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Source: BioScience, 53(2) : 185

Published By: American Institute of Biological Sciences

URL: https://doi.org/10.1641/0006-3568(2003)053[0185:NT]2.0.CO;2

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Microbial Actors in the Evolutionary Drama

Liaisons of Life: From Hornworts to Hippos, How the Unassuming Microbe Has Driven Evolution. Tom Wakeford. Wiley, New York, 2001. 212 pp. $24.95 (ISBN 0471399728 cloth).

Wakeford hiked the fens and watched insects on the waters amongst the woodlands and dairy farms of northern England before his migration, at the age of 16, to Cambridge University in search of a formal education in evolutionary biology. From the beginning, "the orthodox story of life evolving via chance mutations and competitive struggles" (p. 18) never sat well with the naturalist–writer. Indeed, our author found himself "at the bottom of a huge reading list on mathematical modeling" that seemed to ignore all microbiologically informed work. Even the definitive experiments of someone as important as Sir Vincent Wigglesworth were overlooked. Before Wakeford was born, Wigglesworth, in 1952, had shown how sterilized fly eggs died if their food (onions) was deprived of its normal bacilli associates. A teaspoonful of soil contains 10,000 genetically different types of bacteria. Bacteria swim, photosynthesize, and respire not only oxygen but also sulfate and nitrate. They alone convert refractory nitrogen of the air into delectable and useful food components. Why, Wakeford puzzled, did none of the metabolic virtuosities of bacteria and other microbes (e.g., protists and yeast) ever appear in any of his assigned readings in evolutionary biology? Why was the physiological need of flies for their live bacilli not mentioned?

The perspective that helped to develop the ideas of this book was greatly enhanced by a year's course of study in the philosophy and history of science. Now a professional prize-winning writer and biologist at the University of Sussex in England, Wakeford, on completion of his undergraduate degree, took a doctorate at the University of York, where he worked directly with microbial symbioses in the field and the laboratory. This experience, along with an insatiable reading habit, lively conversations, and study at the Marine Biological Laboratory at Woods Hole, Massachusetts, and at the National Centre for Biological Sciences in Bangalore, India, led Wakeford to the thesis of his narrative. The basic idea of *Liaisons of Life* is that microbes are "fundamental to the origin, evolution and current function of every creature we encounter."

These small but complete organisms are best visualized through microscopic analysis in their physical associations with one another and with larger forms of life. From the hornwort, a moss-like plant, to the algae-infested corals of the tropical oceans and fungi-intertwined roots of forest trees, and from the languid hippo to all other mammals, subvisible microbial associations abound. The microbes have silently changed the course of evolutionary history.

One of Wakeford's admirably achieved goals is to explain why, from the 19th-century works of Charles Darwin and Louis Pasteur until now, the microbial world has been ignored in nearly all evolutionary writings. He relates the scientific discoveries to the times and places in which they were made. He shows especially clearly the profound influence of Pasteur's imagery of the "loathsome bacterial mob" and his incessant "war on germs." To this day Pasteur's legacy colors our cultural view of microbiology. Wakeford notes how the study of symbioses "fell afoul of global politics: world wars, nationalism, and anticommunism, to name a few" (p. 17). Symbiosis, as Wakeford claims, was fatally bracketed in



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the minds of its enemies with dangerous political movements.

> Nor did it help that the pioneers in this field were largely from non-English-speaking countries such as France, Germany and prerevolutionary Russia. In the wake of the carnage of World War I and the new threat from the Soviet Union, symbiosis was condemned by mainstream science as a political subversion that could provide explanations neither for humanity's apparent lust for conflict nor for the evolutionary patterns of life. Symbiosis became an international pariah subject, the victim of tacit textbook censorship and McCarthy-like witch-hunts among professional scientists. (p. 17)

I suspect that Wakeford is too impassioned here. He attributes too much to willful maligning of symbiosis research and too little to ordinary belief–system inertia and ignorance. The tide is turning. Protein and nucleic acid sequence studies, cytoplasm transmission genetics, and electron microscopy have all contributed to rising waves of understanding. We now realize that symbiosis is a major source of evolutionary innovation and that microbes are active and incessant agents of evolutionary change. Better that Wakeford were more accurate in his details and less preachy. Nevertheless, it is indisputable that here he has done teachers, students, and the public the fine service of interpretation of facts from disparate sources. By teasing out a fascinating narrative from a jargon-filled, stilted, and obscurantist literature, Wakeford presents the reader, in accessible language, compelling and well-supported evidence for the role of the microbe in the 4000-million-year history of life on Earth.

Scientific papers that concurred with and extended observations of Simon Schwendener (ca. 1870) garnered much evidence that lichens were not plants. The superb naturalist and artist Beatrix Potter had, in the late 1890s, prepared detailed studies, including beautiful watercolor plates, of many British lichens. Indeed, no lichen was a plant—the more she observed, the surer she became that lichens were "dual organisms": a green partner in intimate contact with a fungal associate in each case examined. Though Potter is famous today as the author of the popular and charming Peter Rabbit series of children's books, few know the story Wakeford tells of her thwarted career as a scientific investigator. Not only was her work ridiculed and rejected by the botanists of the day (e.g., Reverend Leighton in his classic book *The Lichen-Flora of Great Britain, Ireland and the Channel Islands* [1871] wrote, "I have purposely omitted any mention of the Schwendenerian Theory of Lichens, as I cannot but regard it as purely imaginary, the baseless fabric of a vision," and well-known naturalist Reverend James Crombie mused, "A useful and invigorating parasitism—who ever before heard of such a thing?"). As a woman, Potter was even refused entry to the open sessions of the Linnean Society, Burlington House, London, where these issues were routinely discussed. In the end, in 1897, her influential and favorite uncle, the chemist Sir Henry Roscoe, was permitted to read her paper for her. The manuscript itself was lost and not until a century later, in 1997, did Potter receive an official—of course, posthumous— apology from that venerable society for its treatment of her undoubtedly correct Schwendenerist analyses of lichens. The term *Schwendenerist* was one of serious abuse: It mocked not only those who claimed that lichens were not plants but any who took seriously the importance of symbiosis in physiology, taxonomy, and evolution. Botanist M. C. Cooke wrote in 1879 that "even if endorsed by the nineteenth century," such ludicrous symbiotic ideals "will certainly be forgotten in the twentieth."

Of course, the main point of Wakeford's well-written book is how wrong Cooke has been shown to be. All 20th- and 21st-century lichenologists are today Schwendenerists, since all of the 14,000 documented species of lichens are at least "dual." None are plants. Schwendenerism, the 19th-century term that labeled and dismissed the concept of the central importance of symbiosis, especially microbial symbiosis, in the evolutionary history of life, has been replaced in the 21st century by symbiogenesis. Symbiosis, à la Anton de Bary, the distinguished botanist, is an ecological idea, the protracted physical contact between organisms of different species, whereas symbiogenesis, the origin of new organisms, organs, tissues, or behavior traits as a consequence of long-term symbiosis, is an evolutionary term. What Wakeford's book shows is the ascendancy of ideas, facts, natural history observations, and molecular biological proofs of the importance of symbiosis as an impetus to evolutionary innovation relative to the sterile anthropocentric rhetoric of neodarwinism.

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ROLL OVER, ADAM SMITH: THE "NEW ECONOMY OF NATURE" OVERLOOKS THE ORIGINS OF MONEY

The New Economy of Nature: The Quest to Make Conservation Profitable. Gretchen C. Daily and Katherine Ellison, eds. Island Press, Washington, DC, 2001. 260 pp. $25.00 (ISBN 1559639458 cloth).

Gretchen Daily and Katherine Ellison are affiliated with Stanford University, where Daily is an interdisciplinary scientist and Ellison a consulting writer. Daily edited *Nature's Services: Societal Dependence on Natural Ecosystems,* an excellent book on the economic importance of ecological integrity. Her teaming with Ellison portends great science writing, as evidenced by their fascinating chapter on pollinators, and their ultimate goal with *The New Economy of Nature* is a noble one: sustainability. Their means to that goal is expressed in the subtitle, *The Quest to Make Conservation Profitable.* The book is enjoyable, owing

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to its easygoing prose. Unfortunately, the authors may have gone on a wild goose chase, joining a lengthening list of sustainability writers who have focused too much on "natural capitalism" to be prudent. Adam Smith would have pinpointed the problem; I'll do my best to "channel."

First, however, a brief overview of contents: The prologue describes a shortcoming in economic policy, namely, the failure to account for natural capital and ecological services (such as pollination and flood control) in the measurement of economic welfare. Daily and Ellison inform us that this is changing, however. "Ecosystem assets have the importance of water and are gradually acquiring the scarcity of diamonds as the human population and its aspirations grow" (p. 11). With that combination of importance and scarcity, every economist this side of Alfred Marshall would say the time is ripe to ascertain the monetary value of these assets and to demand compensation in the market when such assets are liquidated. The rest of the book is about developing this "natural capitalism."

Daily and Ellison toured the world to talk with academics, entrepreneurs, politicians, and various combinations thereof. Adam Smith probably began rolling in his grave at their first stop (Katoomba, New South Wales), where the notion of a "carbon market" was discussed. In the simplest scenario, carbon credits with monetary value would accrue to polluters who lowered carbon emissions or would be acquired from other polluters who lowered carbon emissions. Thus we have incentives for polluters to behave better. In a slightly more complex market, credits could also accrue to whoever plants trees, which then sequester carbon. So far, so good, but then Daily and Ellison suggest, "Some of the billions of dollars generated by the carbon market...might find their way to reforestation of degraded land." Here I imagine Smith huffing, "Generated? What does this mean—generated?!" But let's finish the overview.

The tour includes places like sprawling Seattle, scenic Costa Rica, and wild Amazonia. In New York, where clean water was at stake, the city invested in natural capital by acquiring and preserving portions of its watershed rather than investing in manufactured capital (i.e., water filtration plants) because it was cheaper, thus illustrating how accounting for natural capital may result in conservation. It seems a reasonable point, though Marc Sagoff has already thrown cold water on the story (see "On the Value of Natural Ecosystems," *Politics and the Life Sciences* 21: 19–25).

Town leaders in Napa, California, finally convinced the Army Corps of Engineers to let the river run more naturally, thus providing services such as flood control, fishing, and aesthetic pleasure. All this "had lured developers eager to fill the riverfront with big hotels" (p. 107), leaving us to ponder the net conservation effect.

The pondering continues after a passage about Sydney, Australia, where Daily and Ellison visited a workshop on potential international trade in carbon rights. The primary attendees were exuberant entrepreneurs who embarked upon a catered cruise. "For three hours, as the yacht passed the city's famed opera house and then drifted by immaculate suburban mansions and the gleaming, futuristic downtown, white-jacketed waiters circulated with wine, champagne, and plates of barbecued octopus, lamb, and shrimp. The next evening, after the lectures, the special guests were whisked away on a luxury bus to Lilianfels, where more comforts awaited in the form of cocktails, feather beds, gourmet jelly beans, and two types of chocolate mousse" (p. 30). Daily and Ellison failed to note the irony of this "conservation" cruise and the socioeconomic unsustainability it symbolized.

In Australia (but not on the yacht) they also ran into Jim Shields. As friends, roommates, and graduate students in wildlife science at the University of Washington in the 1980s, Shields and I loved the field but were concerned enough about conservation to engage the political economy of conservation. When Daily and Ellison found Shields, he was presenting his concept of the biodiversity credit, or "bio." They do not clearly explain how the bio would function in the market, but Shields personalized it for me a few years ago. Using analogical terms from my book *Shoveling Fuel for a Runaway Train* (in which the runaway train is the economy and the shovelers are conspicuous consumers), he said, "Think of it as shoveling fuel into the back of the train." According to my old friend, if consumers shovel (buy) the right fuel (bios), it will slow the runaway train (the economy) rather than speed it up. I hope he is right, but it doesn't seem probable, for reasons to be presented shortly. In any event, there is no real market for bios (or carbon credits). Such a "market" may only be foisted into existence, much like the regulatory regime it is intended to obviate.

Like Shields, Daily and Ellison seem to think that, as long as enough shoveling occurs in the back of the train, the rampant shoveling in the front of the train can be counterbalanced. As long as there is enough expenditure on conservation, in other words, the expenditures on nonconservation won't be so destructive, and cumulative expenditure can continue to rise. Adam Smith rolls, because there is no attention paid to what the shovel digs up—that is, where the money comes from.

In *The Wealth of Nations,* published in 1776, Adam Smith ushered in the age of capitalism with observations on the division of labor and the origins of money, without which no market (the matrix of capitalism) would exist. Smith had been to France and studied the *Tableau Economique* (François Quesnay's prototypical model of economic production), and he knew it was agricultural surplus that freed the hands for the division of labor and the exchanging of money. Were it not for agricultural surplus, everyone would be preoccupied with sowing and reaping, and money would be meaningless. The more agricultural surplus, the greater the division of labor and the more money to be spent. Smith's observations resonate with ecological trophic theory, in which it takes plants (producers) to have plant consumers, and plant consumers to have predators. Without the producers serving as the foundation, there is no economy of nature, old or new.

Recall that Daily and Ellison spoke of a carbon market "generating" money.

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Adam Smith rolled because the generation (origins) of money is agricultural or extractive surplus, not the foisting of carbon credits into a far-from-free market. In other words, the human economy is founded upon the liquidation of natural capital. The division of labor and the generation of money for carbon sequestration, ecotourism, and bios are possible only in proportion to that liquidation.

In the 1990s I worked on the San Carlos Apache Reservation, home of the biggest elk in the world. (Jim Shields even helped with an elk survey once.) The tribe sold some elk tags to nontribal members, with the revenue earmarked for habitat improvement. One year we sold three tags for $43,000 apiece. Two of them went to the owner of the largest old-growth sawmill in the Northwest, and I always wondered how many acres of old-growth trees were cleared to *generate* the money for the hunt.

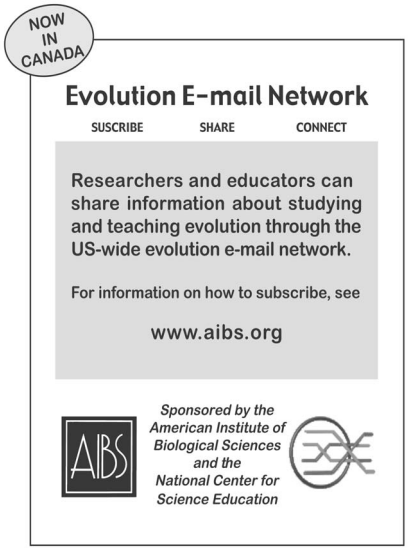
Finding ways to make things cost more is not the solution, because it ultimately puts more pressure on the agricultural and extractive sectors to produce more surplus to generate more money. Nowhere is this clearer than on page 112, where Daily and Ellison describe the result of a sustainable forestry initiative: "To avoid building new roads into the old-growth areas, [Weyerhaeuser] had turned to extracting one tree at a time by helicopter, with 250-foot grapples. As a result, the timber harvest had dropped to a tiny fraction of what [MacMillan Bloedel] had collected before 1993, and costs had skyrocketed." In other words, the logging was much less efficient and the amount of natural capital liquidated elsewhere to purchase a unit of this timber skyrocketed. The book is loaded with such zero-sum examples, especially pertaining to ecotourism.

Daily and Ellison fail to build upon the outstanding foundation of ecological macroeconomics developed over the past few decades. In the United States, two major themes in ecological economics have been economic scale and natural capital accounting, with clear leadership provided by Herman Daly and Robert Costanza, respectively. Neither is mentioned in the text. The lack of reference to Costanza (except for once in a very poorly stocked bibliography) is especially surprising, given his role in developing the concept of natural capital valuation.

The fatal flaw, however, is ignoring Herman Daly's steady-state economics, which would have provided the appropriate macroeconomic framework. Incredibly, while they note the problem of increasing population and consumption, Daily and Ellison never use the phrase "economic growth" (the growing product of population and per capita consumption), missing the opportunity to connect directly to the biggest table in the policy arena. The closest they come to an explicit reference to economic growth is "the scale of the human enterprise" (p. 22). They allude to the issue a few other times, yet the allusions are elusive and illusory. They seem to say, "The increasing scale of the human economy is problematic, but now that resources are becoming scarce enough to be priced in the market, firms can make money on those resources too, so that there will be more ways to make money even as we conserve more natural capital." Roll over, Adam Smith.

For those with a background in ecological macroeconomics, *The Economy of Nature* should be a helpful book. It has a nice style—clear and conversational—and provides real-world examples of natural capital valuation and marketing. Without that background, however, I think it has (along with an increasing number of natural capitalism books) the potential to misguide students and policymakers, especially when they are already heavily exposed to "win–win" political rhetoric about reconciling economic growth with environmental protection.

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LIFE HISTORY: A SYNTHESIS

Life History Evolution. Derek A. Roff. Sinauer Associates, Sunderland, MA, 2001. 527 pp., illus. $54.95 (ISBN 0878937560 paper).

Derek Roff is one of the foremost authorities in life history, with a scholarly output that includes both theoretical and empirical work in population ecology and evolution. This is his second book about life history (the first was *The Evolution of Life Histories,* Chapman and Hall, 1992). In addition, he published *Evolutionary Quantitative Genetics* (Chapman and Hall, 1997), inspired in part by the quantitative genetics chapter from his 1992 book. Roff's latest contribution to our understanding of life history is *Life History Evolution.* This book is an impressive synthesis of the theory and empirical work of the last several decades, and it is an important addition to our understanding of the evolution of the diverse developmental and reproductive patterns found in the natural world.

As in his earlier book on life history evolution, Roff begins the present book with a short overview of quantitative genetics, which includes the derivation of some central models. He then moves into the heart of the book, starting with a discussion of biological tradeoffs. This general discussion of tradeoffs is followed by three chapters on life history evolution, one each for constant, stochastic, and predictable environments. With an exceedingly broad approach involving models and concepts from often discon-

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nected regions of population biology, Roff makes many insightful connections, such as the relevance of game theory models of frequency-dependent selection in life history evolution. His concluding chapter, rather than being a review of topics covered (he concludes each chapter with a review), is a list of 20 topics for future research that he views as particularly important for advancing our understanding of the evolution of life histories.

In each chapter, Roff begins with a presentation of the genetic and optimization models relevant to the central topics. Following the presentation of the principal models is a careful presentation of the empirical research bearing on either the assumptions or the predictions of the models. Presentation of the literature and the links between the theory and the empirical data (when such exist) is the strongest part of the book. Especially enlightening were the occasional discussions of experimental methods that ought to be followed, with examples of studies that fell into or avoided the pitfalls. The recognition and discussion of problems with controls in brood manipulations (e.g., pp. 134–138) is an example of Roff at his best. Strikingly, he shows no taxonomic bias in the data chosen; they come from field and laboratory studies of a wide range of organisms, both botanical and zoological.

My main criticisms of the book concern the detail of the mathematical presentations and the editing. First, although the author states that his aim is to keep the mathematical derivations to a minimum, a very large number of derivations are presented. Deriving so many models that are available to the reader in their original papers, rather than presenting just the assumptions and predictions of each, often overwhelms the "nonmathematical" reader (to use the author's own term from the preface) with mathematical detail. One simple addition could have made the book easier to read: inclusion of a list of symbols and their use (symbols are not listed in the index) at the end of the book or at the end of each chapter. Interestingly, the sixth chapter does include tables of symbols for many of the central models. The failure to include such tables for the bulk of the book drove this reader to try to construct one, and in the process I found that some symbols have multiple meanings. This is trivial when the meaning is explicitly stated, and understandable because Roff was sticking as closely as possible to the original notations. However, symbol meanings are not always explicitly stated with each use, which leads to problems in the presentation of some models.

The book also suffers from poor organization and editing. The structure of the central three chapters risks losing the attention of less dedicated readers. Of the 465 pages of text, the central three chapters make up 66 percent. The fourth chapter alone has 136 pages, including many long mathematical derivations; it covers diverse topics such as the generation and maintenance of genetic variation, evolution of the individual components of life history, evolution of tradeoffs among life history components, and evolution of differences among species. Admittedly, there is an aesthetic appeal to a series of chapters entitled "Evolution in Constant Environments," "Evolution in Stochastic Environments," and "Evolution in Predictable Environments" (chapters 4, 5, and 6, respectively). However,

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subdivision of these chapters (particularly the fourth) would have made reading a less daunting task. There are also a large number of editorial errors both in the text and in the mathematical equations. Although many of the errors are trivial, some of them interfere with understanding and, in a few cases, result in erroneous or incomprehensible presentation of data or research protocols.

These problems may reflect the small number of readers before publication: Only three readers are acknowledged in the preface, and presumably all were colleagues familiar with the subjects covered. Having a larger number of readers—perhaps including some "nonmathematical" biologists—might have resulted in a text more approachable to a wider range of biologists. I suspect that the detailed presentation of a large number of models and empirical research may limit this book's readership to students of life history and may reduce the number of readers who work through the book in its entirety. This is a pity, because the discussions of the assumptions, conclusions, and empirical support for the various models would benefit a much broader range of population biologists, students, and professionals.

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NEW TITLES

A Color Atlas of Pests of Ornamental Trees, Shrubs, and Flowers. David V. Alford. Timber Press, Portland, OR, 2003. 448 pp., illus. $59.95 (ISBN 0881925616 cloth).

Firefly Encyclopedia of Reptiles and Amphibians. Tim Halliday and Kraig Adler, eds. Firefly Books, Toronto, Canada, 2002. 270 pp., illus. $40.00 (ISBN 1552976130 cloth).

Human Ecology: Following Nature's Lead. Frederick Steiner. Island Press, Washington, DC, 2002. 237 pp., illus. $25.00 (ISBN 1559639954 cloth).

Human Molecular Biology: An Introduction to the Molecular Basis of Health and Disease. Richard J. Epstein. Cambridge University Press, Cambridge, UK, 2002. 623 pp., illus. $60.00 (ISBN 052164481X paper).

An Introduction to Arthropod Pest Control. J. R. M. Thacker. Cambridge University Press, New York, 2002. 343 pp., illus. $30.00 (ISBN 0521567874 paper).

Invoking the Spirit: Religion and Spirituality in the Quest for a Sustainable World. Gary Gardner. Worldwatch Institute, Washington, DC, 2002. 62 pp. $5.00 (available at *www.worldwatch.org).*

Plant Growth and Development: Hormones and Environment. Lalit M. Srivastava. Academic Press, San Diego, 2002. 772 pp., illus. $89.95 (ISBN 012660570X cloth).

Protein Physics: A Course of Lectures. Alexei Finkelstein and Oleg Ptitsyn. Academic Press, San Diego, 2002. 354 pp., illus. $80.00 (ISBN 0122567811 cloth).

Why We See What We Do: An Empirical Theory of Vision. Dale Purves and R. Beau Lotto. Sinauer Associates, Sunderland, MA, 2003. 260 pp, illus. $42.95 (ISBN 0878937528 paper).



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