BioQUEST Notes

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Items Of Special Interest In This Issue:

Darwin and Wallace at Burlington House

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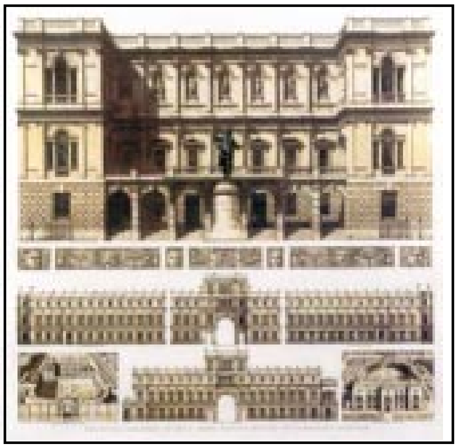

Royal Academy of Arts, Burlington House (1997), etching by Andrew Ingamells,
http://www.artcontact.co.uk/contemporayart.html

The theory of evolution by natural selection, co-founded by Charles Darwin and Alfred Russel Wallace, was announced to the world at a meeting of the Linnean Society held at Burlington House in Piccadilly on 1 July 1858, and published in the Society's Journal on 20 August of that year (Darwin and Wallace, 1858). Neither Darwin, who was home at Down House in Kent, nor Wallace, who was collecting in the Malay Archipelago, were present. Darwin provided a much fuller account of the theory the following year in *On the Origin of Species* (Darwin, 1859), and went on to write several more books, each of which may be considered an elaboration or application of

continued on page 10

Biocomplexity: A Definition Under Development

Robin McC. Greenler
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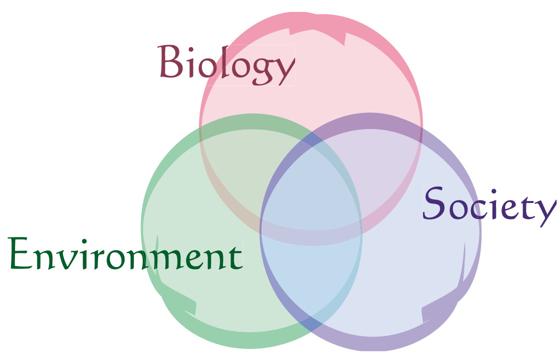
There is a lot of buzz about biocomplexity. The National Science Foundation (NSF) has identified biocomplexity as a priority area for research and education. The theme of the 2001 Annual Meeting of the American Institute of Biological Sciences (AIBS) was *From Biodiversity to Biocomplexity*. However, despite the attention,

continued on page 5

2002 BioQUEST Summer Workshop

From Hard Data to Hard Decisions: Biocomplexity in Undergraduate Education



Beloit College **June 15-24**

http://www.bioquest.org/biocomplexity

For more on this workshop, see page 4

BioQUEST Presentations and Representation

Where We've Been:

November

- The International History, Philosophy, and Science Teaching Organization (IHPST), *Using the Nature of Evolutionary Inquiry as a Guide for Curriculum Development*, Denver, CO
- Quality Undergraduate Education (QUE), *Biology Education Cluster leader,* Atlanta, GA
- *In silico* Biology conference, Georgia Tech, Atlanta, GA

December

- American Society for Cell Biology (ASCB), *Cell Biology Education Editorial Board*, Washington, DC

January

- National Research Council (NRC), *Biology 2010 presenter*, Washington, DC

February

- American Association for the Advancement of Science (AAAS) Annual Meeting, Boston, MA

March

- National Partnership for Advanced Computational Infrastructure (NPACI) All-Hands Meeting, *Dynamic Interactions between Biological, Environmental and Human Systems: Biocomplexity Education*, San Diego, CA
- American Institute of Biological Sciences (AIBS), Research and Education in Evolution, http://www.aibs.org/, Washington, DC
- National Science Teachers Association (NSTA), http://www.nsta.org/, San Diego, CA
- Projects on Design Experiments in Education, http://gse.gmu.edu/research/de/index.html, George Mason University, Santa Fe, NM
- NIH-NSF Panel on Math and Computers in Biology Education, policy meeting, Washington, DC

Where We're Going:

April

- NARST (National Association for Research in Science Teaching), April 7-10, New Orleans, LA
- Girls and Women in Science, April 12-13, Beloit College, Beloit, WI
- National Research Council, *Implementing Case-Based Learning*, April 12-13, Center for Biology Education, University of Wisconsin-Madison, Madison, WI
- National Research Council, Biology 2010 and Biocomplexity Education, April 14-16, Baltimore, MD
- Using Data in Classrooms, April 21-23, Carlton College
- National Research Council, Committee on Undergraduate Science Education, April 21-23, Washington, DC
- National Conference on Undergraduate Research, April 25-27, University of Wisconsin-Whitewater, Whitewater, WI

May

- Chautauqua Short Course, *Evolutionary Bioinformatics Education*, May 8-10, Clark Atlanta University, Atlanta, GA
- 9th ASM Undergraduate Microbiology Education Conference, *BioQUEST Workshop: Introducing Microbes Count!*, May 17-19, Salt Lake City, UT
- National Research Council, Bio2010, May 20-22, Washington, DC
- LifeLines OnLine Community College Faculty Workshop, *Investigative Case-Based Learning*, May 30-June 2, Southeast Missouri State, Cape Girardeau, MO

June

- Gordon Research Conference**,** Theoretical Biology & Mathematics**,** *Chair, Molecular Evolution Session*, June 9-14, Tilton School, NH
- Association for Biology Laboratory Education**,** June 11-15, Louisiana State University, Baton Rouge, LA
- BioQUEST Workshop, *From Hard Data to Hard Decisions: Biocomplexity in undergraduate education*, June 15-24, Beloit College, Beloit, WI
- Society for the Study of Evolution, *Chair, Education Committee*, June 27-July 1, University of Illinois at Champaign-Urbana, Champaign-Urbana, IL

July

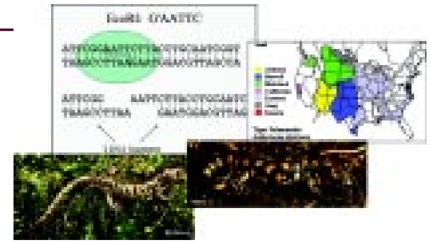
- Society for Mathematical Biology, *Chair, Education Symposium*, July 13-16, University of Tennessee at Knoxville, Knoxville, TN
- Biotechnology 2002 Educators Conference, July 17-20, Virginia Tech, Blacksburg, VA

August

- Botanical Society of America, *Of Cabbages and Kimchee: Investigative case-based learning activities from recipes gone wrong to real-time data acquisition and simulation*, August 4-8, University of Wisconsin-Madison, Madison, WI
- Ecological Society of America, *Biocomplexity in Undergraduate Education: From hard data to hard decisions*, August 4-9, Tucson, Arizona
- *Implementing Problem Solving Strategies: Investigative cases foriology and chemistr*y, Faculty Workshop, Emory University, August 12-16, Atlanta, GA

September

- ACUBE (Association of College and University Biology Educators), September 19-21, Columbia College, Chicago, IL



Have you thought about bringing bioinformatics into your biology classroom?

Interested in sharing an evolutionary perspective while analyzing molecular data?

Would you like to see instruction built around real biology problems and rich datasets?

If so, you should consider joining us for the
Chautauqua Short Course

Evolutionary Bioinformatics Education: A BioQUEST Curriculum Consortium Approach

May 8-10, 2002
Clark Atlanta University, Atlanta, Georgia

This short course, led by John R. Jungck and Sam Donovan, will focus on different ways that the analysis of molecular data is being applied to solve current biological problems in areas such as medicine, agriculture, conservation, and evolution. It will address the relationships between evolutionary theory and the analysis of molecular sequence and structure data. A wide range of sub-disciplines that use bioinformatic analyses will be drawn upon. The focus will be on learning about the causal bases for bioinformatic analyses along with a philosophy of education: problem-posing, problem-solving, and peer review/publication (BioQUEST's three Ps).

The laboratory sessions will deal with medical, cell biology, and conservation examples. The lectures will relate to:
• <u>Evolutionary bioinformatics</u>: Orthology, Paralogy, Xenology, Phylogenetic Probes, and Phylogenetic Profiling;
• <u>BioQUEST's curricular philosophy</u>: Problem Posing, Problem Solving, and Peer Review/Publication; and,
• <u>Theoretical, mathematical, and computational aspects that complicate bioinformatics</u>: homoplasies, computational complexity, numerous tree topologies, scoring multiple sequence alignments, long branch attraction problems, and rate variations.

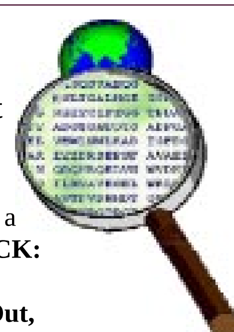
The discussions will focus on how to analyze data, how to implement bioinformatics investigations across the curriculum, and how to develop sustained collaboration.

The course is designed for any biologist who is interested in teaching with bioinformatics.

To apply, visit
<u>http://www.engr.pitt.edu/chautauqua/bioinformatics.html</u>

For more information, contact:
Sam Donovan, donovans@beloit.edu
John Jungck, jungck@beloit.edu

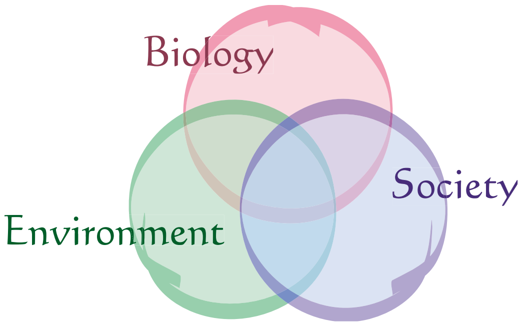
Starting June 1st... BioQUEST's New Bioinformatics Project



BioQUEST's efforts in bioinformatics education will soon be integrated under a new project titled, "**BEDROCK: Bioinformatics Education Dissemination - Reaching Out, Connecting, and Knitting together**". We are focusing on building a community of faculty interested in applying the analysis of molecular data on biological questions across the biology curriculum. The project resources will be available at <u>http://bioquest.org/bioinformatics</u>. Watch for more information in the next *BioQUEST Notes*.

2002 BioQUEST Summer Workshop

From Hard Data to Hard Decisions: Biocomplexity in undergraduate education



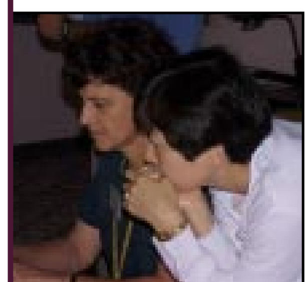
The BioQUEST Biocomplexity Project focuses on bringing the dynamics and richness of biocomplexity-related research into undergraduate learning.

Key goals of the 2002 BioQUEST workshop:

- Collaboratively develop a framework for biocomplexity education
- Create interdisciplinary, problem-solving materials for undergraduate classrooms
- Initiate ongoing collaborations in biocomplexity education

During the 2002 BioQUEST workshop we hope to explore biocomplexity in education through the application of:

- BioQUEST's problem solving approach
- Investigative, case-based learning
- Modeling
- Environmental monitoring
- Geographic information systems
- Bioinformatics
- Analysis of network accessible data
- Numerous software simulations



Featured presenters will include:

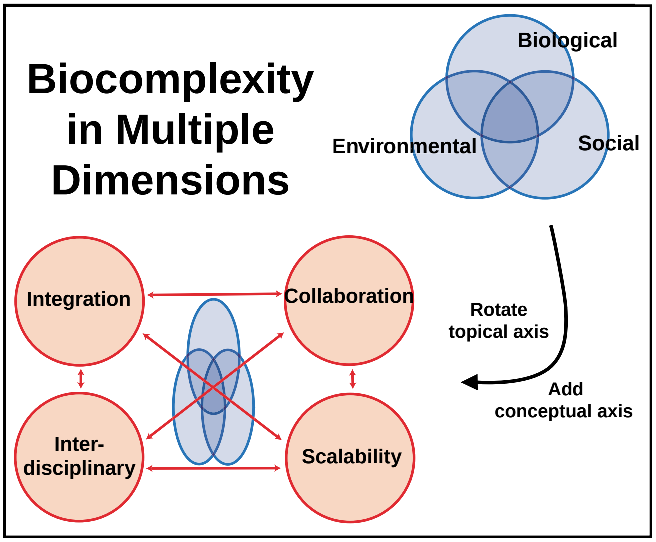
Dr. Louis J. Gross, Professor of Ecology and Evolutionary Biology and Mathematics and Director of The Institute for Environmental Modeling, University of Tennessee at Knoxville

Dr. Claudia Neuhauser, Professor of Ecology, Evolution and Behavior, University of Minnesota, and University of Minnesota Biocomplexity Project, NSF Biocomplexity Initiative

Dr. Peter Lockhart, Senior Research Fellow, Institute of Molecular Biosciences, Massey University, New Zealand

Dr. Peter Taylor, Professor in the Critical and Creative Thinking Program, University of Massachusetts, Boston

This workshop is funded by a grant from the Howard Hughes Medical Institute.



The multidisciplinary content areas of biocomplexity contain common characteristics that align well with goals in educational reform.

Biocomplexity *from page 1*

researchers in this nascent field are still struggling to articulate a concise and complete definition.

The fact that creating a robust definition of this new field has proven to be challenging does not come as a surprise. At its heart, biocomplexity represents the interplay of systems so intricate and dynamic that one individual may frequently comprehend only a part. If the sheer magnitude and complexity creates challenges in our perception, the translation of the concept to tight definition will, likewise, be difficult.

Nonetheless, the concept of biocomplexity has been and is continually being developed, refined, and clarified. Dr. Rita Colwell, director of the NSF and champion of the increased attention and funding to the area, defines the goals of biocomplexity as "understanding how components of the global ecosystem interact—biological, physical, chemical, and the human dimension—in order to gain knowledge of the complexity of the system and to derive fundamental principles from it" (Emmett, 2000). Dr. Colwell maintains that biocomplexity requires taking an integrative perspective across scales and disciplines that will allow us to tackle the intricacies of interactions among diverse disciplines (Colwell, 2001). Alan Covich, president of AIBS, underscores the need for such a biocomplex approach when he notes that, "examining the self-organization, hierarchical structure, and dynamics of communities and ecosystems over time and space requires new approaches and a new generation of nonlinear modeling, designed by collaborators in the natural, social, and computational sciences" (Covich, 2000).

The Ecological Society of America has produced a fact sheet on biocomplexity (http://esa.sdsc.edu/factsheetbiocomplexity.htm) wherein they further the discussion by listing common characteristics of biocomplexity that include:

- nonlinear or chaotic behavior
- interactions that span multiple levels or spatial and temporal scales
- hard to predict (unpredictable behavior)
- must be studied as a whole, as well as piece by piece
- relevant for all kinds of organisms — from microbes to human beings
- relevant for environments that range from frozen polar regions and volcanic vents to temperate forests and agricultural lands as well as the neighborhoods and industries of urban centers.

A research team enters the biocomplexity arena through many different doors. Some teams, responding to a call to address an urgent and complex environmental situation, assemble a broad-based, multidisciplinary team of scientists with the express goal of producing a clearer understanding of the system to decision makers. (And here "scientists" is used in its broadest sense and includes social scientists, engineers and mathematicians.) Other biocomplexity teams form through the linkage of several research programs that are examining common fundamental questions with vastly different systems, organisms, or temporal and spatial scales. Still other researchers find the contemporary label "biocomplexity" is being placed retroactively onto decades of prior ecological, environmental, policy or basic biological research. And indeed, several have pointed out that biocomplexity may be a term for "old wine in new bottles" (Maienschein, 2000).

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Biocomplexity in Education

- Addresses significant contemporary issues
- Requires collaboration, integration and an interdisciplinary approach
- Employs multiple modes of understanding and learning
- Engages students in a diversity of techniques and hands-on inquiry
- Allows for participation in contemporary scientific research (questions and results)

University of Minnesota Biocomplexity Project: http://www.entomology.umn.edu/biocomplexity/, **Corn Borer Lifecycle,** George Heimpel, University of Minnesota, Dept. of Entomology

Biocomplexity *from page 5*

As the field of biocomplexity emerges, it is becoming clear that it holds rich opportunities for education. Many biocomplexity research programs in the lab or field have education derivatives for the classroom. The nature of biocomplexity lends itself to rich pedagogical approaches and the nature of many of the research tools used are readily accessible in undergraduate classrooms. A productive route to deepening one's grasp of biocomplexity and its opportunities for education lies in the examination of case studies of active biocomplexity research. The following projects represent a few of the biocomplexity research areas within which BioQUEST sees great education potential and with which BioQUEST is beginning to collaborate.

University of Minnesota Biocomplexity Project

The University of Minnesota Biocomplexity Project is a collaboration of researchers who are analyzing and modeling the consequences of massive perturbation in biological communities. Tied together by this broad focus, they are bringing many areas of expertise to bear on the examination of the interactions of ecological, genetic and historical factors on spatially explicit, non-equilibrial systems. Four specific systems that they are currently examining include: Corn borer and Bt and non-Bt corn; prairie fragmentation and mating structure of native populations; Corn smut and corn; and Rhizobia associated with common bean.

The corn borer and Bt-corn team is examining the evolution of resistance to genetically engineered Bt-corn. In part they are investigating the dynamics of the policy-driven planting of non-Bt resistant corn refugia areas within Bt resistant corn fields. It is clear that the size and spacing of these refugia are important factors, and that natural predators of the corn borer can also play a critical role. The prairie fragmentation research group is examining the role of spatial habitat structure in the pollination and genetic transfer of certain plants native to North America's tallgrass prairies. The researchers are asking questions about the correlation between spatial characteristics of isolated populations and patterns of mating and progeny fitness. The corn smut team is exploring how the biogeographic history and spatial dynamics of corn (Zea mays) affects the population dynamics and evolution of corn smut (Ustilago maydis). The Rhizobia team is exploring the ecology and coevolution of host-Rhizobia relationships. The scope of their research covers both cultivated and wild native legume hosts and therefore looks at disturbances associated with agricultural cultivation as well as fragmented native ecosystems.

From the outside, each of these projects looks like a traditional, robust research program at a large university. What makes these different is that they are all linked with common questions. They can examine how issues of time and spatial scale may affect underlying ecological principles. They can look for small or large universalities between very different environmental systems or between strongly disparate organisms. The distinctions between the "pieces" and the "whole" become blurred as one collaborator's "whole" (corm smut) may be another's "piece." (Bt and non-Bt corn plants). This kind of research collaboration, knit together with a broad focus, is a prime example of one way that biocomplexity research can proceed.

ATLSS Project

The ATLSS Project (Across Tropic Level System Simulation) is asking some similar questions but in a wholly different context. The project, involving Dr. Louis J. Gross of the University of Tennessee is concerned about how to effectively create models of community-level ecological interactions that include individual variation in both organisms and local habitat.

The project is exploring how to best model the effects of various hydrologic regimes on the plant and animal life in the Everglades and Big Cypress Swamp of South Florida.

continued on next page

Biocomplexity

from page 6

While water flow controls the trophic dynamics of the system, there are complex patterns of spatial heterogeneity and temporal variability within the system. As the trophic interactions occur at varying spatial and temporal scales, the use of a single modeling approach to predict impacts of hydrological change is inappropriate.

At higher trophic levels individual-based models that account for individual variation in factors such as sex, size, age, health, and social status and spatial variation such as habitat, roads, and topography are necessary in order to predict accurately the effects of various hydrologic scenarios. Lower trophic levels such as benthic insects, periphyton and zooplankton and functional groups of fish and macroinvertebrates need different modeling systems structured to their populations and life history characteristics. All these models are then integrated across the Everglades and Big Cypress Swamp landscape and coupled to GIS maps for cover type. With this data, one can more effectively assess the effects of alternative proposed hydrologic restoration scenarios on trophic structures.

The ATLSS team is driven by a concrete policy need. More accurate modeling regimes will provide policy makers the critical scientific information they need in order to make recommendations about scope, type and nature of the restoration efforts for the region. These recommendations will define the legal, economic and social implications of a large-scale land-use initiative. The research team is trying to characterize phenomena that are not consistent across spatial or temporal scales. The system must be studied from both a reductionist and integrationist perspective. This scenario would challenge the most traditional research approaches. The ALTAS program is responding to a policy need that will utilize whatever best research information is currently available. The task therefore is to integrate the information that has been gained from traditional research into the best contemporary understanding. This is often the challenge of biocomplexity—while the problem is too big to understand fully yet, the legal, economic, or environmental actions demand a synthesis of current best understanding.

The Gulf of Mexico and the Hypoxia Zone

Biocomplexity work by Dr. Nancy Rabalais of the Louisiana Universities Marine Consortium and Dr. R. Eugene Turner of Louisiana State University looks explicitly at the interactions of science and policy in the context of the Mississippi River and hypoxia zone in the Gulf of Mexico. Broad evidence over the past two decades has revealed strong and dynamic links between anoxia in the Gulf of Mexico and land use practices in the Mississippi watershed basin. Land use practices include watershed flood control and navigational channelization, landscape alterations (such as deforestation and conversion of wetlands to agricultural lands), and nitrogen input (Rabalais, et al., 2002).

Obviously these interactions cross temporal, spatial, political, and ecosystem boundaries. But perhaps less obvious to the public is the degree of interdisciplinarity necessary within the sciences. To examine this issue fully requires a remarkable collaboration of scientists from vastly different specialties. Parts of this analysis hinge on an understanding of hydrology, terrestrial and aquatic ecology, zoology and botany, as well as chemistry, geology, and environmental engineering.

In addition to the scientific complexity, the research involves a huge constituent of stakeholders, interacts with a vast body of legal regulation and has far-reaching economic implications. How does this expansive human policy arena interact productively with a growing and

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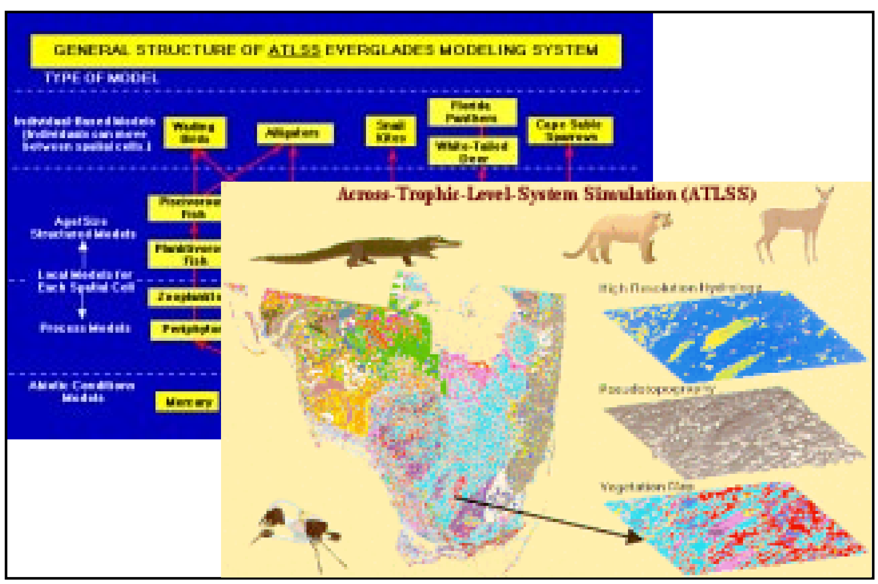
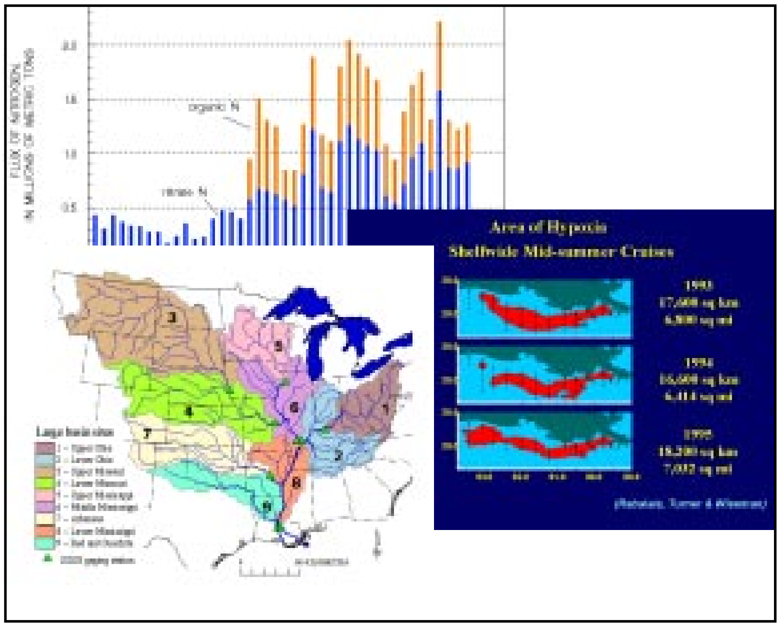


ATLSS Everglades Modeling System: www.atlss.org, **ATLSS Mutli-level Geographic Information System Model:** www.fcsc.usgs.gov/Ecosystem_Modeling

Biocomplexity *from page 7*

incomplete understanding of the science of the linked riverine-ocean system? These are exactly the questions being asked by Rabalais and her colleagues. The tremendous scope of the issue, the myriad of interactions, the need for a broad, informed and collaborative team of professionals and the urgency for practical, implementable solutions are all trademarks of this developing area called biocomplexity.

Clearly, there is a compelling need for biocomplexity research. The study of biocomplexity is computationally intensive and frequently includes modeling, spatial analysis and manipulation of data from large databases (genomic, climatological, environmental, etc.). Fortuitously, recent mathematical studies of complex phenomena and the current availability of powerful supercomputing capabilities are facilitating much of the work.



Mississippi Watershed, Basin and Subbasins: http://wwwrcolka.cr.usgs.gov/, **Nitrogen Inputs into Gulf of Mexico:** http://wwwrcolka.cr.usgs.gov/, **Hypoxia in the Gulf of Mexico:** http://www.csc.noaa.gov/products/gulfmex/html/rabalais.htm

While the synthesis of the field of biocomplexity is still young, we cannot afford to wait for the field to "settle" to begin to integrate this new paradigm of scientific research into undergraduate education. Too frequently we hesitate to bring new and leading-edge science into the classroom. However, if we want to produce citizens and scientists who can contribute practically and conceptually to the field of biocomplexity, we would be well advised to expose them now to the kind of synthetic, multidisciplinary, and computationally intensive approach typical in biocomplexity. If we wish to, as Rita Colwell put it, "develop a view of earth that is startlingly different from that of the past" (Colwell, 1998), then we must concurrently work with the scientists of the present and of the future. And it is with both scientists of the present and future that BioQUEST wants to begin.

References

Across Tropic Level System Simulation Biocomplexity Project, http://atlss.org/

Colwell, RA. 1998. Ecological science in the new millennium: A bold step into the next thousand years. Ecological Society of America NewSource 61: 2-3.

Colwell, RA. 2001. "World enough, and time": A global investment for the environment. Bioscience 51(11): 908-914.

Covich, A. 2000. Biocomplexity and the future: The need to unite disciplines. Bioscience 50(12): 1035.

Emmett, A. 2000. Biocomplexity: A new science for survival? The Scientist 14(19):1.

Gross, L. 1999. Computational Ecology. Ecological Society of America NewSource 65: 1-4.

Maienschein, J. 2000. Old wine in new bottles. Nature 407: 21.

Neuhauser, C. 2001. Mathematical challenges in spatial ecology. Notices of the AMS(48)11:1304-1314.

Rabalais, NN., Turner, RE., Scavia, D. 2002. Beyond science into policy: Gulf of Mexico hypoxia and the Mississippi River. Bioscience 52(2): 129-142.

University of Minnesota's Biocomplexity Project, http://www.entomology.umn.edu/biocomplexity/.

BioQUEST Library Volume VI

Purchasing Information

The BioQUEST Library Volume VI, distributed by Academic Press, contains over 75 software simulations, tools, datasets, and other supporting materials from many areas of biology. The Library package includes two CDs, one for Macintosh and one for Windows. Each CD contains all of the modules that will run on that platform. The documentation and other related information for all of the modules is available in electronic form on both CDs.

Volume VI can be purchased in packages for single or multiple users. Packages are available in three different sizes.

- An individual package for **1** user: $149.95 + tax
- A three package lab-pack: $295.00 + tax
  Valid for use by up to **3** individuals at the same time
- A ten package lab-pack: $695.00 + tax
  Valid for use by up to **20** (twenty) individuals at the same time

Networked or distributed learning users should make a good faith estimate of the maximum number of simultaneous users and buy the appropriate number of packages. Special licensing terms can be arranged for institutions with more than 60 simultaneous users. Users who previously purchased a site license for the Library are eligible for a special upgrade price.

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Contact Virginia Vaughan at vvaughan@hamilton.edu

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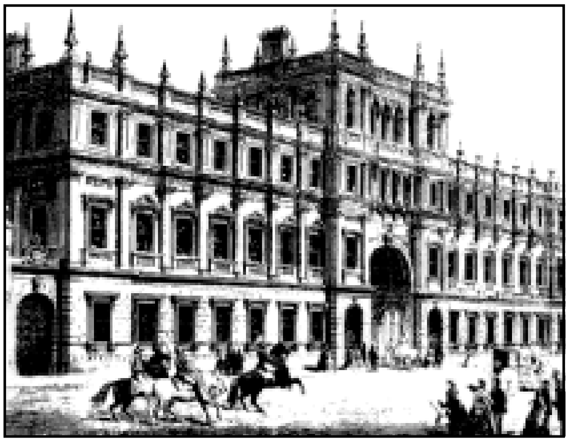
Darwin and Wallace

from page 1

the theory. Wallace remained in the East Indies until 1862. After returning to England he too wrote several books, the best known being his applications of evolution to zoogeography (Wallace 1876, 1880).



Burlington House, from Royal Society of Chemistry, http://www.rsc.org/members/bh_hist.htm

Although the theory at its inception was attributed to both men, it is usually associated primarily with the name of Darwin; indeed, even Wallace entitled one of his books *Darwinism* (1889), and always considered Darwin to be at least *primus interpares*. Some, however, have thought that Darwin's lion's share of the credit is undeserved, and that Wallace has been wronged, both by Darwin and by history (Brackman, 1980; Brooks, 1983; Quammen, 1996). The accusations against Darwin are that he 'stole' one or more ideas from Wallace, and that the circumstances of the reading and publication of the Linnean Society papers were somehow unethical. Although ostensibly arguing on Wallace's behalf, these authors must dismiss Wallace's own accounts (e.g. 1870, 1889, 1905) of the contributions made by Darwin and himself. In this essay I argue that these accusations are baseless, and that a fair reading of the historical evidence shows that the high and friendly regard (Kottler, 1985) in which the two men held each other throughout their lives was well deserved on both their parts.

What might Darwin have stolen from Wallace? The first suspect might be natural selection itself, but the historical evidence is overwhelming that this is not the case, as even Darwin's detractors would admit. It is worthwhile recounting some of this history, as it sets the context for later events. The following account draws on Mayr (1982), Kottler (1985), Bowler (1989), Desmond and Moore (1991), Browne (1995), Ruse (1999), and Raby (2001).

When Darwin returned from the *Beagle v*oyage in late 1836, he was not yet an evolutionist, but by mid-1837, when he began his first notebook on transmutation, he was. By late 1838, after considering a number of possibilities, he had come upon natural selection as the mechanism of transmutation, and he was to consider this the chief (though not exclusive) mechanism for the rest of his life. In 1842 he wrote a 35 page outline of his views which has come to be known as the *Sketch.* He elaborated this into a 230 page *Essay* (published, along with the *Sketch,* in 1909) in 1844. At this time he first revealed his theory of natural selection, showing the *Essay* to the botanist J.D. Hooker. The theory in the *Sketch* and the *Essay* is the same as that of the *Origin.* As Wallace had not yet published on the subject, Wallace had no influence on Darwin's formulation of natural selection.

Wallace's evolutionary history begins a few years after Darwin's return to England. He became a transmutationist in 1845 after reading Chambers' (1844) *Vestiges of the Natural History of Creation*. From 1848 to 1852, with the "species question" in mind, he conducted fieldwork in South America with Henry Bates. Setting out for the East Indies in 1854, again for the deliberate purpose of gathering evidence to address the species question, Wallace, like Darwin, needed a mechanism, but, unlike Darwin, he did not fail to publish his incomplete views. In 1855 he wrote and published in the *Annals and Magazine of Natural History* what is known as his Sarawak paper. In it he stated that new species come into being near in time and space to allied species, but without supplying a mechanism for their origin.

The paper sparked little public reaction. Darwin thought it just another vaguely transmutationist work. The geologist Charles Lyell, however, thought it very important, and said so to Darwin. In 1856, Darwin explained his theory to Lyell, and Lyell pressed him to begin his "big book on species": *Natural Selection* (Darwin, 1975). This Darwin did.

The idea Darwin's detractors most suspect of having been stolen from Wallace is the "principle of divergence". Unlike natural selection, most biologists would be hard pressed to say exactly what Darwin meant by this, if they have even heard of it at all. Kohn (1981, 1985) and Kottler (1985), two historians, have analysed this concept. Part of the biologist's difficulty is that Darwin, as Kohn notes, included in this principle several ideas (the branching nature of phylogeny, sympatric speciation, interspecific interactions, ecological specialization) which, while familiar enough individually, do not to us today seem to form an ineluctable whole.

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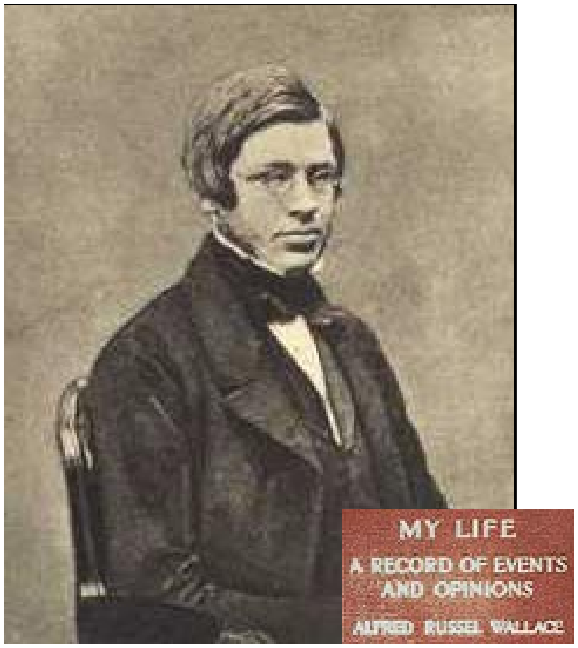

Alfred Wallace circa 1848

Darwin and Wallace

from page 10

Both Kohn and Kottler consider Darwin's and Wallace's concepts of the principle of divergence significantly different, so that Darwin could not have gotten his ideas from Wallace. Kottler argues that in his Ternate paper of 1858, Wallace considered only linear or phyletic divergence (i.e. anagenesis), while Darwin's principle embraced not only this, but branching divergence as well (i.e. the divergence from each other of two or more species descended from a single common ancestor). Kohn concludes that Darwin had formulated his principle of divergence by January 1855; Darwin (1958), in his autobiography, implies he had done so by early 1856; according to Kottler, Darwin had formulated his principle by 1857 at the very latest. Thus, by any of these datings, Darwin could not have been influenced by the Ternate paper of 1858.

My own brief analysis shows that most of the components of Darwin's concept were already present in his writings well before Wallace published at all. In his 'B' notebook, written in the late 1830s, Darwin includes his first sketches of the branching tree (or coral) of life (Darwin, 1987:177, 180). In the 'D' notebook, in September 1838, he uses the metaphor of the "wedge", with every species trying to fill gaps in the economy of nature (Darwin, 1987:375-6). And, in a note dated January 1855, he writes of "diversity of structures supporting more life" (i.e. ecological specialization leading to greater diversity) (Kohn, 1985:256). I thus do not see that Wallace, in either the Sarawak or Ternate papers, supplied anything wanting in Darwin's conceptual armamentarium. It takes nothing from the perspicacity of Wallace, or the import of his views for the world at large, to conclude, as do both Kohn and Kottler, that *for Darwin*, Wallace's Ternate paper was an "intellectual non-event".

In the spring of 1858 Darwin received Wallace's famous Ternate paper, which contained Wallace's theory of evolution by natural selection. Although there are some differences between Darwin's and Wallace's formulations, they were both much more impressed by the similarities. Wallace asked that Darwin pass the paper on to Lyell. Darwin was much distressed by the paper, as it contained, he thought, his own views in miniature. Darwin passed the paper on to Lyell, not wanting to do anything unfair to Wallace, but at the same time not wanting his own 20 years' work to go unrecognized. Darwin was much distracted at this time by an outbreak of scarlet fever in his household, in which several fell ill, and his son Charles died. Lyell and Hooker arranged for a reading of Wallace's paper, along with an excerpt from Darwin's *Essay* and a letter from Darwin to Asa Gray, at the next meeting of the Linnean Society. In presenting them, Lyell and Hooker arranged them, delicately perhaps, in chronological order.

Darwin's detractors argue that Darwin stole more bits of the principle of divergence when he received the Ternate paper, that he lied about when the manuscript and other of Wallace's correspondence arrived, and that he destroyed letters to cover up his actions. The first of these claims is, as we have already seen, belied by the fact that Darwin had by this time already formulated his principle of divergence. The second is based on unlikely suppositions concerning the uniformity and regularity of postal service from the Dutch East Indies to England in the 1850s (Kohn, 1981; Raby, 2001). The third is based on

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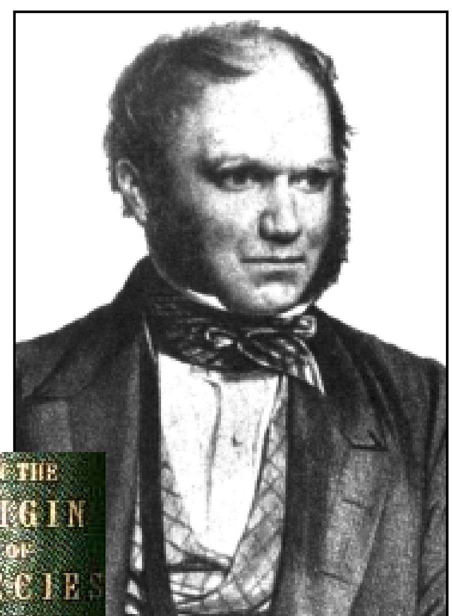
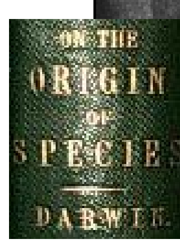
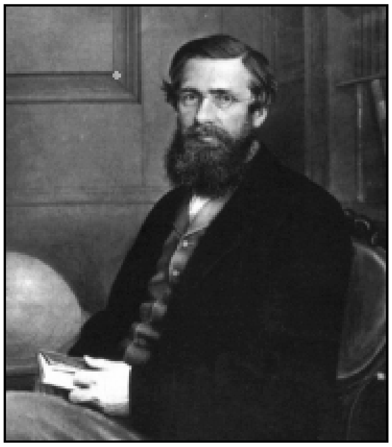




Charles Darwin circa 1849

Darwin and Wallace *from page 11*

unfamiliarity with the circumstances under which Darwin's correspondence was saved and stored: Darwin used to routinely cut up his correspondence, saving relevant portions in topical folders, while discarding the rest, and significant parts of what he did save were later lost to water damage (Kohn, 1981).

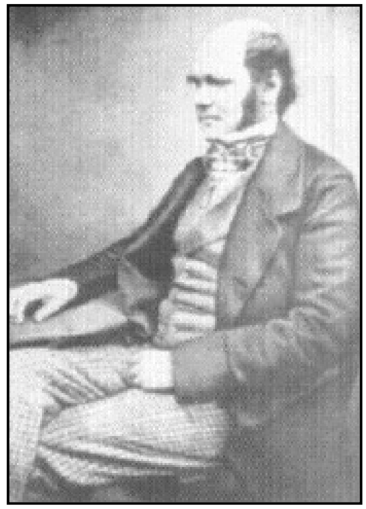


Alfred Wallace circa 1864

Finally, even if Darwin did not steal anything from Wallace, or lie about it, was it not unsavory to have Darwin's excerpts published along with Wallace's paper? Again, I think not. At the time of the arrival of Wallace's paper, Darwin was well along in the writing of *Natural Selection*. Wallace did not ask that Darwin publish his paper, but that he should show it to Lyell. Darwin, had he wanted to be unfair to Wallace, could easily have read it, sent it on to Lyell, gotten it back, and then returned it to Wallace, with the advice that it was indeed worth publishing, and that if Wallace would just tidy it up here and there and return it, he (Darwin) would submit it forthwith for publication. Given the delays involved in correspondence with the East Indies, it might have taken six months for such an exchange to occur (Raby, 2001), giving Darwin ample time to publish his views before Wallace.

Lyell and Hooker's actions in fact advanced the publication of Wallace's views further than Wallace could have hoped. On the other hand, not to publish Darwin's views at the same time would have been a grave injustice to Darwin, since Lyell and Hooker knew that Darwin had been working many years on the species problem, and had a much more substantial, though incomplete, manuscript in hand. Had Wallace been published alone, and received sole credit for natural selection, it would be regarded today as a much more curious and unjust turn of events than what did transpire.

Simultaneous publication in fact was a "win-win" situation for Darwin and Wallace. Darwin established that he in fact had thought of natural selection first, and also received a strong stimulus to complete a fuller presentation of his views. Wallace established that his discovery of natural selection was, though later, entirely independent of Darwin's. The circumstances allowed Wallace to later rightly insist that he not be classed with those forerunners, such as W.C. Wells and Patrick Matthew, who stated the principle of natural selection, but "failed to see its wide and immensely important applications" (1870: iv): Wallace did see its wide and immensely important applications. Simultaneous publication gave Wallace the *nihil obstat* of Darwin, Lyell and Hooker, and thus a guarantee that his paper would be read and taken seriously, and not be overlooked, as he thought his Sarawak paper had been. Indeed, Wallace wrote home that their action "insures me the acquaintance of these eminent men on my return home" (Wallace, 1905, I:365). Later, in *My Life*, Wallace wrote, "I not only approved, but felt that they had given me more honour and credit than I deserved." In the event, there was little reaction to the Linnean Society papers, so that it was Darwin's glowing mention of Wallace on page 1 of the *Origin* that firmly established Wallace as the co-discoverer of natural selection.



Charles Darwin circa 1954

Although the circumstances of independent discovery could have led to an ugly priority dispute, they did not. Both Darwin and Wallace realized the value and nature of each other's contributions, and both were content to share credit with the other. Although they later differed on a number of issues (Kohn, 1985), they remained friends and colleagues for life, standing figuratively side by side, fighting together the intellectual battle for their theory of evolution by natural selection against its many and powerful foes.

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References

Appleman, P, ed. (2001). *Darwin: a Norton Critical Edition*. 3rd ed. New York: W.W. Norton.

Bowler, PJ. (1989). *Evolution, the History of an Idea*. 2nd ed. Berkeley: University of California Press.

Brackman, AC. (1980). *A Delicate Arrangement*. New York: Times Books.

Brooks, JL. (1983). *Just Before the Origin: Alfred Russel Wallace's Theory of Evolution*. New York: Columbia University Press.

Browne, J. (1995). *Charles Darwin: Voyaging*. Princeton, N.J.: Princeton University Press.

Chambers, R. (1844). *Vestiges of the Natural History of Creation*. London: Churchill.

Darwin, CR. (1859). *On the Origin of Species*. London: John Murray.

Darwin, CR. (1909) *The Foundations of the Origin of Species*. Two Essays Written in 1842 and 1844. F. Darwin, ed. Cambridge: Cambridge University Press.

Darwin, CR. (1958). *The Autobiography of Charles Darwin 1809-1882*. N. Barlow, ed. New York: W.W. Norton.

Darwin, CR. 1975. *Charles Darwin's Natural Selection*. R.C. Stauffer, ed. Cambridge: Cambridge University Press.

Darwin, CR. 1987. *Charles Darwin's Notebooks 1836-1844*. P.H. Barrett, P.J. Gautrey, S. Herbert, D. Kohn and S. Smith, eds. Ithaca, N.Y.: Cornell University Press.

Darwin, C. and **Wallace, AR.** 1858. On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. Journal of the Linnean Society (Zoology) 3:45-62. Reprinted in Appleman (2001).

Desmond, A. and **Moore, J.** 1991. *Darwin*. New York: Warner Books.

Kohn, D. 1981. On the origin of the principle of diversity (review of *A Delicate Arrangement*). *Science* 213:1105-1108.

Kohn, D. 1985. Darwin's principle of divergence as internal dialogue. Pp. 245-257 in D. Kohn, ed. *The Darwinian Heritage*. Princeton, N.J.: Princeton University Press.

Kottler, MJ. 1985. Charles Darwin and Alfred Russel Wallace: two decades of debate over natural selection. Pp. 367-432 in D. Kohn, ed. *The Darwinian Heritage*. Princeton, N.J.: Princeton University Press.

Mayr, E. 1982. *The Growth of Biological Thought*. Cambridge, Mass.: Harvard University Press.

Quammen, D. 1996. *The Song of the Dodo*. New York: Scribner.

Raby, P. 2001. *Alfred Russel Wallace: A Life*. Princeton, N.J.: Princeton University Press.

Ruse, M. 1999. *The Darwinian Revolution*. 2nd ed. Chicago: University of Chicago Press.

Wallace, AR. 1855. On the law which has regulated the introduction of new species. Annals and Magazine of Natural History 2nd Ser. 16:184-196.

Wallace, AR. 1870. *Contributions to the Theory of Natural Selection*. London: Macmillan.

Wallace, AR. 1876. *The Geographical Distribution of Animals*. London: Macmillan.

Wallace, AR. 1880. *Island Life*. London: Macmillan.

Wallace, AR. 1889. *Darwinism*. London: Macmillan.

Wallace, AR. 1905. *My Life*. 2 vols. London: Chapman & Hall.

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