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Biological Boundaries

Dissertation Abstract

Modern biology serves as an umbrella term for the various sub-disciplines which pursue the myriad causal relations of life. The Modern Evolutionary Synthesis left out developmental biology and ecology and the efforts in the late 20th Century to amend this oversight have been exemplary. Despite ecological and evolutionary developmental biology's many recent successes I think the greatest addition of Evo-Eco-Devo to the Modern Synthesis will be the insight that a return to questions of process is fundamental for thinking on evolution to progress. For, if the incredible variety and differences in morphological form and life history that is exhibited in the natural world is not explained by differences in genes but rather by the regulation of these genes, then a corresponding shift from understanding component parts (i.e., genes) and the information purportedly carried by them to an understanding of how these parts interact and a view that understands information as arising from these interactions is needed.

The justification for upper level explanations of process and form should not emanate solely from the failures and ignorance which result from looking for explanation at the lower levels. Rather, a more positive program must be established that formulates precise observations of process across various biological phenomena and tries to piece these together into a body of knowledge about living form and process. To wit, as one moves along a biological hierarchy from the more basic units of biological organization (e.g., genes) through to the more complicated, inclusive organizational structures (e.g., cells, tissues, organ systems, individual organisms, superorganisms, groups, etc.) the features and properties at the lower levels do not translate easily to those of the upper level. That is, a hierarchical biological organization

identifies an organizing principle (e.g., size, flow of energy, flow of information, etc.) in which each level depends in some way upon lower levels, but this does not guarantee that properties at the upper levels will be reducible to those of the lower level. Whether or not there are emergent properties moving up a hierarchy will depend upon boundary principles. Thus, an investigation as to which biological boundaries exist, how these are drawn, whether and when they break down, etc. is much needed, as is a re-evaluation of mereology in biology. To this end, the recent trend towards systems biology and an integrative approach is welcome, as is the search for concepts and methods that try to explain how systems' properties emerge and evolve. In order to bridge the successes of reductionist biology and a philosophy of science that favors a more integrative approach we have to pursue what is fundamentally a boundary-crossing science across various sub-disciplines. The research program I propose in what follows looks at boundary formation and boundary break-down as essential activities to life-processes. My hope is that an exploration and appreciation for these boundary processes will help to bridge and integrate the various sub-disciplines for a fuller understanding of evolution and life in general. Ultimately, looking at boundary formation and breakdown processes will serve as a framework from which heuristic guidelines may contribute to progress in biological understanding.

Chapter 1 introduces the theme of boundary formation and breakdown and shows how this distinctive feature of the living has profound consequences for many areas of biological theory, particularly evolutionary biology.

Chapter 2 of the dissertation explores the notion of biological information by looking at the ongoing debate between Developmental Systems Theorists (DSTists) and more reductionist views of information. The latter group views information as emanating from and encoded within genes or a genetic program while the former takes a more holistic approach to the sources and uses of information during development of the organism. The biological information debate has resonances with the traditional debate in biology between reductionism and holism, but has an interesting consequence for those who are usually left without an adequate mechanism to defend their particular world-view. Namely, the DSTists, who are more holistic in their approach can avail themselves of the more powerful and open-ended mathematical notion of information in defending their claims that information for development and for evolution can arise from multiple sources. Surprisingly, few DSTists have noted this potential mechanism or used it to their advantage. Additionally, I continue the theme of boundary division and energy use by viewing how information is related to energy.

Though the relationship between energy, specifically trophic energy, and information (understood as a lack of entropy) is difficult and somewhat obscure, I suggest ways in which information can be thought of as stored energy, i.e., energy stored in a particularly ordered way. The notion of activity has long been considered a hallmark of the living. And, in many ways the idea that life is a process or an activity runs counter to the idea that life is a program or a blueprint. Nonetheless, both ideas can involve the notion of reversing the randomness of thermodynamic entropy. If we equate entropy with disorganization and see living organisms as essentially feeding on and converting energy into a stored form – information – that can be used to transmit energy efficiently between generations (heredity), but which is liable to failures and losses leading to variation. And, we see these processes of energy conversion embodied by organisms competing differentially for resources (which we can also equate with energy) then a picture in line with modern evolutionary theory emerges. Boundaries, particularly boundaries used to form capacitors for biological information, turn out to be crucially important both for the storage, integrity and transmission of this information. Boundaries determine what energy forms a part of the system, how it is incorporated and stored, and finally, what energy (in the form of other organisms) is kept out. Understood in this way, boundary formation and dissolution forms an important touch point between investigations of evolutionary and developmental processes (especially those involving information).

Chapter 3 investigates the divisions or boundaries between life-stages in the life-cycle of organisms with complex life cycles. Each life stage has a characteristic body plan corresponding to its ecological niche and these differences can sometimes be very dramatic, so much so, that it is difficult to identify the different life-stages as all corresponding to one life-history (or organism). Consider the morphological and ecological differences between the pelagic, free-floating, non-feeding, indirect developing larvae (pluteus) of the Echinoidea and their relatively sessile, filter-feeding, adult forms as urchins. And, even when the embryo stage is similar between species, the adult forms can have very different morphologies (e.g., the differences between pencil urchins, heart urchins, sea biscuits and sand dollars).

There are many ways to think of a life-history that splits its time between different developmental morphologies and environments. We can think of the life-history as consisting of different competing genetic programs (one for each stage of development and under genetic control) or as involving tradeoffs between different ecological demands (and determined by ecological factors), or some combination of these with various sources playing an informational, developmental and co-determining role in the formation of the boundary. Under all of these interpretations, the juvenile (larval) developmental plan and the adult plan compete for life-history time and expression, shifting aspects of the developmental boundary between the two life-stages later (paedomorphosis) or earlier (peramorphosis) in development. Changes in the rate of development or alterations in the start or end-points of the developmental shift will lead to different results [respectively, for Paedomorphosis: neoteny, post-displacement and progenesis; and for Peramorphosis: acceleration, predisplacement and hypermorphosis]. Together these perspectives on shifts in development are known as heterochrony and though the phenomena exhibited were described since Haeckel, they have seen their most recent revival beginning with the work of (Gould, 1977) and (Calow, 1983).

These different ways of parsing a life-history have led to different interpretation not only of heterochrony but of the evolutionary processes that give shape to complex life cycles and to the process of metamorphosis. This chapter explores the differences between interpretations that privilege one out of a number of contributing factors at the expense of other sources of information. Both the ecological and the genetic perspectives push different factors to the background and each perspective thus comes up short of giving a full causal account of the phenomenon. Synthetic models are an improvement since they try to paint a fuller picture of the phenomena involved but they too are hampered by limited consideration of cause, either internal or external to the organism, rather than looking at the relational properties of a process interpretation of the organism. Finally, attempts from developmental systems theory (DST) are investigated. These hold the greatest promise for capturing the phenomenon but are still in a fledgling state of theory development. Their greatest advantage is that they do not privilege one source of information a prior over others, but remain open to discovering all of the causal factors involved in the building up of organismic form. With respect to metamorphosis and CLCs this turns out to be a useful perspective which allows proper consideration of the division and bounding of different stages of a life cycle.

Chapter 4 on the concept of accommodation looks at the process of forming individuality at each level of organization. Here I will address difficulties in the concept of biological individuality as well as those in the related questions of what counts as an organism. Determinations of each concept draw upon boundary conditions, so perhaps it is not surprising that since I do not find boundaries to be categorical or easy to fit into necessary and sufficient conditions, that I also do not find categorical individuality and organism concepts to be very useful. Instead, I opt for different individuality and organism concepts for addressing different biological questions. So long as clarity and explicitness are used in delineating the investigation, a functioning model of individuality can be used; subsequently, the model can be refined so as to get at a deeper understanding of causal relations and processes. In any case, individuality is likely to be the result of feedback mechanisms which further functional integration and respond to the fitness demands that a process tends to inhabit. That is, a process of accommodation occurs between individuals and their environments such that each responds to the challenges and perturbations presented by the other.

Living organisms have the advantages of developing sub-systems that are reproduced from generation to generation such that developmental capacities are transferred and ways of adjusting to the environment are internalized. The environment's greatest advantage is that it is not alive in the same way that its subsystems are, so it can suffer grave disturbances that push it towards disorder (entropy) at least locally and still recover. Besides spatial and distributions differences, time scales which are fundamental to evolutionary processes, have different effects on sub-systems (organisms) and their larger environment. The interactions between organisms and environments are shaped by these differences in spatial and temporal scales. I explore the importance of these differences later in chapters 8 & 9 when I lay out the important boundary crossings relevant to environmental interactions.

Chapters 5 & 6 explore immunological boundaries and notions of selfhood. Some of the most interesting payoffs for using boundary crossings as a research heuristic come in looking at the vertebrate immune system. Studies of the Immune System are underrepresented in the Philosophy of Biology so these two chapters are just the beginning of what should be a much larger project. Part of the reason for the under-representation may be the incredible complexity of the system along with the speed with which understanding in the field develops. Nonetheless, it holds many riches for philosophers of biology and I try to mine some of these in these two chapters.

Understood as a process of boundary formation and dissolution the competing perspectives of the Immune System as identity forming (as a self/non-self distinguishing system) and the Immune System as a regulatory system can both be brought together under one more encompassing interpretation – the Immune System is about regulation and persistence of normal function, it does this by creating functional boundaries that maintain proper functioning of sub-systems, but it also does this by creating boundaries to ward off invading pathogens that would disrupt function. By warding off these invading pathogens, the Immune System can also be used to identify self from non-self cells, though there are important exceptions to a rigid self-identification (i.e., there are non-self cells that are allowed to persist within the organism, self-cells that are rejected, etc.) We do not have to choose between competing Immune System interpretations since we can use either perspective depending upon what better meets our research goals. Furthermore, both perspectives add to a causal account since sometimes the immune system is acting to further refine selfhood and sometimes it is acting to ward off invading pathogens. The dynamics of these interactions must be understood as part of a larger process of living involving boundary building and breakdown processes; the immune system fulfills multiple functional roles because the living system has to navigate all of these in order to maintain identity and proper functioning while at the same time keeping other processes from coopting or corrupting these.

Chapter 7 looks at the ways in which boundaries structurally and functionally integrate different life processes, making these processes more robust to perturbations. Robustness – a feature of systems or their parts which allows for continued function in the face of perturbations – is a critical aspect of homeostasis and I explore the extent to which boundaries assist in forming homeostatic environments both within the organism and beyond the organism. Since all living organisms must constantly compensate for changes both within and beyond themselves, it is energetically costly to maintain equilibrium. Nonetheless, the evolution of life forms clearly shows a propensity for using boundaries to increase robustness and thereby mitigate the effects of selection. Robustness has been accomplished at multiple hierarchical levels of biological form and function – levels which are defined by the characteristic boundaries that delimit them. A related concept which has received significant attention in developmental and evolutionary biology is modularity. Boundaries and boundary conditions form an integral part of modules and modules are critical to the possibility and establishment of robust processes and structures. An investigation of the interplay between these three concepts (boundaries, modules and robustness) illustrates the complex dynamics of living systems forced to respond to fitness challenges at multiple levels and from multiple fronts.

The notion that natural selection can “see” or “not see” a change at a particular level of organization is presented as a way of understanding the fitness effects of evolutionary forces other than natural selection. That is, the idea that fitness effects can be modulated by developmental strategies such as boundary formation is anathema to a perspective that considers natural selection as a force that has omniscient and ultimate omnipotence over biological form and function; however, it is well in line with a view of evolution that considers natural selection one of many forces at play in the survival and change of lines of living processes.

Chapters 8 & 9 look at the importance of crossing boundaries between science (mainly biology), humanities and the social sciences (mainly ethics). Chapter 8 investigates whether scientists should participate in the philosophical and ethical discussions regarding their work or whether this specialization (ethical thinking) is better left to the experts. I come down on the side of scientific participation in ethical discussion but also think it imperative for ethicist and philosophers to enter the lab and do some scientific research of their own. Arm-chair philosophy is perhaps appropriate for metaphysics but to understand philosophy of science and the ethical issues involved really necessitates active involvement in the activity of science. Ethical issues at the edges of scientific research demand active engagement on several levels, from practical to epistemic. Science is a practice and as such is a process of inquiry, perturbation, observation and discovery. Ethics is a similar embodied type of practiced or embodied knowledge. Bridging the divide and trying to understand each other’s discipline helps both scientists to do better science and the ethicist to discover and confront the real ethical problems.

This chapter also sets up a particular framework based on boundaries and boundary crossings to investigate the source of many ethical dilemmas in the boundary crossing sciences arising out of new forms of technology. I look at ethical issues in nanotechnology, but the observations I draw are similarly applicable to the other boundary crossing sciences of the last century (i.e., nuclear energy, genetic modification, synthetic biology, etc.). Boundary crossings involving dispersal (spatial boundaries), penetrance (structural boundaries), persistence (temporal boundaries) and unpredictability (imaginative boundaries) turn out to be the most threatening both to humans and to the environment. Looking at these boundary crossings concurrently with investigating a science that promises to breach these, is one way of anticipating and discovering the ethical issues that might arise.

Revealing research on boundaries is important but experience in crossing boundaries is better. So, the last chapter is a case study that attempts to test the hypothesis that a participant-observer, who is informed and interested in ethical issues, can enhance the ethical awareness of nanotech researchers by being embedded in a nanotech facility and taking part as an active lab member in the scientific research being done there. The benefits for me as a researcher were manifest and are elaborated in the chapter. The benefits to the scientists were measure in both a qualitative and quantitative study. The former was an attempt to tease out the societal implications of the work being conducted at the lab by way of two methods: 1) the regular involvement of the ethicist in the technical and scientific research at the facility, and 2) via repeated interactions and discussions with the scientists. The quantitative study attempted to collect questionnaires of ethical issues relevant to the research being conducted at the facility. And though the questionnaire did become incorporated into the admissions procedures for researchers as they commence use of the facility, the numbers and quality of answers received and the failure of scientists to truly engage with the questionnaire has not produced sufficient data to make a true quantitative assessment of the impact of having an ethicist in the lab.

Perhaps this points to the importance of having more active engagement, bridge-building and live interaction between researchers from different fields working together to solve shared problems.