompted the development of several different hierarchical theories in evolutionary biology, ecology, complexity and systems sciences, and some areas of cognitive science and will most likely pave the way for future advances.

We should recall—at least as a brief testimony—some antecedents. Even leaving aside the work in the late nineteenth century and early twentieth century on emergent evolution (George H. Lewes, John S. Mill, C. Lloyd Morgan, Charles D. Broad), there are at least two other earlier broad periods or clusters of theories that dealt with and contributed to the development of concepts akin to that of level of organization.

In the 1930s and 1940s, at least two separate yet partially connected theoretical departures, organicism and systems science, addressed fundamental aspects of biological organization in explicitly hierarchical terms (see Haraway 1976). On the one hand, researchers Joseph Needham, Alex B. Novikoff, James K. Feibleman, and others attempted to develop a scientifically sound organicist view that gave rise to the *theory of levels of integration* (Needham 1937; Redfield 1942; Feibleman 1954). On the other hand, von Bertalanffy and other biologists—for instance, Paul Weiss—had already begun developing a systems view, initially based on biological systems (later generalized as a *General System Theory*), in which a multilevel hierarchical approach was central. The latter view, unlike that of the purely organicist perspective, was able to connect with the ensuing period of further theoretical exploration of biological hierarchies (see Umerez 1994 and Etxeberria and Umerez 2006 for a more detailed treatment and further references).

The work on hierarchy theory flourished throughout the late 1960s and into the 1980s. In parallel with more general and epistemological discussions related to reductionism (i.e., Ayala and Dobzhansky 1974), detailed hierarchical theories were formulated, both as general approaches to biological organization (see, for instance, Whyte et al. 1969; Weiss 1971; Pattee 1973) and as more specific accounts of relevant phenomena in certain areas of biology—mainly evolutionary biology (Eldredge and Salthe 1984; Eldredge 1985; Salthe 1985; Grene 1987) and ecology (Allen and Starr 1982; O'Neill et al. 1986). All these contributions offered detailed and precise accounts of interlevel relations (Umerez 1994; Umerez and Moreno 1995).

In short, with the exception of the older work of the 1930s and 1940s, and the development of systems science, a hierarchical perspective had seen major advances in the organizational and evolutionary perspectives in the period between the late 1960s and the mid-1980s. Some of the proponents of these approaches have continued to defend hierarchical and multilevel views that are quite specific in their characterization of the sense in which they use "level of organization" and how they relate those levels among them in a hierarchical ordering.

In the philosophical domain, William Wimsatt had developed a distinctive approach in the 1970s (i.e., 1974, 1976; see Wimsatt 2007), with its roots in the work of Simon (1962). Wimsatt's view was further developed and transformed by later scholars, contributing to current neomechanistic perspectives.

As a result of this body of work from previous decades, there is a rich choice of definitions of *level* available to the contemporary scholar. For the purpose of this analysis, two representative examples are selected that emphasize different aspects regarding interlevel relation.

The first approach takes a more static compositional view, exemplified by Wimsatt's definition: "By level of organization, I will mean here compositional levels—hierarchical divisions of stuff (paradigmatically but not necessarily material stuff) organized by part-whole relations, in which wholes at one level function as parts at the next (and at all higher) levels." (Wimsatt 1994, 222). The second approach offers a more dynamic relational sort of definition, which encompasses composition, as in the following definition by Salthe: "Level: a representation of scale in a functional hierarchy such that higher levels regulate lower ones and lower ones give rise to higher ones. In the present application, the higher ones also include the lower ones as subsystems." (Salthe 1985, 295).

Significantly, a more recent definition—stemming from the first approach—connects both perspectives by subsuming the relational aspect under the idea of organization: "levels that are related as parts to wholes with the additional restrictions that the parts are components. The relata are mechanisms and components and the relationship is organization: lower level components are organized to make up a higher-level mechanism." (Craver 2009, 396).

The following section attempts to disentangle what is generally implicit in this idea of organization as used in the context of biological hierarchies.

The plethora of meanings of the concept of level enables some authors to develop taxonomies, classifying the diversity of the concept (see early examples in, e.g., Bunge 1960 or Whyte, Wilson, and Wilson 1969). See the meticulous analyses by Carl Craver (2007, 171ff; 2009, 389ff; 2015, 3ff) for more recent attempts to systematize the various versions of this fundamental concept.

Most—if not all—of these classifications of different meanings of *level* clarify how the term is used in different contexts, but they are presented as a juxtaposition of different meanings that are diligently distinguished, though typically they are not interrelated. As useful as these taxonomies are, it would also be valuable to provide ways of relating those different meanings in order to be able to establish a common ground for direct comparison among them. The view presented in the next section is an attempt to offer such a comprehensive, integrative approach.

3. Articulated View

The goal of the articulated view presented here is not to substitute other general approaches to definitions or taxonomies but to supplement them by trying to explicitly account for the trait organization, understood as a very specific kind of relationship among levels. Thus, the articulation is an attempt to disentangle the notion of "level of organization" by means of an epistemological reconstruction of the content of the concept, as a result of determining the kinds of relations among elements and their processes that are implicit when it is used in hierarchical approaches.

As a general starting point, levels are the various groups of elements connected with other such groups at a different scale[5] by virtue of a given relation and within a particular system. The only limitation implied by this intuitive concept is that the constitution of systems must be based on some type of *specific relation* among groups of elements (i.e., levels). The peculiarities of the relation in each particular case or the rendition of the concept of level is the object of a detailed epistemological reconstruction. This intuitive notion is taken as a heuristic starting point to further inquire into the nature of those specific relations and it is not, therefore, offering a particular definition or a criterion for a definite taxonomy. It should instead be complementary and compatible with several definitions and partitions into distinct levels of organization, since the present analysis should be applicable to any of them.

The analysis is clustered around five fundamental features that cover any possible meaning of the term and are ordered according to their degree of generality. These features are *composition*, *integration*, *emergence*, *control*, and *organization*. They represent, precisely, different kinds of relations among groups of elements or processes, which become articulated into an overall picture (Umerez 1994).

The reconstruction proceeds from the more general to the more specific. It starts from a potential common minimum for any concept of level of organization, related to the idea of composition, and gradually discloses further conditions, restrictive of that generality toward more specific and operative concepts. The idea is that in order to better understand biological *organization* we may attempt to consider organization as a cluster of different, but related, kinds of levels, each one with different types of traits and characteristics common to other systems (or ways of ordering things or phenomena) but which, when integrated, deploy the features of fully fledged biological organization, as in "levels of organization."

In terms of Salthe's *specification hierarchy* (1993), we could present those different kinds of levels according to the progressive specification of their relation:

{composition {integration {emergence {regulation {organization}}}}}

This articulation does not by itself support any particular definition, taxonomy, or ordering against any other. On the contrary, it should serve as an epistemological tool relevant to the analysis and contrast of all of them. The intention is to make explicit some characteristics about the relations among elements that give rise to levels, such as when they are involved in what is referred to as biological organization, with the ambition to clarify what any version of levels of organization in biological systems should (and, explicitly or not, typically does) fulfill.

The organization of biological systems—from the most simple to the most complex—entails instances of the aforementioned kinds of relations among the elements and processes involved. Those relations might be involved to varying degrees in each different system, and might give rise to a distinct ordering of elements in each case. It is important to note that this ordering is not universal or given, but always depends on the particular system, process, or operation that the explanation in terms of levels of organization is seeking to illuminate.

The articulation suggested herein serves as an additional tool for adequate comparisons among alternative hierarchical schemes and across different fields of inquiry.

3.1. Levels of Composition

First, we must analyze what "levels of composition" refers to. In this regard, at least four characteristics must be considered: (1) nestedness, (2) relation of partial ordering, (3) homogeneity and heterogeneity of component parts, and (4) the discreteness or continuity of the arrangement.

The relation among levels based on composition is the most general and basic, with the exception of *aggregation*, which is taken as the antithesis of organization (as in the aggregative case,[6] sensu Wimsatt 2000, 2006). In its generality, level of composition may be conceptually close to the notion of subsystem, but some further specifications are needed to clarify its meaning.

3.1.1. NESTEDNESS Nestedness is understood as "the requirement that upper levels contain lower levels," or the property that "entities of smaller scale are enclosed within those of larger scale" (Allen and Starr 1982; Salthe 1985). It is unclear, however, whether the notion of composition should be restricted to physical inclusion or containments or may encompass wider compositional meanings, such as those derived from functional and dynamical properties. If the former is correct, then difficulties arise with how to describe the relation among organisms and demes or populations and ecosystems, or the relationship between membranes and cells. Levels of different composition are superposed, but by virtue of some specific relation (which must be explicit) that allows the proper use of level. For instance, in cases where the relation is functional (e.g., informational), not spatial, and the overall (organized) system can nevertheless be referred to as *composed of* those functionally related levels.

Since the concept of level of composition has to be applicable in these more complex cases, the minimal characterization of the relation of composition must be sufficiently broad in its definition to avoid mere nestedness as a mandatory condition.

3.1.2. RELATION OF PARTIAL ORDERING In general, levels should maintain a partial ordering relation among them. In mathematical and formal terms, *order* is defined as the relation among members of a set according to which some members precede or follow others. A partial ordering on such a set is a relation ≤ that is "transitive, reflexive, and antisymmetric" (Blackburn 1994, 272). This order is set in each case with respect to a specific criterion or measure, such as containment, size, rate, enabling or constraining action, command, etc. Levels of composition show a partial ordering relation. This condition might seem too restrictive as a minimal condition because it imposes a very specific relation modality, but a careful analysis reveals that this condition is indeed necessary. Without a partial order relation, the very notion of level may become meaningless: levels that are reversible according to the same relation would be possible as well as different levels at the same very level, undermining the prospects of a cogent and theoretically useful sense for the concept.

This clearly does not imply that the particular order between two levels cannot be reversed according to different criteria (for instance, size or containment, as in the case of the genes with respect to the cell, against function, as in the case of gene expression with respect to cellular metabolism).

3.1.3. HOMOGENEITY OR HETEROGENEITY OF COMPONENTS It is also necessary to address the issue of whether we are dealing with, at each level, just homogeneous (undifferentiated) or heterogeneous (differentiated) components. In this regard, for organizational perspectives (as well as mechanistic ones), it is important to note that at each level we are primarily dealing with differentiated parts, not just equivalent component parts. Therefore, in general, the relation of composition should be able to accommodate both cases, which would be distinguished later on according to further specifications of relations.

At this point, it is worth emphasizing one aspect that will be discussed in subsequent sections. Being able to accommodate both homogeneous and heterogeneous entities means that, as far as the characterization of composition is concerned, the two are indistinguishable. In other words, the *relation of composition* by itself does not distinguish between being composed of homogeneous or interchangeable components and being composed of heterogeneous and noninterchangeable components. If this distinction is relevant, as it happens to be in biological systems, some further specification will have to be added to account for it. This is precisely what explanations in the biological sciences consistently seek. An important part of biological knowledge consists of specifying the particular ordering and different roles of different kinds of components, and the way in which these heterogeneous components are integrated within their level *and* relate to those at contiguous levels.

3.1.4. DISCRETE LEVELS Finally, and briefly, since it amounts to a question of convention in the meaningful use of words, it is important to emphasize that levels must be discrete, at least heuristically (even if they are artificially discretized from a continuum), in order to be a useful conceptual tool.[7]

3.2. Levels of Integration

This relation addresses the question of how *parts* are constituted into *wholes*, instead of just components into aggregates. Thus, it is a nuance that specifies a particular kind of relation of composition. All levels of integration are levels of composition in the broad sense established earlier (and they would consequently fulfill the simpler conditions to be aggregates), but not all levels of composition are levels of integration.

The idea of integration, in its most traditional sense, refers to the "making up or composition of a whole by adding together or combining the separate parts or elements" (OED). In the context of complex and biological systems, it means, first, that the relation by virtue of which a set of equivalent component parts produce a common dynamical pattern or a coordination of processes that holds them together or maintains a particular steady state. Second, it means that the relation by which the combination of various distinct component parts gives rise to a complex whole or a complex state with the same properties of relative stability and unified performance.

The relation of integration is the first step to exclude what, in terms of Bechtel (following Wimsatt's characterization of aggregativity), might be called the "null case" with which to confront other cases: "the null case in which organization is absent . . . components are put together but no order is imposed" (2008, 150n7). The relation of integration produces a coherent higher level (*cohesive* sensu Collier 1986) and may give rise to a form of self-contained unit, characterized by its own properties and an extreme integration of its parts (in complex systems). This feature is present in systems ranging from basic self-organized systems, such as far from equilibrium dissipative systems, where an ordered pattern at the global macro-level arises from dynamics of entities at the microlevel, to more complex systems, such as lipid compartments or protocells.

3.3. Levels of Emergence

If integration specifies the relation of wholes to its parts, the relation of emergence further specifies a particular kind of process of formation of (at least) some of these wholes. It classically implies the two features of nonpredictability and qualitative novelty. Though often unnoticed, it also classically implies the grounding of the higher levels on the lower levels, such that the existence of the higher levels is dependent on the existence of lower-level entities.

3.4. Levels of Regulation (Control)

Regulation is the relation by which higher levels, derived in some sense (through integration and emergence) from the lower ones, in turn exert some sort of influence on those very lower levels. This relation among levels should encompass both the disputed forms of downward causation (Campbell 1974), as well as those apparently more simple cases of cybernetic-like regulation (or control).[8]

3.5. Levels of Organization

The relation of organization among levels entails the combination of the other four, more encompassing, levels of specification, all of which are simultaneously present: "The organization of an entity refers to the arrangement of its component parts and their operations (functions) and to how they result in the capacities of the whole or the phenomena in which it appears. Often, organized entities are complex and hierarchical: their parts are themselves organized entities" (Etxeberria and Umerez 2013).

Therefore, when considering organization, we are referring to complex systems implying some form of interrelation among elements that goes well beyond mere composition: such systems manifest integrated global emergent properties, capable of regulating the behavior (dynamics) of their constituents.

4. Causal Plurality: Constraint

In addition to the two reasons that have been presented in the previous two sections (a disregard of developments in scientific hierarchical approaches and a restricted view of organizational relations), there is another and more general reason underlying the philosophical suspicion about interlevel relations that is related to the fundamental issue of causality. In fact, most criticisms that downplay the role of interlevel relations (especially top-down relations) in hierarchies are concerned with the problems of overdetermination or postulating more than one cause for the same effect.[9]

To admit that events or processes at higher levels have some decisive influence on the events or processes at lower levels may conflict with the alleged causal sufficiency of lower levels. Typically, this problem is framed in the context of the principle of the *causal closure of the physical domain*, which roughly states that "any physical event that has a cause at time t has a physical cause at t" (Kim 1993, 280). Such a view is grounded in physicalist ontology, asserting that all that exists is the physical world (rejection of nonphysical entities) (Blackburn 1994, 287). This principle is typically supplemented with the so-called problem of *causal explanatory exclusion*, that "seems to arise from the fact that a cause, or causal explanation, of an event, when it is regarded as a full, sufficient cause or explanation, appears to *exclude* other *independent* purported causes or causal explanations of it" (Kim 1993, 281).

A thorough examination of this issue is well beyond the scope of this chapter. Nevertheless, here again an imbalance may be detected between these philosophical reservations and the determination to overcome epistemological difficulties that characterize the explicitly hierarchical approaches adopted in evolutionary biology, ecology, or complexity and systems sciences.

Aside from the specific theoretical construction of each particular area and approach, the way to overcome these philosophical problems is sought, in most cases, through a common strategy that involves (1) the deployment and vindication of a more plural and complex understanding of causal relationships, made specific through (2) the intentional adoption of several additional concepts, such as the idea of constraint.

This effort is patently clear, for instance, in the development of the hierarchical theory of evolution, where the awareness of the need to expand the scope of causal interactions is present from the very beginning: "A hierarchical approach includes wider possibilities of causation within additional levels, as well as upward and downward causation between levels" (Vrba and Eldredge 1984, 169). As the following quote shows, the hierarchical approach has since been developing conceptual tools for a very detailed individuation and analysis of the causal factors involved in the appearance of evolutionary patterns: "Complex evolutionary patterns integrate variational dynamics of sorting processes that occur at different levels, with their effects propagated indirectly to other levels within the genealogical hierarchy via downward and upward causation. Hierarchy theory provides a theoretically and operationally unified framework for unraveling causal processes responsible for generating evolutionary patterns by identifying the involved individuals and their properties, hierarchical levels where these individuals reside, and their interactions within and across levels as well as between the two hierarchies" (Tëmkin and Eldredge 2015, 204).

There are also views that take a more general perspective, claiming that any appeal to selection process still requires an expansion of what counts as causal explanation: "My claim, thus, is that in selection processes these functional or relational properties can be causally efficacious, which means that properties other than physical properties can have causal powers. To put it in the form of a slogan: selection processes make the causal world exuberant" (Vicente 2013, 139–140).

Significant cases are also found even in some areas of molecular biology, though in the absence of scientific, explicit hierarchical approaches. For instance, the analysis of the folding of proteins aided by chaperones is couched in such terms that philosopher Alan Love interpreted it as an instance of interlevel, top-down causal explanation. In a review article, Christopher M. Dobson summarized the point: “It is apparent that biological systems have become robust not just by careful manipulation of the sequences of proteins but also by controlling, by means of molecular chaperones and degradation mechanisms, the particular state adopted by a given polypeptide chain at a given time and under given conditions. This process can be thought of as being analogous to the way in which biology regulates and controls the various chemical transformations that take place in the cell by means of enzymes” (Dobson 2003, 888).

Reflecting on this case, Love offers a straightforward reading in causal terms: “Explanations of protein folding that rely on chaperones are a form of top-down causal explanation. . . . The top-down causal explanation of protein folding is in terms of macromolecules and their components, and the hierarchical relations that apply to protein structure are delineated precisely” (Love 2012, 119).

In all of these examples, there is not only the recognition that in some cases an explanation based on physical properties as such is not appropriate but also an explicit acknowledgment that complex events or processes, such as many biological phenomena, often require or allow for complementary or alternative causal accounts that are not reducible. In sum, this amounts to questioning both the causal closure of the physical world and the principle of causal explanatory exclusion. To effectively address these issues, it is necessary to provide scientifically and empirically sound accounts and models capable of integrating interactions among levels of this sort.

The second aspect common to hierarchical approaches is the incorporation of special conceptual tools that supply the specific operational materialization of the relations among levels of organization. One such set of concepts may be summarized under an inclusive interpretation of the idea of constraint.

Constraint is a term that has slightly different meanings in different scientific disciplines. In several fields of biology and complexity sciences, *constraint* (among other terms with approximately the same meaning as *boundary condition*) is used to account for phenomena whose explanation is not exhausted by reference to the general and standard causal factors at one level, and requires taking into consideration factors at other levels. The development of more specific characterizations of constraint are attempts to spell out the interaction among levels of organization by deriving them from epistemologically legitimate concepts grounded in the physical sciences or in their explanatory stock.

In general, *constraint* "refers to a reduction on the degrees of freedom of the elements of a system exerted by some collection of elements, or to a limitation or bias on the variability or possibilities of change in the kind of such elements" (Umerez and Mossio 2013, 490). The action of constraint is inherently hierarchical because it does not interact *dynamically* (because it operates at a different rate) with the elements it is going to influence but interacts globally as a boundary condition or an initiating condition (Salthe 1985).

The concept in its usual meaning of "a limiting factor" has been routinely used to describe the operation of several natural and artificial devices or processes. Examples of constraints range from surfaces (e.g., table tops) to switches; from eddies or convection phenomena (such as Bénard cells) to other pattern formation cases or flocking behaviors, from membranes or enzymes to canalization or other developmental determinants, and from genetic or epigenetic instructions to sorting or other selective processes.

The unveiling of the implicit implications of the concept of constraint against the monist causal assumptions (those introduced at the beginning of this section) may be attributed to Michael Polanyi. He was the first author to discuss this notion as the distinguishing feature of biological organization (Polanyi 1968), even though he did not use the term *constraint*. Indeed, he used the more generic concept of *boundary condition* in order to introduce the idea of a dual control over the chemical processes occurring within an organism, where a higher level would additionally harness the dynamics of the lower level. He did, though, distinguish between two kinds of boundaries, test-tube type and machine type (Polanyi 1968, 1208), which indicates the intended generality of his attempt, since the latter expands significantly the scope of phenomena covered by the former.

This meaning of interlevel constraint, as an additional but necessary (complementary) ingredient to explain the workings of living systems, was further developed by Howard Pattee. By then he was investigating (in the context of the problem of the origin of life) how to account for the reliability of hereditary mechanisms, departing from a point of view grounded in physics (1966, 1967, 1968, 1969a, 1972). In these works, Pattee had already begun to use the concept of constraint as an appropriate explanatory tool, derived from physics (mechanics) to describe the functioning of hereditary systems as a combination of two separated dynamical realms at different levels. Quite naturally, he endorsed Polanyi's dual control perspective for his hierarchical theory, distinguishing structural from functional hierarchies (Pattee 1969b, 1973) and developing a broader theory of biological organization (see Pattee 2012; Umerez 2001, 2009). Additionally, the more technical distinction between holonomic and nonholonomic constraints (formulated according to their definition in physics) became fundamental for his formulation of those kinds of hierarchical relations (as well as for his treatment of the problems of the origin of life and heredity).[10]

The use of the concept of constraint and other related concepts as a limiting factor has become customary in many areas of the biological sciences and usually does not pose explicit epistemological issues. The early formulations of Polanyi and Pattee, though, help us to notice the underlying significance of such a concept to challenge the conventional view of causality: it makes room for a more pluralistic perspective, accepting as genuine input diverse forms of interaction among levels of organization.

5. Conclusions

In summary, it has been observed that some current philosophical approaches that are not rigidly reductionist tend nevertheless to downplay the significance of interlevel relations in biological and complex systems. In each case, the particulars of the rationale for such position may differ, but a conjunction of three related reasons constitute a common ground underlying most of them. These three reasons are (1) a partial disregard of the contribution of hierarchical approaches that (2) facilitates the perseverance of a compositional view that takes organization for granted and that (3) does not compel us to challenge the intimidation of potential causal overdetermination against top-down causal accounts.

To better frame the challenge, let us recall that Joseph Needham had already reminded us that understanding organization is the key concern of biological inquiry:

> Recognition of the objectivity and importance of organizing relations had always been an empirical necessity, forced upon biologists by the very subject matter of their science, but the issue was always confused by their inability to distinguish between the organization of the living system and its supposed anima. With the abolition of souls and vital forces the genuine organizing relations in the organism could become the object of scientific

study. . . . Today we are perfectly clear . . . that the organization of living systems is the problem, not the axiomatic starting point, of biological research. Organizing relations exist, but they are not immune from scientific grasp and understanding. On the other hand, their laws are not likely to be reducible to the laws governing the behavior of molecules at lower levels of complexity." (Needham 1937, 15–16 [1943, 242–43])

The articulated view presented in this chapter is an attempt to unfold the implicit content of the notion of level of organization as it is currently used in various areas of the biological and complexity sciences. Thus it is claimed that, in hierarchical approaches, *level of organization* designates a very definite form of compositional level that requires further conditions that specify the kind of composition involved. Those additional specifications of the peculiarities of the relation of composition include the more restricted relations of integration, emergence, and regulation among components that, collectively, give rise to the inclusive relation of organization as such.

The articulation through those five kinds of progressively restrictive relations among elements (composition, integration, emergence, regulation, organization) that give rise to kinds of levels allows us to distinguish between different perspectives and definitions of level without confronting them. Depending on the subject of inquiry, an intermediate kind of relation among those might be sufficient. Only the specification order needs to be preserved: each kind implies the less specific relations but not necessarily those that are more restrictive. Thus all of them imply relations of composition of some sort and, for instance, emergence or regulation must also entail integration. It is only when biological organization is involved that all kinds of relations are required. Conversely, the relation of composition does not imply any others and, hence, it is too weak, by itself, to account for properties or behaviors that depend on organization.

This is evident even in those approaches that are reluctant to admit stronger kinds of interlevel relations because their proponents are also compelled to specify that their explanations and models deal with "organized collections of components" (Craver and Bechtel 2007) and not with just "haphazard parts" (Craver 2008). In other words, the organized nature of those collections of components in biological systems does not derive from their sheer condition of being a component part but from something else that is more specific. According to the articulated view, this "something" is the relations of integration, emergence, and regulation: a group of components acquires the condition of organized if its constitution (composition) involves some instance of those additional kinds of relations.

The actual material implementation of this organizational disposition is due to the action of some form of constraint or boundary condition over the potential components or collections of them. As pointed out in the previous section, reliance on constraints entails a thorough consideration of the interaction among levels and addressing the potentially causal nature of such interactions, both bottom-up and top-down.

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Notes

1. It was originally stated by Donald T. Campbell in 1974 in reference to the action of natural selection: "(Downward causation) Where natural selection operates through life and death at a higher level of organisation, the laws of the higher level selective system determine in part the distribution of lower level events and substances. Description of an intermediate-level phenomenon is not completed by describing its possibility and implementation in lower level terms. Its presence, prevalence, or distribution (all needed for the complete explanation of biological phenomena) will often require reference to laws at a higher level of organization as well. Paraphrasing Point 1, for biology, all processes at the lower levels of a hierarchy are restrained by, and act in conformity to, the laws of the higher levels" (Campbell 1974, 180).

2. Deflationary: Depriving the concept of substantive epistemological content, claiming that it does not add anything in explanatory terms.

3. Eliminativism: A position that defends the convenience to eliminate from our discourse what is considered to be a superfluous (or erroneous) entity or concept and to replace it with a more basic and fundamental one.

4. To mention a few, see Allen and Starr 1982, Eldredge 1985, O'Neill et al. 1986, Pattee 1973, Salthe 1985, Weiss 1971, Whyte et al. 1969.

5. Scale as a generic graded measure of some basic variable (size, time, rate, etc.).

6. "To be aggregative, the system property would have to depend upon the parts' properties in a very strongly atomistic manner, under all physically possible decompositions. . . . Aggregativity is the complete antithesis of functional organization" (Wimsatt 2000, 272; Wimsatt 2006, 675).

7. A very different issue, which is not going to be addressed here, is the general philosophical discussion regarding the ontological or merely epistemological status of levels of organization together with the more technical one about how accurately we can succeed in demarcating them (in "carving nature at its joints"). For instance, Allen and Starr (1982) take an explicitly epistemological stance whereas Salthe (1985) tends toward a more ontological one.

8. The issues involved in the understanding of these two last kinds of relations among levels, *emergence* and *regulation* (or *control*), are so wide, deep, and controversial that they deserve and require a full treatment that doesn't fit within the limits of this chapter. For now, the point is to stress the necessity to include them when dealing with any version of levels of organization, although here the analysis is limited to elaborate the more approachable but currently highly relevant relation of *composition*.

9. Overdetermination: An event is overdetermined if there exists more than one antecedent event, any of which would be a sufficient condition for the event occurring (Blackburn 1994, 274).

10. Holonomic constraints are auxiliary conditions that limit permanently the number of degrees of freedom of a system and are, therefore, the basis for structural hierarchies, while nonholonomic constraints are variable auxiliary conditions that limit in time the number of degrees of freedom of the system, being the basis for the functional hierarchies typical of living systems. The latter are dynamical structures that establish time-dependent relations among degrees of freedom but introduce a different temporal scale.

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