PERSPECTIVES

Integrating Functional, Developmental and Evolutionary Biology into Biology Curricula

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Abstract: A complete understanding of life involves how organisms are able to function in their environment and how they arise. Understanding how organisms arise involves both their evolution and development. Thus to completely comprehend living things, biology must study their function, development and evolution. Previous proposals for standardized post-secondary biology curricula have relied upon surveys of current practice, producing a curriculum that omits development and conflates evolution with ecology. To produce undergraduate biology programs that focus on the core essence of biology, curricula must address these three pillars undergirding biology: function, development, and evolution. Focusing the curriculum in this way may ease the difficulty of squeezing the burgeoning growth of biological knowledge into biology degree programs. A number of different approaches are possible, ranging from ensuring that these three principles are woven into the core biology courses to having specific required courses for each. Whichever approach is taken, it is imperative that biological function, development and evolution are integrated with each other such that students graduate with an understanding that these three concepts are inextricably entwined with, and dependent upon, each other.

Key words: curriculum design, functional biology, evolutionary biology, developmental biology, integrated biology

During his long and productive career, Ernst Mayr advocated that biological phenomena had two sources of causation: proximate and ultimate (Mayr, 1996). Proximate causation involves the mechanisms of immediate utility and explains how organisms are able to live in their immediate surroundings. This is the focus of functional biology (e.g. cell biology, physiology, genetics, and metabolism). Ultimate causation, in contrast, considers how species are produced. A full explanation of any given organism, Mayr argued, had to address both proximate and ultimate causation: the left and right hands of biology are function and evolution. Mayr's thesis had its origins in the mid-twentieth century when he was involved in the construction of the modern evolutionary synthesis in which genetics was wedded with evolution (Smocovitis, 1992). Gene expression provided the proximate explanation and evolution the ultimate explanation of how organisms and species arise.

Scott Gilbert et al. (1996) have suggested that Mayr's dualistic view of biology misses a key aspect of how organisms come into existence: ontogeny. Evolution results from changes in the developmental program. Changes in development produce different structures, functions, and behaviors in individual organisms which affect their ability to reproduce. Evolutionary theory explains how the fittest organisms are selected by their environment to have increased reproductive success. In contrast, development explains how the fittest organisms are produced. Evolutionary biology considers the survival of the fittest whereas developmental biology considers the arrival of the fittest. The mechanisms by which development and evolution occur are dependent upon how cells and organisms function in their respective environments. Differing functional abilities determine which individuals survive to reproduce. Changes in the developmental program lead to differences in the functional abilities of reproducing organisms. Thus, evolutionary biology is derived from developmental biology which is derived from functional biology: ontogeny mediates between the ultimate and proximate causations of organisms (Gilbert et al, 1996). Some may consider developmental biology simply a result of gene expression. Ontogeny, however, cannot be completely reduced to genetics because of the presence of morphogenetic fields: the modular entities of cells and their secreted proteins responsible for the production of identifiable functional structures within an organism (Gilbert et al, 1996). Biology curricula need to attend to this re-synthesis which incorporates development into the modern evolutionary synthesis of evolution and genetics (Hlodan, 2009); development bridges the gap between proximate and ultimate causations in the evolutionary synthesis of the mid-twentieth century (Carroll, 2008).

Previous papers which proposed standardized curricula for post-secondary biology degree programs have relied upon surveys of current practice, producing a curriculum that omits development and conflates evolution with ecology (for examples see

Heppner et al, 1990; Cheesman et al, 2007). Surveys may produce an accepted standard or consensual curriculum but do not consider the theoretical foundations of biology. They assume that the biological principles will be adequately covered and integrated across the biological curriculum. Such an approach produces a curriculum based on disparate facts rather than on integrated theory and produces a representation that is current *status quo* but does not necessarily advance biology education.

Any academic discipline, however, must focus its education of the next generation of practitioners on its practice and principles not simply on subject matter. A discussion of the practice of biological science and its place in biology curricula is beyond the scope of the present article which addresses only the theoretical aspect of biology curricula. Making principles the focal point gives biology educators a means of focusing curricula despite the exponential growth of biological knowledge. Currently, educators are faced with a difficult choice when considering how to include growing current knowledge into the finite time of existing required courses. By attending to principles rather than to memorized facts, educators may instead choose from among the wealth of current biological knowledge to exemplify how the principles of biology are manifested in the living universe. Others have also suggested that a conceptual rather than content approach to course design may be a better way of enhancing students' understanding of biology (Sundberg and Dini, 1993). This conceptual approach, moreover, may be extended to the design of biology curricula (Bybee, 2002) as exemplified by the recent report published by the AAAS (Brewer and Smith, 2011). This most recent call for curriculum change in biology undergraduate education (Brewer and Smith, 2011) is excellent in its focus on core competencies (ability to apply the process of science, use quantitative reasoning, modeling and simulation, tap into interdisciplinary nature of science, communicate and collaborate, and understand the science-society relationship) and concepts (evolution, structure-function, information storage and retrieval, energy and matter transformation, and systems). However, similar to previous calls for curriculum change, it also omits one of the three conceptual pillars of biology; developmental biology is limited to a list of sub-disciplines which only provide supporting evidence for evolution.

To produce undergraduate biology programs that focus on the core essence of biology, curricula must address these three pillars undergirding biology: function, development, and evolution. Rather than having degree programs emphasize sub-disciplines and courses they could instead consider the principles and then require students majoring in biology to complete whichever courses are necessary to convey the principles. Thus, rather than degree programs requiring courses in fields such as genetics, physiology, cell biology, ecology, biochemistry, microbiology, evolution, or molecular biology, they could instead require that majors graduate with an understanding of how prokaryotic and eukaryotic organisms function, develop, and evolve. The reductive (e.g. genetics and molecular biology) and holistic (e.g. behavior and ecology) biological sciences have their place within this scheme as different approaches to investigating the three fundamental biological pillars. For example, genetics considers the role that genes play in biological function, development and evolution. Similarly ecology considers the role of the environment in how life functions, develops and evolves.

In essence, to understand life, to study life, students need to comprehend how organisms work; how they overcome the problems of gas exchange, reproduction, waste removal, and energy conversion. The solutions employed by cells and organisms to overcome the challenges presented by their internal and external environments require an understanding of functional biology (metabolism, molecular biology, gene expression, anatomy and physiology). This would enable students to explain how organisms manage to maintain themselves while their environments change.

Students also need a foundation in understanding how life comes into existence. This must address two inter-related questions whose answers are dependent upon proximate mechanisms. First, how do organisms function while developing? This can occur through simple cell division in unicellular organisms in addition to the more complicated self-assembly of multicellular organisms. The study of these phenomena includes a consideration of cell communication, genetic control, cell motility, and developing structure/anatomy. Second, how do organisms evolve? What mechanisms produce Earth's biodiversity? This includes a consideration of selection theory, population genetics and ecology. These two aspects of how life arises are intimately entwined as evolutionary change necessarily derives from changes in developmental programs. Conversely, developmental programs evolve by natural selection of the procreating adults that development has constructed.

Both aspects of how organisms come into existence (development and evolution) are dependent upon how organisms function. Developing organisms must necessarily live/function in their developmental environments. Organisms are selected to develop and procreate based upon their relative ability to function.

Historical contingency clearly plays a role in evolution but, other than serendipity, the developmental program is the major constraint of organisms' ability to evolve over generations

(Gilbert, 2006); it limits what is available to be selected by the environment. The developmental history determines what features are available to be modified over generations. The history of an organism's evolution is written into its developmental program determining its future possible evolutionary paths.

Post-secondary biology curricula must ensure that graduates have a firm foundation in its principles and thus necessarily consider how organisms function, assemble (development) and are selected (evolution). However, developmental biology is missing from the AAAS list of major topics to be included in producing biologically literate students (AAAS, 1989). It is included in the BSCS (1993) guide but its integration with functional and evolutionary biology is only made explicit in the penultimate paragraph of the development essay by John Tyler Bonner. In addition, the most recent recommendation for renewal of biology curricula (Brewer and Smith, 2011) omits ontogeny in its list of core concepts required by all biology students.

If the three themes of function, development and evolution undergird a coherent theory of biology, then they must be woven across the curriculum of undergraduate degree programs in the biological sciences. Students must be introduced to these three conceptual pillars in any freshman biology course providing students with a rudimentary base of our current understanding of how life is possible. Currently, courses often treat the biological principles such as evolution as separate topics rather than as an integrated system (Musante, 2008). This may be appropriate in subsequent more advanced courses in which the focus is on their detailed mechanisms. A senior capstone course could then reconsider how all three themes are related and inextricably tied to each other. Alternative curricular sequences of biological concepts could be developed that best utilize the particular faculty expertise in any given biology department. Evolution might be consistently addressed in all courses negating the necessity for a specific evolution course. Similarly, function may be addressed in anatomy, cell or evolution/diversity courses negating the need for a specific course in biological function. I suggest, however, that a senior course that specifically integrates all three themes may be required to emphasize the point for students before they graduate. I have found that such integration may occur very well in third- or fourth-year developmental biology courses, and in fourth-year seminar and history and philosophy of biology courses.

Interestingly, the latest survey of US undergraduate biology curricula suggests that functional biology is well represented at the cellular and molecular level but not at the organismal level in the consensual biological core of required courses (Cheesman et al, 2007). In addition, a good percentage of biology degree programs do not require their students to complete courses in both embryology (developmental biology) and evolution. Thus the de facto core curriculum excludes development and lists evolution interchangeably with ecology. It is unclear from the surveys whether the omission of development and evolution in institutions' list of required core courses is because these themes are adequately addressed in other required courses, is simply a result of the historical contingency of their degree program, or if the particular biology programs still subscribe to Mayr's dualist philosophy which inadequately addresses the role of development in how organisms are assembled to become procreating adults.

If ontogeny does bridge the gap between proximate and ultimate causation in biology (Carroll, 2008) then it is critical that undergraduate biology curricula reflect current research and teach biology as an integrated discipline (Futuyma, 2007) which would include the explicit synthesis of biological function, development and evolution. Surveying biology degree programs to determine the required core courses is interesting to assess current common practice but does not consider this growing understanding of how life is integrated. Revising biology curricula to reflect this current understanding is possible via many different course combinations but would require a first year course which introduces how these three concepts are inter-dependent upon each other in addition to concerted effort at the department level to provide the broad overview of the entire major. Regardless of how it is achieved, Gilbert et al's (1996) resynthesis of development with evolution and function needs to be an important aspect of an integrated biology curriculum.

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