Unity and Disunity in Biology

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Biology is extremely diverse in its methodologies, concepts, theories, and goals. It is also developing rapidly and revealing deeper complexities at almost every level of organic organization. For these and other reasons, biology is becoming increasingly specialized and fragmented. Is there a remedy for this state of affairs? Are there historical or philosophical resources to help? Can biologists communicate more effectively and establish a new, truly all-inclusive modern synthesis? Toward answering these questions, we discuss the need for the specialist and the generalist in the biological sciences and argue that these two roles are not mutually exclusive. Indeed, although comparatively rare, the specialist–generalist is illustrated by the achievements of Charles Darwin and Louis Pasteur, among others. We also discuss the crosscutting science concepts identified by the National Academy of Sciences Board of Education, particularly in the context of teaching an integrated and specialized biology.

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We live in an age of biology. The biological sciences are increasingly taking center stage as a consequence of persistent ecological and social pressures, as well as a variety of other factors, including the priorities of funding agencies. Important discoveries are being made almost daily at every level of biological organization, from intracellular processes to the operation of entire ecosystems. Discoveries are also being made that reveal greater complexity at every level. The number of scientific journals is increasing at a remarkable rate (figure 1a), as is the number of journals devoted to biology (figure 1b). For example, the number of scientific articles published just in 2006 was a staggering 1,350,000 (Björk et al. 2008). The growth in science publication is so fast that some citation indexes are incapable of keeping up with it (Larsen and von Ins 2010). As a result of this growth and past trends, some see the biological sciences as continuing to become more specialized and the specializations as becoming more conceptually isolated, as is indicated by the two following quotations, separated by 44 years:

> One may rejoice in seeing the prodigious rate of growth of the store of human knowledge.… But the magnitude of this store has far outstripped the capacity of even the most powerful human intellects to assimilate all the knowledge. Irretrievably gone is the time when a scientist… could be a person broadly familiar with the contemporaneous state of science as a whole. (Dobzhansky 1964, p. viii)

> Major advances in biological knowledge come about through the interplay of theoretical insights, observations, and key experimental results and by improvements in technology that make new observations, experiments, and insights possible. The fragmentation of biology into many sub-disciplines means both that the mix of these components can differ dramatically from one area to another and that the development of theoretical insights that cut across sub-disciplines can be difficult. (NRC 2008, p. 7)

It is certainly the case that our textbooks expand in size and often become outdated in short order, just as more and more specialized journals appear on the shelves of our virtual and real libraries. Indeed, some colleagues feel that it is becoming extremely difficult to know what to teach, given time constraints in our lecture halls and laboratories.

We readily acknowledge that growth in the body of scientific knowledge does not necessarily indicate growth in the fragmentation of that body of knowledge. However, evidence for an increasing fragmentation in biology is abundant. Consider, for example, the journal *Nature*. This journal was founded in 1869 to encompass all of science. Today, however, there are 26 *Nature* spin-offs devoted just to biology, ranging from *Nature Chemical Biology* and *Nature Genetics* to *Nature Structure and Molecular Biology* and *Nature Reviews Microbiology*, in addition to biology-oriented articles in *Nature Photonics*, *Nature Physics*, and *Nature Materials* (*www.nature.com/siteindex/index.html*). Similar evidence for the fragmentation in biology can be garnered by perusing journals as diverse as the *American Journal of Botany* and the *Proceedings of the National Academy of Sciences*, both of whose inaugural issues lacked sublistings of biological categories but whose current issues abound with them.

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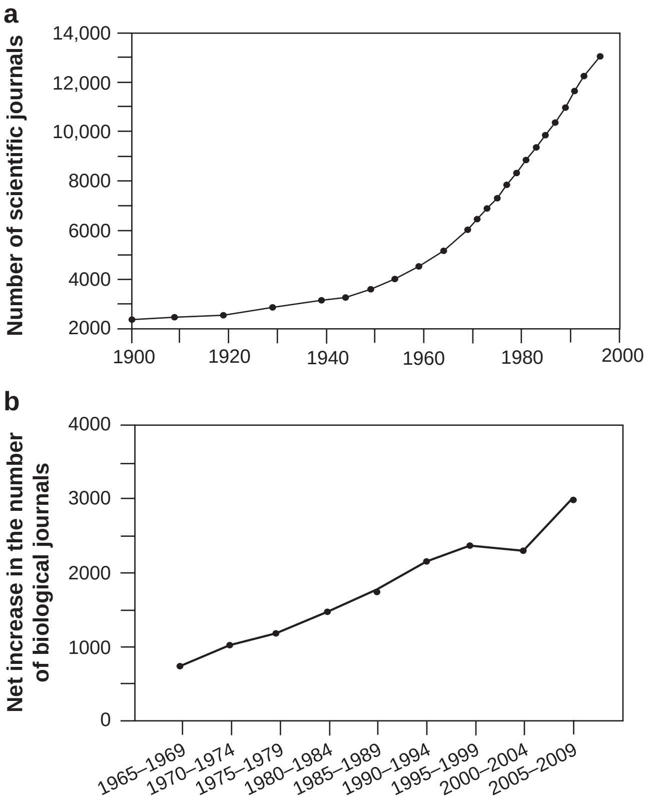

Figure 1. (a) The number of scientific journals (worldwide) and (b) net growth in the number of biological journals throughout the twentieth century. The data for panel (a) are derived from Mabe and Amin (2001); those for panel (b) were derived from the UlrichsWEB Global Serials Directory, using an advanced search for "serial type: journal; content type: academic/scholarly; subject area: biological sciences and agriculture OR medicine and health; format: print OR online."

This zeitgeist in the age of biology raises a number of important theoretical and practical questions. First, are the biological sciences really in danger of becoming too fragmented? Second, if the answer is *yes*, can we identify conceptual or theoretical commonalities that will reunite them? And third, how do we make sure that the current generation of biology students is sufficiently prepared to become the next generation of biologists while still respecting a need for the plant biologist, the molecular biologist, and the microbiologist?

In the following sections, we explore these questions in the context of two affirmations that are undoubtedly idealistic but nevertheless true. First, in theory (albeit perhaps not in practice), there is no intellectual disconnection among any of the natural, physical, or sociological sciences. The practitioners in each scientific area, knowingly or unknowingly, draw on the methods, concepts, and theories of each of the other sciences in one way or another, and the research in each area informs and provides perspective on all of the other areas—as is illustrated by the contributions of the physiologist Adolf Fick (who established the laws of passive diffusion by studying transmembrane solute movement in kidneys), the botanist Robert Brown (who identified random molecular motion by examining pollen in a liquid medium), the physicist Gotthilf Hagen and the physician Jean Poiseuille (who mathematically characterized the flow of fluids in thin tubes by studying blood flow), and René-Just Haüy (who became "the father of crystallography" by virtue of dropping a friend's specimen of calcareous spar) to mathematics, physics, chemistry, biology, and many of the social sciences. The pursuit of science is therefore an interconnected enterprise, because the advancements in one science can ultimately advance all other sciences. Indeed, the philosophy of science and the history of science show us that chemistry, physics, mathematics, sociology, and so on interface at many levels in each of the biological sciences. Nevertheless, we also recognize that each of the different biological sciences is becoming increasingly specialized and that it is becoming harder to fully integrate the developments occurring in the various biological sciences. Pressure to secure external funding and internal decisions about tenure and promotion also tend to favor the specialist and often select against the generalist, whom some view as a dilettante (Wayne and Staves 2008).

Second, we believe that no level of biological organization can be fully understood without understanding how all of the other levels of biological organization affect it and how it affects them. Every organism is an integrated phenotype, and every organism affects and is affected by its environment. Indeed, it benefits every science to recognize the relationships of the parts to the whole. For this reason, we believe that every biologist should be able to effectively teach an introductory course in biology as well as a course in his or her specialty area. However, in our experience, this idealistic view of who should teach (and how biology should be taught) is not the norm. Many graduate students are being trained to be technically adroit but conceptually narrow minded, and many new faculty members are being hired for their research expertise with little or no consideration of their teaching abilities. As a consequence, many biological subject areas are dropping out of our curricula; formerly integrated departments are being fragmented into separate units dedicated exclusively to organismic or molecular biology; and introductory biology classes are either team taught or abandoned entirely in favor of area-specific courses.

Each of the biological sciences needs the specialist and the generalist. Both are necessary to shift scientific paradigms or to create new ones (Kuhn 1962). For this reason, we believe that graduate students must learn the core biological concepts and how to integrate them actively into one another in addition to learning the details of their chosen field of study. In this way, each student can make an informed decision regarding the type of scientist he or she wants to become (in light of the effects that this decision will have on his or her scientific calling). We must cultivate students that can simultaneously see the forest and the individual tree (or the coral reef and the polyp) if for no other reason than that these individuals are just as likely to be the next great communicators of science and the discoverers of new scientific vistas.

In the rest of this article, we present our reasons for making these claims; illustrate them by drawing on the achievements of Charles Darwin and Louis Pasteur, among other scientists; and conclude with an argument that students must learn not only the core biological concepts but also how to actively interrelate these concepts to one another and to those drawn from other disciplines.

The unity of science

Science is a conceptual framework that has at least three important attributes: It is a body of knowledge that is steadfastly self-critical, steadily accumulating, and increasingly explanatory. Scientists investigate natural causality by accumulating empirical observations, continually interpreting the meaning of these observations, and persistently subjecting interpretations to rigorous empirical testing. The pursuit of science begins with initially scattered observations that lead to tentative interpretations. Over time and with sustained observations and testing, these interpretations become more focused and precise in their nature. Some interpretations will be discarded as false, whereas others will eventually achieve the stature of a scientific theory, which will nevertheless always be subjected to empirical scrutiny. Indeed, one of the attributes of a good theory is its resilience to more and more rigorous tests. The biological sciences share all of these attributes and are therefore not unique among the sciences. They also share another attribute with the other sciences: Their purpose is to better understand nature in general and to understand our species in particular. All of this has been said before and with greater eloquence:

> The sciences bestow, as is right and fitting, infinite pains upon that experience which in their absence would drift by unchallenged or misunderstood. They take note, infer, and prophesy. They compare prophesy with event, and altogether they supply—so intent are they on reality—every imaginable and extension of the present dream. (Santayana 1998 [1905], p. 393)

> It seems plain and self-evident, yet it needs to be said: The isolated knowledge obtained by a group of specialists in a narrow field has in itself no value whatsoever, but only in its synthesis with all the rest of knowledge and only inasmuch as it really contributes in this synthesis toward answering the demand, “Who are we?” (Schrödinger 1951, p. 5)

However, the methodology shared among the sciences does not guarantee cohesiveness among them or even within each of them. Some reasons for disunity in biology are less obvious than others. Consider terminology, for example. The *basal body* of the cell biologist is called the *kinetosome* by the protozoologist, who calls the cell biologist’s *undulipodium* a *flagellum*, which is a very different structure from the *flagellum* studied by the bacteriologist. Likewise, what is known to the phycologist as a *siphonocladous* tissue is called a *symplast* by the bryologist, which is known to the zoologist as a *syncytium*. Language is not the only barrier to communication among the biological sciences. Increasingly monocular scientific journals, specialized conferences and symposia, focused and stringent funding priorities, departmental politics, and institutional policies are among the other sociological influences and pressures that have driven wedges among the various biological sciences and that have nurtured increased specialization at the expense of seeing biology as a unified whole. In addition, a pecking order exists among the biological sciences, wherein some view certain fields of study as trivial or unneeded, a perspective that is often institutionally cultivated on the basis of the size of grants or classroom enrollments. Publication costs contribute to this state of affairs, because publication is contingent on funding, and funding is contingent on publication. One consequence of this vicious circle is the disappearance of less popular lines of research. To paraphrase Chargaff (1976), what we consider to be chic science is conditioned by funding.

The specialist–generalist

The history of science shows us that there is no question in any science that is too small for empirical pursuit but that the answer to any question gains in importance when it is understood and integrated into a broader interdisciplinary context. A prudent scientist does not wait to see the bigger implications of even a small answer, because someone else surely will see them (and take credit for it). The specialist needs to see every discovery in its broader context, just as the generalist must appreciate the importance of the answers to the most specialized questions. We freely admit that this specialist–generalist mindset is neither easy to achieve nor widespread. However, the effort is well worth it. Many great discoveries began with seemingly small questions, and the answers to small questions have often led to overarching scientific theories. Why does my wine turn sour? What is that fungus doing to those bacteria in my Petri dish? Why are there seashells in rocks at the top of that mountain? Why are some peas yellow and others green? These and many other seemingly banal questions about the world around us have led to some of the greatest scientific discoveries and some of the most profoundly influential and far-reaching scientific theories.

One of the best-known examples of how the answer to a small question can fine-tune a grand theory can be seen in Charles Darwin’s detailed study of barnacles (Cirripedia), which lasted 8 long years (1846–1854; see Love 2002, Stott 2003). Darwin’s interest in invertebrate zoology dates back to his days in Edinburgh, where he met Robert E. Grant in 1826. However, Darwin’s highly focused interest in barnacles can be traced to two discoveries in 1835, during his now-famous voyage on the *Beagle*—the occurrence of small, shell-less, burrowing parasitic cirripedes in gastropod shells and the discovery of developmental stages in their eggs that were similar to those of crustacea. Before the publication of John V. Thompson's findings in 1830, most naturalists classified barnacles as molluscs. However, Darwin's observations, which were consistent with Thompson's, suggested an entirely different classification. In 1846, Darwin undertook a detailed reevaluation of undescribed cirripedes collected during his voyage, particularly a strange specimen collected in South America (originally called *Arthrobalanus minutus*, but later renamed *Cryptophialus minutus*), which had an articulated shell reminiscent of a crustacean's. In light of the deplorable state of how these creatures were classified up to 1846, Darwin gradually adopted the views of von Baer, Milne-Edwards, and others that classification was best based on embryological features and a detailed understanding of homology. As a result of his fastidious study of barnacles and the tremendous variation within individual species, Darwin became increasingly convinced that species could and did change over time and evolve into new species. His observations of rudimentary parasitic males in the genus *Ibla* and of "complemental" males on hermaphrodites in both *Ibla* and *Scalpellum* contributed particularly to his adoption of a transformationalist perspective.

The publication of the first volume of Darwin's (1851) study earned him the Royal Medal of the Royal Society of London in 1853 and cemented his reputation as a world-class scientist. More important, his intense focus on what some today might consider a very narrow specialty helped develop and crystalize what is arguably the most unifying theory in the biological sciences.

Another example of the specialist–generalist is Louis Pasteur, who began his career as a chemist (Duclaux 1920, Geison 1995, Debré 1998). Pasteur knew from previous work that solutions made from the crystals of any tartrate salt could rotate polarized light to the right, whereas solutions made from the crystals of sodium ammonium paratartrate synthesized in the laboratory could not. Pasteur's single-mindedness helped him see that the tartrate crystals had asymmetrically inclined facets on the right side, whereas the sodium ammonium paratartrate crystals had inclined facets either on the right or on the left side. He separated the two kinds of paratartrate crystals, dissolved each group, and found that the crystals with facets on the right side rotated polarized light to the right, and those with facets on the left rotated polarized light to the left. He also found that a solution made from a 1:1 mixture of the two types of crystals had no effect on polarized light. Pasteur concluded that the inability of paratartrate to rotate polarized light was due to the canceling or compensating effect of the two mirror images. He also guessed that only living organisms could produce chemicals that were optically active. He tested this idea by feeding a fungus (*Penicillium glaucum*) paratartrate and found that, as the fungus grew, the ability of the nutrient medium to rotate polarized light to the left increased. Pasteur serendipitously developed the biotechnology necessary to isolate a particular stereoisomer.

While studying fermentation as a chemist, Pasteur realized that putrefaction, like fermentation, was caused by microbes and that life takes part in the process of death. Microbes facilitate the cycle of life by making available to the living the nutrients tied up in dead organisms, including sulfur compounds that contribute to the smell of decay. From the onset of his work with wine-producing grapes, Pasteur realized its potential medical benefits and that the germ theory of the diseases applied to those of the human body as well as to those of grapes. Pasteur then correlated the presence of an unwanted microbe, *Bacillus anthracis*, with anthrax and *Streptococcus pyogenes* with septicemia and puerperal (childbed) fever. While Robert Koch, a country doctor who worked in his home laboratory and won the Nobel Prize for Physiology or Medicine for his work in 1905, extended Pasteur's germ theory to other diseases, such as tuberculosis and cholera, Pasteur went on to develop vaccines, including those for rabies, anthrax, and cholera, which plagued both humans and animals. Pasteur, along with Ignaz Semmelweis, Joseph Lister, and Robert Koch, also saw the importance of simple measures and insisted that physicians should wash their hands between performing autopsies and delivering babies. Not being constrained by any artificial boundaries, Pasteur's mind's eye could see the future of medicine, not in a crystal ball, but in a crystal of tartrate.

As a third example of how a highly focused study can provide fundamental insights into biology as a whole, consider the work of Moser and colleagues (1992). In this study, the rates of electron transfer determined in a number of biological and synthetic systems were compared with the standard electron transport rates predicted by the theories of Marcus (1956) and Jortner (1976). The conceptual basis of this study rests on the theoretical predictions that electron transfer depends on three fundamental properties of the system in which the electron transfer occurs: the edge-to-edge distance between the electron donor and acceptor (d), the free energy difference associated with the electron transfer process (ΔG), and the energy associated with the reorganization of the medium in which the electron transfer occurs (λ). Marcus (1956) predicted that for any given value of d, the maximum rate of electron transfer occurs when $\Delta G = \lambda$—that is, when the free energy released by the electron transfer exactly matches the free energy change induced in the environment by the electron transfer. Early support for Marcus's theory came from Gunner and Dutton's 1989 study of electron transfer rates in isolated photosynthetic reaction center complexes, in which the native electron acceptors were replaced by structurally related compounds in order to alter the $\Delta G°$ of the reaction while keeping λ, which is a characteristic of the protein environment in which the electron transfer occurs, and d constant. Moser and colleagues (1992) went on to generalize this same type of analysis to a number of different biological and synthetic electron transfer systems. Their analysis revealed that, for each of the biological electron transfers they examined, the values of $\Delta G°$ and λ were equivalent, which resulted in the maximal rate of electron transfer for that reaction. In other words, for any given distance between an electron donor and acceptor in a protein, evolution had tweaked the characteristics of the protein environment of this electron transfer to maximize the rate of the reaction. From an evolutionary perspective, the rates of electron transfer reactions are important because they contribute to the efficiency of the reaction—in particular, by minimizing the contribution of competing, nonproductive reactions. Because electron transfers underlie the fundamental cellular reactions of biological energy transformations, the importance of optimizing these reactions is clear. Although Moser and colleagues' 1992 paper was written for the specialist, its authors wrote as generalists, as is evidenced by the following quotation:

> Natural selection has shaped the present form of electron-transport proteins by applying the engineering principles we have outlined.… This biological "blueprint" sketches the central features of the function of some of the most important electron-transport systems in nature and clarifies the design requirements for the construction of analogous systems in the laboratory. (p. 802)

It should not escape attention that the formulation of the modern evolutionary synthesis was the result of the collaboration of diverse specialists (e.g., the geneticist Theodosius Dobzhansky, the ornithologist Ernst Mayr, the paleontologist George G. Simpson, the botanist G. Ledyard Stebbins), all of whom adopted a global evolutionary perspective intended to be all inclusive. This enterprise was stimulated in part by the development of population genetics by Ronald A. Fisher, John B. S. Haldane, and Sewall Wright, among others, between 1918 and 1932. However, it required the collaboration of numerous specialists to resolve many—if not all—of the conceptual and theoretical problems resulting from the high degree of specialization and feeble lines of communication among biologists in the early part of the twentieth century (Mayr 1982, Smocovitis 1996). The modern synthesis attempted to unify all of the biological sciences and illustrates the tremendous importance of training scientists to see how their research fits into the bigger picture.

Cultivating the specialist–generalist

The following quotation illustrates the importance of focusing on specific problems (the mindset of the specialist) and the importance of seeing how each solution fits into the grander scheme of things (the mindset of the generalist).

> More subtle, but also more lasting for those who know enough to see them, are two beautiful aspects of life: its unity and its diversity. (Dobzhansky 1964, p. 114)

The achievements of Darwin, Pasteur, and others show that these two mindsets are not mutually exclusive and that both need to be cultivated and rewarded. The specialist is needed to expand the body of knowledge within a discipline; the generalist is needed to synthesize newly gained knowledge and to integrate it with previous knowledge. In this way, students need not learn all of the details of biology but should, rather, come away from courses with an understanding of the interrelationships that are integrated in modern biology and with the ability to think critically about and to apply biological information to relevant questions, particularly to questions that are outside the scope of topics covered in courses.

But how do we accomplish this? How do we train students so that they become specialist–generalists? More generally, how do we reunite the biological sciences?

This last question motivated the American Association for the Advancement of Science, the National Science Foundation, and other stakeholders in the training of future biologists to publish a call for the transformation of undergraduate biology education (Brewer and Smith 2011). In response to this effort, four biological core domains were identified in a report developed by the National Research Council (NRC) Board on Science Education (NRC 2012). These domains are that from molecules to organisms, ecosystems, heredity, and biological evolution. Brewer and Smith (2011) also contains a chapter in which seven fundamental concepts spanning all of science are identified. These are patterns; cause and effect; scale, proportion, and quantity; systems and system models; energy and matter, structure and function, and stability and change.

The NRC (2012) report is an important first step, because it provides a model with which to reunify the biological sciences. However, to paraphrase the mathematician Samuel Karlin, who made fundamental contributions to both game theory and biomolecular sequence analysis, the purpose of a model is not to fit the available data but to sharpen our questions. Will the model developed by the NRC Board on Science Education cultivate the specialist–generalist? We believe that the answer is *not necessarily*. In our experience, introductory biology courses teach most if not all of the four biological core domains and the seven crosscutting concepts, but they typically lack an integrated approach. Blood circulation in animals is taught in one lecture, water movement in plants is taught in another lecture, and the underlying cellular processes that drive both are taught in yet another. The NRC model is a list of concepts that should be taught, but it provides no model for how these concepts can be integrated; the breadth of concepts does not translate into conceptual synthesis. Therefore, the critical issue is how to teach biology. Recognizing core concepts is an important first step, but it is equally important to effectively communicate these concepts in an integrated way. The model that most generally describes the undergraduate and graduate educational experience is one in which the breadth of science is introduced early on, but as training proceeds, the educational experience becomes more specialized. However, our understanding and appreciation of how biology is unified (i.e., how fundamental biological concepts articulate with one another) is typically not taught in the classroom. Rather, it is gleaned through practical experience and self-discovery outside the classroom or, more commonly, in a research environment, when the ability to truly understand information demands an integrative perspective. Recent studies in science education and cognition have emphasized the benefits of shifting this integrative experience to coincide with the breadth of the introductory biology experience (e.g., NRC 2003). We need to teach biology in the context of the process of science, with an overarching understanding that learning should start with generalities that provide the context to understand all of the details that are learned subsequently.

Training teachers how to teach is not an easy task, and, in our experience, there are equally effective teachers who have very different styles. If the three of us were asked to give the same lecture, it is probable that some of our students would not even recognize that our lectures dealt with the same topic. Therefore, we believe that there is no single formulaic way to teach any subject, but we also earnestly believe that every attempt to teach biology must emphasize how core biological concepts are interrelated, not just with each other but also with the other sciences. Fluid transport in animals, plants, fungi, and bacteria is a single concept, and it cannot be taught effectively without drawing on the concepts of cohesion, adhesion, bulk flow, and passive diffusion. It is equally ineffective to teach energy flow in plants, animals, microbes, or entire ecosystems without drawing on the concepts of chemistry and physics and using the tools of mathematics (Nobel 2005, Wayne 2009, Niklas and Spatz 2012).

It is unlikely that all biologists will agree with the core domains in biology identified in the NRC (2012) report or with the seven crosscutting concepts in science (Brewer and Smith 2011). So, what should we all agree on? We should accept that biology is unified in theory by its fundamental concepts but fragmented in practice, because the interrelationships among these concepts are often not actively pursued. We should accept that the degree of specialization will likely intensify as the depth of our scientific knowledge grows, but we should also accept the need to train students to have an integrative perspective that makes them think globally early in their academic experience and to continually appreciate the importance of this perspective as they become specialists. We must train our students to be enthusiastic generalists first and specialists second, so that they can achieve a new (and truly all-inclusive) modern synthesis.

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