Conveying the intellectual challenge of ecology: an historical perspective

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The roots of ecology are historically extremely diverse, with contributions from many fields of science. A sampling of ways of thinking ecologically, ranging from the early 19th to the early 20th century, reveals the richness of ecological science. By examining historical examples from biogeography, natural history, the science of energy, and biomedical sciences, we can appreciate the many different contexts in which ecological thinking has evolved, whether as part of larger projects to systematize and unify knowledge of the world, or in response to particular problems that were solved by taking a fresh approach. It is important, when educating students and the public, to convey this diversity of ecological thought and the nature of ecology as an integrative discipline.

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Ecologists have long endeavored to improve ecological literacy. This goal goes beyond informing students about environmental issues: one must excite their interest in ecological science, regardless of whether or not they intend to pursue the more advanced technical and mathematical education that modern ecology requires (Golley 1998). The challenge is to motivate people to tackle difficult ecological problems. Fifty years ago, G Evelyn Hutchinson (1953) observed that, while students did not hesitate to dive into complicated activities concerned with "electronic amplifiers and with the explosive combustion of hydrocarbons", they traditionally viewed the majority of complex activities as boring duties. "What we have to do", Hutchinson wrote, "is to show by example that a very large number of diversified, complicated, and often extremely difficult constructive activities are capable of giving enormous pleasure". The kind of pleasure that Hutchinson was thinking of involved the formulation of theory, discovery, and problem-solving. Repairing the biosphere and the human societies within it, he believed, ought to be as much fun as repairing the family car. While people today are better informed about environmental problems , engaging students in ecological research and conveying what ecology is about to the public is still challenging because of the complexity of the science.

In a nutshell:

- Historical examples illustrate some of the key features that constitute ecological ways of thinking, which combine general theory, logical argument, and an understanding of how environmental and historical context affects the behavior of organisms and the distribution of species
- Ecological thinking, with its roots in the quantitative ideals of Newtonian science, has helped to elucidate the broad cycles of matter and energy that govern systems
- Solving problems in evolutionary biology, epidemiology, and biomedicine have depended on adopting an ecological perspective
- Awakening students to the intellectual challenge of ecological research and teaching them to integrate knowledge from different fields begins by exposing them to diverse forms of creative ecological thinking across the spectrum of the life sciences

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I will draw on historical examples to illustrate ways of thinking that are characteristic of an ecological approach to the study of nature. My list is by no means complete. I touch only lightly on the classics of the ecological canon, which are discussed elsewhere (Real and Brown 1991; Keller and Golley 2000). Instead, I include some lesser known examples from medical science to highlight different contexts in which thinking ecologically has been important. Students should appreciate that this kind of thinking integrates methods derived from many fields of science and has a particular perspective that has evolved over decades of careful observation and thought. They may not realize, for instance, that ecology has roots in Newtonian science, or that some ecologists esteem Louis Pasteur because of his ability to think ecologically. This article offers a sampling of different forms of problem solving, starting with the prehistory of ecology in the 19th century, to illustrate a few of the key components of that perspective and some of the important generalizations that have resulted from thinking ecologically. The components highlighted here are: (1) the drive for a general theory or unifying worldview, culminating in the concept of the ecosystem; (2) the discovery of the role of history in explaining species diversity and distribution; (3) the discovery of the complexity of species relationships; (4) the application of logico-mathematical arguments as heuristic devices (rules of thumb or guidelines that do not guarantee optimal solutions); and (5) the recognition that how organisms behave is dependent on context.

Scientific natural history

Ecology in the early 20th century was often described as "scientific natural history" (Elton 1927). Although that definition now seems old-fashioned, such a description remains useful in that it reminds us of how innovative it once was to combine natural history and science (or, as it was then called, natural philosophy). Ecological thinking emerged in the early 19th century, at the intersection of natural history and natural philosophy. The expression "natural history" meant the description of nature (primarily taxonomy), while "natural philosophy" generally referred to the elucidation of the laws of nature. Natural history was transformed in the early 19th century by making it also a "philosophical" inquiry – that is, a search for the laws of the history and distribution of species and, within the science of anatomy, a search for the laws of structure (Rehbock 1983). The term "scientific natural history" denotes this important intellectual transformation, which set the stage for the development of ecological science later that century.

Behind this transformation was the authority of Newtonian science. In the 18th and early 19th centuries, under the impetus of scientists such as Antoine Lavoisier (1743–1794) and Pierre-Simon Laplace (1749–1827), Newtonian ideals of exact science were extended into chemistry, the life sciences, and even into social science (Hankins 1985). Analytic reasoning and precise measurement were the hallmarks of these advances. Here we can locate one of the fathers of ecology, Alexander Humboldt (1769–1859), a Prussian mining official, explorer, and naturalist who, inspired by Lavoisier's achievements in chemistry, conceived of a new science, "terrestrial physics", which unified various branches of the earth sciences and biogeography (Figure 1). Humboldt, although sometimes thought of as a Romantic natural philosopher because of his interest in poetry and aesthetics, drew inspiration from Newtonian science, especially as developed in the Parisian school of Lavoisier and Laplace (Dettelbach 1996). Stimulated by Lavoisier's reform of chemistry, Humboldt envisioned a new type of naturalist as "physicist". Merging natural philosophy with natural history meant that within natural history the search for unifying laws of nature and the use of quantitative methods and mathematical analysis became criteria of good science. Humboldt was a stickler for collecting exact numerical data, but the larger goal was to understand how order, or a state of equilibrium, was obtained from the interplay of conflicting forces. His ability to extend Newtonian principles into new subjects demonstrated the possibilities of developing "scientific natural history" and stimulated the later generation of scientists who became the first ecologists (Nicolson 1996). Humboldt also incorporated aesthetic elements into his popular works. Science was meant to awaken a sense of awe, for contemplating nature was a deep source of pleasure, much like the experience of seeing a great work of art (Humboldt 1850).

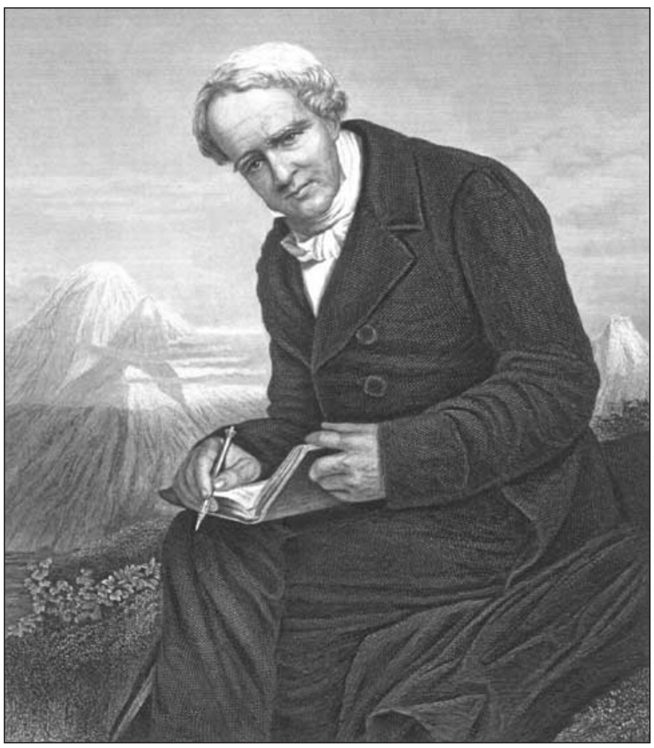

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Figure 1. *Humboldt's concept of a new science of terrestrial physics stimulated the later development of ecology.*

Among Humboldt's admirers was Charles Darwin (1809–1882), who added a crucial dimension to ecological thinking by arguing that knowing the relationships of organisms with each other and to their environment helps to explain how adaptations arise and how species are created from other species. Darwin's world travels as a young man made him into an ecological thinker, in part because his experiences contradicted his naive expectations, causing him to look at nature with fresh eyes. Disarmingly simple observations often had far-reaching significance. In *The Origin of Species*, Darwin used the distribution of species on the Galápagos archipelago as crucial evidence against the idea that species were independently created (Darwin 1964). The Galápagos Islands exhibited an unexpected pattern that stimulated Darwin to reflect on the causes underlying the distribution of species (Darwin 1964). He expected that species would be closely adapted to their physical environments, so that similar environments would have similar species. But the species on the Galápagos Islands showed affinities to those located on the adjacent coast of South America, between 500 and 600 miles distant. Not only the land birds, but also other animals and plants bore the "unmistakeable stamp of the American continent". Yet the islands were quite different in their climate and conditions of life from South America. In fact, these islands physically resembled the Cape Verde archipelago off the coast of Africa, which the Beagle had visited earlier (Figure 2). Despite the geological similarity of the two island groups, Darwin exclaimed, "what an entire and absolute difference in their inhabitants!" (Darwin 1964).

Figure 2. *Despite the physical resemblance of the Galápagos Islands to the Cape Verde Islands off the coast of Africa, the inhabitants of the two island groups were completely different. Noting the difference, Darwin realized the importance of the history of migration as an explanation of species distribution.*

The history of species migration and colonization was key to understanding why species inhabited certain regions. Competition among the islands' inhabitants would also crucially determine their success, he believed. Darwin concluded that naturalists were wrong to emphasize the physical conditions of a country as the most important for its inhabitants. They had not appreciated either the significance of competitive relations or the crucial role of history in determining the distribution of species. Ocean islands, Darwin realized, provided excellent testing grounds for his evolutionary hypothesis. For Darwin, the discovery of the importance of history helped him to understand that species were not specially created, but evolved. Modern ecology similarly seeks a balance between explanations based on history, that is, on particular sequences of contingent events and regularly acting causes that occur more predictably. The role of rare and possibly even unique events in shaping the earth's history has received more attention in the past three or four decades, the most celebrated example being the link made between a major asteroid impact and the extinction of dinosaurs (Alvarez 1997). In teasing out the relationship between pattern and process, ecology recognizes two different ways of thinking about processes, the challenge being to understand their relationship (Wilson 1992; Ricklefs and Schluter 1993). The importance of understanding the role of history in the formation of ecological systems lies in realizing that it might not be possible to reconstruct a system that has been seriously altered: nature will not automatically "bounce back" and return to its original state.

Darwin realized that nature's patterns arose from the activities of organisms connected to each other in myriad ways, each dependent on many others for survival. Tracing the chain of relationships could lead to surprising conclusions. Why were there more bees in areas close to villages? Because village cats killed the field mice that otherwise destroyed the combs and nests of bumble bees. In a more complicated chain of connections, Darwin noted the interdependence of cattle, parasitic flies, insectivorous birds, and vegetation in parts of South America that he had visited, creating a chain of reactions "in ever-increasing circles of complexity". Darwin was also fascinated to discover that the grazing habits of cattle on the English heath completely prevented forests from being established (Figure 3). Peering between the heath stems, he found little trees kept down by browsing, one of which he judged by its rings to be 26 years old. When the land was enclosed to prevent common access for grazing, it was quickly covered with vigorous young firs (Darwin 1964).

Ecological thinking involves an awareness of the chains of connection between species. While these relationships are both direct and indirect, the indirect effects may only be discovered after painstaking research (Wootton 1996). Darwin's brief examples were meant to stimulate others to make more exact inquiries, and from these measurements, censuses, and experiments the science of ecology took form. His descriptions of these chains also reveal an important stimulus to ecological study: human transformation of lands. With the enclosure of common lands, ending traditions of land use extending back into the Middle Ages, an unintended but impressive ecological experiment unfolded quickly as heath turned to forest. Every act of colonization around the world introduced new species into landscapes, while agricultural entrepreneurs exploited the variation of domesticated animals and plants to create new forms for human benefit and amusement. The world was rapidly changing in front of Darwin's eyes, changes which both provoked his curiosity and shaped his ideas about evolution; they also prompted interest in what would later be called ecology. The more humans changed the world, the more necessary it became to probe the operations of nature, understand exactly what those human effects were, and learn how to better control and predict their impacts. Ecology was the scientific response to the transformations underway in the age of empire and industry.

The search for a unified worldview

Darwin described his theory of evolution using the metaphorical term "natural selection", which expressed the idea that some individuals were better equipped to survive the struggle for existence than others. John Herschel reportedly dismissed Darwin's theory as the "law of higgledy-piggledy" (Ruse 1979, 248–49), expressing the difficulty that many physicists had in understanding

Figure 3. The ability of large herbivores to suppress the growth of forests intrigued Darwin and remains an important subject of ecological research.

Darwin's concept of selection. Some of the greatest scientists of the time, including William Thomson (Lord Kelvin) and James Clerk Maxwell, did not accept Darwin's mechanism of evolution, for both scientific and religious reasons. They could not grasp how the historical process of descent and modification that Darwin postulated could produce what looked like directed change over time.

These physicists did, however, contribute to ecological thinking, albeit inadvertently, by formulating the first and second laws of thermodynamics in the mid-19th century: the law of conservation of energy and the principle that energy is degraded through its transformations, being converted eventually to heat and becoming unavailable to do work. The science of energy, developed by William Thomson and other physicists and engineers in Britain, and by Hermann von Helmholtz in Germany, provided unifying laws that brought together physics, chemistry, and biology (Smith 1998). The unification of worldview that Humboldt sought was completed in the new science of energy, which taught that, like a great engine, the world system was driven by transformations of energy derived from the sun. In popularizations of these ideas, the relevance of an energetic viewpoint for understanding the nature of the world, its history, and the relationship between organisms and environment was perceived (Youmans 1873).

The ecological articulation of this kind of thinking would wait for 20th-century thinkers such as Vladimir Vernadsky, G Evelyn Hutchinson, Arthur Tansley, Raymond Lindeman, Eugene Odum and others, who developed our understanding of biogeochemical cycles and the concept of the ecosystem (Hagen 1992; Golley 1993). The feedback loops created by the cycling of matter and transformation of energy were seen to underlie the ecological systems that sustain our world. The development of the ecosystem concept was an outgrowth of decades of ecological study and increased emphasis on the quantitative measurement of these exchanges. Starting especially with the work of Eugene Odum (1913–2002) in the 1950s, these ideas shaped and invigorated the discipline of ecology after the Second World War. In remembering how long it took to articulate the ecosystem concept, we should appreciate what an important act of intellectual creativity it was to conceive of the ecosystem in abstract terms as the cycling of matter and flow of energy. Apart from one rather idiosyncratic analysis of the "great world engine" in energetic terms published in the 1920s by Alfred J Lotka (1924), who was trained in physical chemistry, it was not obvious that ecological relations should be analyzed in terms of energy flow. The relationship of thermodynamics to ecology is now considered fundamental (Pielou 2001; Jørgensen 2002), but such was not the case prior to the 1940s.

Logical argument as a route to knowledge

Critics of Darwin's theory also complained of its circularity. If evolution occurs by survival of the fittest, and those that survive are automatically deemed to have been the fittest, then are we merely asserting that organisms that can't live, die? Darwin's great insight into how evolution occurs is not, in fact, captured in this simple tautology. We must assume that in many instances survival occurs because the organism possesses some advantage over its competitors, and in looking for that advantage we are led to a deeper understanding of the complexity of ecological relationships. The point, as Darwin emphasized, is that we do not know in advance exactly what favored one organism over another: the observation of differential survival and reproduction stimulates us to look more deeply into nature for an answer. This was one of Darwin's most important general lessons: naturalists who believed they understood a great deal about the world were in truth highly ignorant and needed to return to the study of nature with sharper questions and a finer level of analysis. From these sharper questions the science of ecology was created.

Scientific reasoning involves the creative use of logical arguments. As Sir Harold Jeffreys (1937) argued in his analysis of scientific inference, the trick is to use such arguments to provide new knowledge and not be caught in empty circularity. G Evelyn Hutchinson (1903–1991) saw how Jeffreys' ideas might apply to ecological problems. Hutchinson (1965) considered the study of the influence of the environment on evolution to be one of the central concerns of ecology. He was interested in the Darwinian problem of how closely related species lived together in the world, which led to his formalization of the concept of the ecological niche. Towards the end of his career, concerned about criticism that this type of argument was not scientific, Hutchinson explained its creative potential. Hutchinson (1978) pointed out that arguments such as the principle of competitive exclusion are logico-mathematical theories, derived from a set of postulates about the external world. Such arguments cannot be verified in an absolute sense, but they can be falsified. If similar species do live together, this observation, apparently falsifying the competitive exclusion principle, suggests that a closer investigation should be made of how they manage to do so. A number of alternative hypotheses might be proposed, such as niche separation, frequency-dependent competition, or the effects of predation, and these can be investigated in particular cases. Hutchinson explained that the use of logical arguments is to uncover possibilities about what might occur in the world; the next step is to uncover whether these possibilities occur in nature.

Logico-mathematical arguments are also useful when trying to explain a theory to an audience that is reluctant to accept it. Sir Ronald Ross (1857–1932) discussed one example of this educational function in the early 20th century. Ross had worked out the biological basis of the transmission of malaria by tracing the complicated life cycle of the malarial plasmodium, which is transmitted to humans by anopheline mosquitoes (Figure 4), discoveries for which he was awarded the Nobel Prize in medicine in 1902. However, Ross found that many people rejected his explanation because they could not see a causal connection between the incidence of malaria in humans and the presence of mosquitoes. People did not believe that eradicating mosquitoes could lower the incidence of malaria.

Ross faced three obstacles: common prejudice against his thesis, lack of quantitative information about mosquito populations and rates of infection, and poorly designed field experiments that were unable to validate his thesis. Not having time to collect data or conduct rigorous experiments, and knowing the importance of acting on the malaria problem immediately, Ross developed his argument logically and supported it by mathematical calculations to persuade people that he was correct about the relationship between mosquito populations and malaria (Ross 1905, 1911, 1923). He dubbed his method the "Theory of Happenings", a label meant to suggest the wide applicability of his method not just to epidemiology but to other areas of public health, demography, evolution, and even commerce and politics. His problem statement was the inverse of arguments later used in ecology

Courtesy of J Gathany

Figure 4. *Ronald Ross used mathematical arguments to persuade a skeptical public of the connection between malaria and the abundance of anopheline mosquitoes, making him one of the earliest contributors to theoretical population ecology.*

to investigate the design of nature reserves; whereas an ecologist would now ask what size, shape, or configuration of land would best protect a species from extinction (Williams *et al.* 2004), Ross asked what size and configuration of land would best ensure that a disease-carrying insect would remain rare or absent from a region where eradication measures were enforced.

The importance of context

Hutchinson observed that the evolutionary play occurs in an ecological theater, or to put it less poetically, organisms behave in a way that is dependent on context. René Jules Dubos (1901–1982), the noted microbiologist and environmentalist, described how understanding the importance of context led him to an important discovery early in his career. Dubos is known for his work on microbial diseases and the development of antibiotics, but also wrote extensively on environmental issues from a humanistic standpoint, and gave us the maxim "think globally, act locally" (Dubos 1980). Despite spending most of his career in a medical environment, Dubos was trained as an agronomist and was influenced by the work of Russian soil scientist Sergei Vinogradskii in the 1920s (Ackert 2004). Dubos was impressed by Vinogradskii's insistence that microbiologists were making a serious mistake by studying microbes in artificial laboratory cultures rather than in their natural environments, because they did not behave "naturally" in artificial environments (Piel and Segerberg 1990). While admitting the practical difficulty of trying to investigate the complex natural environment, Dubos appreciated the wisdom of this key ecological idea. His doctoral research compared the ability of different organisms to decompose cellulose in soil under different environmental conditions (Dubos 1928).

Dubos took a postdoctoral position with Oswald T. Avery at the Rockefeller Institute for Medical Research, now Rockefeller University. Avery's group was working on the chemistry and immunological properties of pneu-

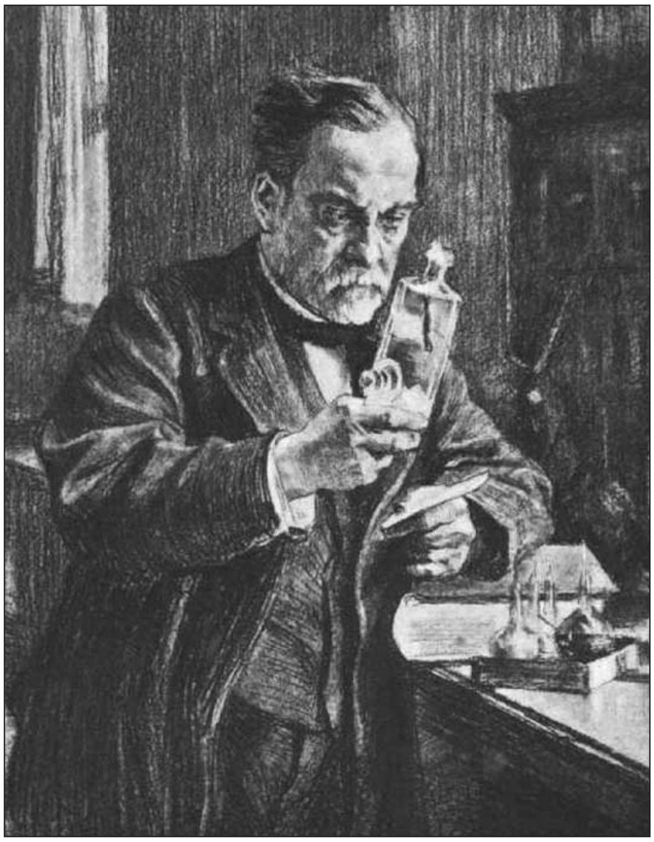

Figure 5. *Louis Pasteur's ecological approach to the study of microbes was emulated by René Dubos, who found that bacterial metabolism depended on the environmental context.*

monia-causing bacteria. The virulence of one type of pneumococcus was known to be due to a protective sugar coating, which prevented white blood cells from destroying the bacteria. Dubos' project was to find an enzyme that would destroy the sugar capsule surrounding the pneumococcus. He reasoned that there must exist in nature microorganisms that could attack the sugar. From samples of soil and sewage, he found a bacterial culture in which the polysaccharide was decomposed and then isolated the bacterium that decomposed the sugar. Separating the enzyme with which it accomplished the task was the final step.

At this point, Dubos departed from standard laboratory methods and instead took an ecological perspective on the problem. When he cultured the bacterium in the enrichment medium normally used by bacteriologists, it grew abundantly but did not produce the enzyme needed. Instead, the enzyme was only produced when the bacterium was struggling in a poor medium that contained only the capsular polysaccharide. Dubos was able to isolate the enzyme because, contrary to the advice of his colleagues, he insisted on growing the bacterium only in a weak solution of the polysaccharide. This discovery, he wrote, brought him face to face with one of the most interesting biological principles he had ever seen, namely that cells have multiple potentialities and these operate only when the cell is placed in an environment where it is compelled to use them (Piel and Segerberg 1990). A Finnish scientist, H Karström, simultaneously discovered the same phenomenon and gave the name "adaptive enzymes" to these proteins that were produced only when the organism needed them for survival. That microorganisms changed their enzymatic constitution in response to the environment led Dubos to realize that such responses were important in determining the nature of infectious diseases.

Dubos' scientific model was Louis Pasteur (1822–1895) (Figure 5), originator of the germ theory of disease and of fermentation, which related chemical processes and diseases to specific types of microbes. Dubos argued that Pasteur's great achievements stemmed from an ecological view of life and his intuitive understanding that microbes had crucial roles to play in the economy of nature (Piel and Segerberg 1990). Microbes were the great recyclers of the chemical substances of the world; their role is still recognized as an important and imperfectly understood aspect of global processes (Post *et al.* 1990). Pasteur also recognized that the environment had a determining influence on the morphology and chemical activities of microbial species. Dubos believed that Pasteur's greatness as a scientist, as illustrated especially in his studies of fermentation and putrefaction, were consequences of his sophisticated ecological understanding that the functions of bacteria varied, depending on the environment. Dubos emulated the ecological thinking of Pasteur and Vinogradksii, which he believed was critically important for relating the science of bacterial metabolism and physiology to the understanding of infectious processes (Dubos 1954). This form of reasoning is especially important for understanding diseases such as cholera, for instance, where the bacterium causing the disease inhabits both aquatic environments and the human intestine, behaving differently in each environment (Cottingham *et al.* 2003).

■ Ecology as an integrative science

These problems and ways of thinking were consolidated into the modern discipline of ecology as scientists came to realize that ecology provided an approach to problems that distinguished it from other disciplines. As Eugene Odum (1977) argued a quarter of a century ago, the various ways of thinking ecologically must be integrated in order to solve society's problems. Students also need to be taught to integrate knowledge, following the models of people like Humboldt, Darwin, and Pasteur, three of the greatest scientists of the 19th century. The first step is to convey what it means to think ecologically about a problem and what scientists have gained from this perspective. These examples show how ecology relates to, and arises from, different realms of scientific thought across the spectrum, from Newtonian science to natural history, to biomedical science. Nor should we forget that ecology also tells a story about the beauty of the world.

Ecological thinking, in its various guises, does not happen automatically or easily; it is the product of two centuries of scientific thought and investigation on many fronts. It requires considerable sophistication and breadth of knowledge. One can scarcely imagine a better way to develop students' intellectual abilities to their highest level than by mastering the different perspectives and methods involved in ecology. Students may not easily grasp the essential ingredients of ecological thinking from modern textbooks, which plunge them quickly into complex topics. By stepping back to gain a more general view, one can convey some of the characteristics that underlie ecological thinking and show how they can be applied in fields outside ecology – they are just as important for students aiming for careers in medicine, engineering, or the social sciences, for instance.

Modern ecology encompasses intellectual approaches across a spectrum ranging from analytic and reductionist to synthetic and holistic (Pickett *et al.* 1994; Jørgensen 2002). This diversity makes ecology hard to define as a science, but is not surprising in a science that seeks to understand the entire biosphere. Ecologists have to consider problems on very different scales, over short and long terms, and to alter their perspectives depending on the kinds of problems they are investigating. Hutchinson, for example, recognized that population ecology and ecosystem ecology required very different perspectives, yet he considered them to be aspects of one science (Hutchinson 1978). Ecologists also have to explore the dynamism of our world under difficult circumstances, when information is missing, when controlled experiments are difficult to arrange, and when random events introduce uncertainty into calculations even in the best of times.

Given its difficulty, ecology could be considered a quixotic undertaking that has prevailed, despite a culture that favors molecular biology. It has done so because it has unveiled a subtle understanding of how ecological systems function and how we benefit from nature (Wilson 1992; Daily 1997; Levin 1999; Beattie and Ehrlich 2001). Ecological thinking has led to two of the most important general conclusions of modern biology, namely the understanding of how biological diversity arises, and of how ecological systems are regulated by cycles of matter and flows of energy. Ecological science has imbued us with a sense of urgency in responding to the global changes wrought by our own hands, but it also shows us what kind of creative thinking is needed to come up with solutions.

If one were to poll the members of the Ecological Society of America and ask them to cite one or two favorite examples of creative ecological thinking, no doubt a great diversity of views would be offered and there might well be disagreement as to the validity of some choices. The danger in a very complicated subject like this is that disagreements about how to do science can become so sharp that whole areas of research are dismissed. Hutchinson feared that this was happening when he defended the use of logico-mathematical arguments in ecology. The challenge is to integrate diverse ways of thinking, so that they can be seen as mutually reinforcing and not mutually exclusive. By conveying this diversity and range of thought in a positive light, ecologists can open students' minds to the challenges and rewards of ecological study and also help the public to understand the nature of the science and its accomplishments.

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References

Ackert LT. 2004. From the thermodynamics of life to ecological microbiology: Sergei Vinogradskii and the cycle of life, 1850–1950 (PhD dissertation). Baltimore: Johns Hopkins University.

Alvarez W. 1997. *T. rex* and the crater of doom. Princeton, NJ: Princeton University Press.

Beattie A and Ehrlich P. 2001. Wild solutions: how diversity is money in the bank. New Haven, CT: Yale University Press.

Cottingham KL, Chiavelli DA, and Taylor RK. 2003. Environmental microbe and human pathogen: the ecology and microbiology of *Vibrio cholerae*. *Front Ecol Environ* **1**: 80–86.

Daily GC (Ed). 1997. Nature's services: societal dependence on natural ecosystems. Washington, DC: Island Press.

Darwin C. 1964. On the origin of species, a facsimile of the first edition. Cambridge, MA: Harvard University Press.

Dettelbach M. 1996. Humboldtian science. In: Jardine N, Secord JA, and Spary EC (Eds). Cultures of natural history. Cambridge, UK: Cambridge University Press.

Dubos RJ. 1928. Influence of environmental conditions on the activities of cellulose decomposing organisms in the soil. *Ecology* 9: 12–27.

Dubos RJ. 1954. Biochemical determinants of microbial diseases. Cambridge, MA: Harvard University Press.

Dubos RJ. 1980. The wooing of earth. New York: Charles Scribner's Sons.

Elton CS. 1927. Animal ecology. London: Sidgwick and Jackson.

Golley FB. 1993. A history of the ecosystem concept in ecology: more than the sum of the parts. New Haven, CT: Yale University Press.

Golley FB. 1998. A primer for environmental literacy. New Haven, CT: Yale University Press.

Hagen JB. 1992. An entangled bank: the origins of ecosystem ecology. New Brunswick, NJ: Rutgers University Press.

Hankins TL. 1985. Science and the enlightenment. Cambridge, UK: Cambridge University Press.

Hutchinson GE. 1953. On living in the biosphere. In: Hutchinson GE. The itinerant ivory tower: scientific and literary essays. New Haven, CT: Yale University Press.

Hutchinson GE. 1965. The ecological theater and the evolutionary play. New Haven, CT: Yale University Press.

Hutchinson GE. 1978. An introduction to population ecology. New Haven, CT: Yale University Press.

Humboldt A. 1850. Views of nature: or, contemplations on the sublime phenomena of creation; with scientific illustrations, 3rd edn. London: Henry G. Bohn.

Jeffreys H. 1937. Scientific inference, 2nd edn. Cambridge, UK: Cambridge University Press.

Jørgensen SV. 2002. Integration of ecosystem theories: a pattern,

3rd edn. Dordrecht, Germany: Kluwer Academic Publishers.
Keller DR and Golley FB (Eds). 2000. The philosophy of ecology: from science to synthesis. Athens, GA: University of Georgia Press.
Levin S. 1999. Fragile dominion: complexity and the commons. Reading, MA: Perseus Books.
Lotka AJ. 1924. Elements of physical biology. Baltimore: Williams and Wilkins.
Nicolson M. 1996. Humboldtian plant geography after Humboldt: the link to ecology. *Brit J Hist Sci* **29**: 289–310.
Odum EP. 1977. The emergence of ecology as a new integrative discipline. *Science* **195**: 1289–93.
Pickett STA, Kolasa J, and Jones CG. 1994. Ecological understanding: the nature of theory and the theory of nature. San Diego: Academic Press.
Piel G and Segerberg O. 1990. The world of René Dubos: a collection from his writings. New York: Henry Holt.
Pielou EC. 2001. The energy of nature. Chicago: University of Chicago Press.
Post WM, Peng TH, Emanuel WR, *et al.* 1990. The global carbon cycle. *Amer Sci* **78**: 310–26.
Real LA and Brown JH (Eds). 1991. Foundations of ecology: classic papers with commentaries. Chicago: University of Chicago Press.
Rehbock PF. 1983. The philosophical naturalists: themes in early nineteenth-century British biology. Madison, WI: University of Wisconsin Press.
Ricklefs RE and Schluter D (Eds). 1993. Species diversity in ecological communities: historical and geographical perspectives. Chicago: University of Chicago Press.
Ross R. 1905. The logical basis of the sanitary policy of mosquito reduction. *Science* **22**: 689–99.
Ross R. 1911. Some quantitative studies in epidemiology. *Nature* **87**: 466–67.
Ross R. 1923. Memoirs, with a full account of the great malaria problem and its solution. London: John Murray.
Ruse M. 1979. The Darwinian revolution: science red in tooth and claw. Chicago: University of Chicago Press.
Smith C. 1998. The science of energy: a cultural history of energy physics in Victorian Britain. Chicago: University of Chicago Press.
Williams JC, ReVelle CS, and Levin SA. 2004. Using mathematical optimization models to design nature reserves. *Front Ecol Environ* **2**: 98–105.
Wilson EO. 1992. The diversity of life. Cambridge, MA: Harvard University Press.
Wootton JT. 1996. The nature and consequences of indirect effects in ecological communities. *Annu Rev Ecol Syst* **25**: 443–66.
Youmans EL (Ed). 1873. The correlation and conservation of forces: a series of expositions. New York: D Appleton.

