INFORMATION AND ENTROPY IN BIOLOGICAL SYSTEMS

Short title: Information and Entropy

Contact information:

- John C. Baez, Department of Mathematics, University of California, Riverside, CA, 92521, baez@math.ucr.edu
- Marc Harper, UCLA-DOE Institute for Genomics and Proteomics, 611 Young Drive East, Los Angeles, CA 90095, marcharper@ucla.edu
- John Harte, The Department of Environmental Science, Policy and Management, 305 Hilgard Hall, University of California, Berkeley, CA 94720, jharte@berkeley.edu

Summary: The goal of this investigative workshop is to synthesize different ways of applying information theory, and the closely connected concept of entropy, to biological systems. In ecology, entropy maximization methods have proved successful in predicting the distribution and abundance of species. Entropy is also widely used as a measure of biodiversity. Work on the role of information in game theory has shed new light on evolution: as a population evolves, it can be seen as gaining information about its environment. Finally, the principle of maximum entropy production has emerged as a fascinating yet controversial approach to predicting the behavior of biological systems, from individual organisms to whole ecosystems. By bringing together top researchers in these diverse areas, this workshop will let them trade expertise about the different roles information and entropy can serve as tools in biology, and address some long-standing conceptual problems.

Keywords: Shannon entropy, relative entropy, maximum entropy, biodiversity, evolutionary game theory

Proposed Dates: October 22-24, 2014.

Conflicts of interest: None.

1. Central Theme

Ever since Shannon initiated research on information theory in 1948, there have been hopes that the concept of information could serve as a tool to help systematize and unify work in biology. The link between information and *entropy* was noted very early on, and it suggested that a full thermodynamic understanding of biology would naturally involve the information processing and storage that are characteristic of living organisms. However, the subject is full of conceptual pitfalls for the unwary, and progress has been slower than initially expected. Premature attempts at 'grand syntheses' have often misfired. But applications of information theory and entropy to specific highly focused topics in biology have been increasingly successful, such as:

- the maximum entropy principle in ecology,
- Shannon and Rényi entropies as measures of biodiversity,
- information theory in evolutionary game theory,
- information and the thermodynamics of individual cells.

Because they work in diverse fields, researchers in these specific topics have had little opportunity to trade insights and take stock of the progress so far. The aim of the workshop is to do just this.

In what follows, participants' names are in boldface, while the main goals of the workshop are in italics.

Dewar is a key advocate of the principle of Maximum Entropy Production, which says that biological systems—and indeed all open, non-equilibrium systems—act to produce entropy at the maximum rate. Along with others, he has applied this principle to make testable predictions in a wide range of biological systems, from ATP synthesis [13] to respiration and photosynthesis of individual plants [16] and plant communities. He has also sought to derive this principle from ideas in statistical mechanics [12, 15], but it remains controversial. *The first goal of this workshop is to study the validity of this principle.*

While they may be related, the principle of Maximum Entropy Production should not be confused with the MaxEnt inference procedure, which says that we should choose the probabilistic hypothesis with the highest entropy subject to the constraints provided by our data. MaxEnt was first explicitly advocated by Jaynes. He noted that it is already implicit in the procedures of statistical mechanics, but convincingly argued that it can also be applied to situations where entropy is more 'informational' than 'thermodynamic' in character.

Recently **Harte** has applied MaxEnt in this way to ecology, using using it to make specific testable predictions for the distribution, abundance and energy usage of species across spatial scales and across habitats and taxonomic groups [22–24]. **Ostling** is an expert on other theories that attempt to explain the same data, such as the 'neutral model". **Dewar** has also used MaxEnt in ecology [14], and he has argued that it underlies the principle of Maximum Entropy Production. *Thus, a second goal of this workshop is to familiarize all the participants with applications of the MaxEnt method to ecology,* *compare it with competing approaches, and study whether MaxEnt provides a sufficient justification for the principle of Maximum Entropy Production.*

Entropy is not merely a predictive tool in ecology: it is also widely used as a measure of biodiversity. Here Shannon's original concept of entropy naturally generalizes to 'Rényi entropy', which depends on a parameter $\alpha \geq 0$. This equals

$$H_\alpha(p) = \frac{1}{1-\alpha} \log \sum_i p_i^\alpha$$

where p_i is the fraction of organisms of the ith type (which could mean species, some other taxon, etc.). In the limit $\alpha \to 1$ this reduces to the Shannon entropy:

$$H(p) = -\sum_i p_i \log p_i,$$

As α increases, we give less weight to rare types of organisms. **Cobbold** and **Leinster** have described a systematic and highly flexible system of biodiversity measurement, with Rényi entropy at its heart [9]. They consider both the case where all we have are the numbers p_i, and the more subtle case where we take the distance between different types of organisms into account.

Baez [3] has explained the role of Rényi entropy in thermodynamics, and together with **Leinster** and **Fritz** he has proved other theorems characterizing entropy which explain its importance for information processing [2]. However, these ideas have not yet been connected to the widespread use of entropy in biodiversity studies. More importantly, the use of entropy as a measure of biodiversity has not been clearly connected to MaxEnt methods in ecology. Does the success of MaxEnt methods imply a tendency for ecosystems to maximize biodiversity subject to the constraints of resource availability? This seems surprising, but a more nuanced statement along these general lines might be correct. *So, a third goal of this workshop is to clarify relations between known characterizations of entropy, the use of entropy as a measure of biodiversity, and the use of MaxEnt methods in ecology.*

As the amount of data to analyze in genomics continues to surpass the ability of humans to analyze it, we can expect automated experiment design to become ever more important. In **Lee** and **Harper**'s RoboMendel program [25], a mathematically precise concept of 'potential information'—how much information is left to learn—plays a crucial role in deciding what experiment to do next, given the data obtained so far. It will be useful for them to interact with **Bialek**, who has expertise in estimating entropy from empirical data and using it to constrain properties of models [5–7].

However, there is another link between biology and potential information. **Harper** has noted that in an ecosystem where the population of each type of organism grows at a rate proportional to its fitness (which may depend on the fraction of organisms of each type), the quantity

$$I(q||p) = \sum_i q_i \ln(q_i/p_i)$$

always decreases if there is an evolutionarily stable state [20]. Here p_i is the fraction of organisms of the ith genotype at a given time, while q_i is this fraction in the evolutionarily stable state. This quantity is often called the Shannon information of q 'relative to' p. But in fact, it is precisely the same as **Lee** and **Harper**'s potential information! Indeed, there is a precise mathematical analogy between evolutionary games and processes where a probabilistic hypothesis is refined by repeated experiments.

Thus, a fourth goal of this workshop is to develop the concept of evolutionary games as 'learning' processes in which information is gained over time. We shall try to synthesize this with **Bergstrom** and **Donaldson-Matasci**'s work [4, 17, 18] on the 'fitness value of information': a measure of how much increase in fitness a population can obtain per bit of extra information. Following **Harper**, we shall consider not only relative Shannon entropy, but also relative Rényi entropy, as a measure of information gain [21].

A fifth and final goal of this workshop is to study the interplay between information theory and the thermodynamics of individual cells and organelles. **Rieper** has studied the 'work value of information': that is, the amount of work that an agent can extract from a system per bit of information about its microstate [10]. She has also studied the role information plays in the reproduction of cells [11]. And in a celebrated recent piece of work, **England** used thermodynamic arguments to a derive a lower bound for the amount of entropy generated during a process of self-replication of a bacterial cell [19]. Interestingly, he showed that *E. coli* comes within a factor of 3 of this lower bound.

In short, information theory and entropy methods are becoming powerful tools in biology, from the level of individual cells, to whole ecosystems, to experimental design, model-building, and the measurement of biodiversity. The time is ripe for an investigative workshop that brings together experts from different fields and lets them share insights and methods and begin to tackle some of the big remaining questions.

Rationale for NIMBioS support

The study of entropy and information in biological systems is a highly interdisciplinary pursuit, with key players coming from mathematics, physics, mathematical biology, genomics, neuroscience, evolutionary biology, and population biology. While there is a strong overlap between their interests, the diverse group of researchers we are trying to bring together work in all these different fields, so they have never met all in one place. Thus, this workshop represents precisely the sort of opportunity for synthesizing the state of the art and identifying future research directions that NIMBioS is specially suited to provide.

Networks and Collaborations

This investigative workshop can serve as the starting-point for several collaborations and one or more NIMBioS working groups. There is particularly strong potential for interaction between researchers working on MaxEnt methods in ecology and those using entropy as a measure of biodiversity, since there is an overlap both in mathematical concepts used and in the systems being studied. There are also strong shared interests between researchers applying information theory to evolutionary game theory, those studying the fitness value of information, and those applying information theory to automated experiment design.

References

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[12] R. C. Dewar, Maximum entropy production and non-equilibrium statistical mechanics, in *Non-Equilibrium Thermodynamics and Entropy Production: Life, Earth and Beyond*, eds. A. Kleidon and R. Lorenz, Springer, New York, 41–55.

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[15] R. C. Dewar, Maximum entropy production as an inference algorithm that translates physical assumptions into macroscopic predictions: don't shoot the messenger, *Entropy* **11** (2009), 931–944.

[16] R. C. Dewar, Maximum entropy production and plant optimization theories, *Phil. Trans. Roy. Soc. B* **365** (2010) 1429-1435.

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[19] J. L. England, Statistical physics of self-replication, *J. Chem. Phys.* **139** (2013), 121923.

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[25] C. Lee and M. Harper, Basic experiment planning via information metrics: the RoboMendel problem, arXiv:1210.4808 (2012).

2. Participants

John Baez	Department of Mathematics, University of California, Riverside	Ph.D.: Mathematics. Mathematics of Information and Entropy
Carl T. Bergstrom	Department of Biology, University of Washington	Ph.D.: Biological Sciences. Information Theory in Evolutionary Biology
William Bialek	Lewis-Sigler Institute for Integrative Genomics, Princeton University	Ph.D.: Biophysics. Information and Entropy in Biology
Christina Cobbold	Department of Applied Mathematics, University of Glasgow	Ph.D.: Mathematical Biology. Entropy and Measures of Biodiversity
Roderick Dewar	Research School of Biology, Australian National University	Ph.D.: Mathematical Physics. Entropy Production in in Biological Systems
Matina C. Donaldson-Matasci	Department of Ecology and Evolutionary Biology, University of Arizona	Ph.D.: Biology. Information Theory in Evolutionary Biology
Jeremy L. England	Department of Physics, Massachusetts Institute of Technology	Ph.D.: Physics. Entropy of Self-Replicating Systems
Tobias Fritz	Perimeter Institute for Theoretical Physics	Ph.D.: Mathematics Mathematics of Information and Entropy
John Harte	Department of Environmental Science, Policy and Management, University of California, Berkeley	Ph.D.: Physics. Maximum Entropy in Ecology
Marc Harper	Bioinformatics Program, University of California, Los Angeles	Ph.D.: Mathematics. Information in Evolutionary Game Theory
Chris Lee	Bioinformatics Program, University of California, Los Angeles	Ph.D.: Structural Biology. Information Theory for Experiment Planning
Tom Leinster	School of Mathematics U. of Edinburgh	Ph.D.: Mathematics. Entropy and Measures of Biodiversity
Annette Ostling	Department of Ecology and Evolutionary Biology, University of Michigan	Ph.D.: Energy and Resources. Stochastic Models in Ecology
Blake Pollard	Department of Physics University of California, Riverside	B.A.: Physics. Entropy and Probability Theory
Elisabeth Rieper	Centre for Quantum Technologies National University of Singapore	Ph.D.: Physics. Entropy in Cellular Biology

International participants

Christina Cobbold — Cobbold is an expert on mathematical modelling of ecological processes in population and evolutionary ecology. Together with **Leinster**, she has proved some useful theorems generalizing Shannon and Rényi entropy in a way that takes species similarity into account when measuring biodiversity [9]. She is a member of the Boyd Orr Centre for Population and Ecosystem Health at the University of Glasgow.

Roderick Dewar — Dewar is the leading figure in attempts to derive the controversial principle of 'maximum entropy production' and apply it to biological systems [12]- [15]. This principle, not to be confused with Jaynes' widely used 'maximum entropy principle' in statistical reasoning, says that a certain class of systems out of thermal equilibrium tend to maximize their rate of entropy production. One important goal of this workshop is to discuss the validity of this principle.

Tobias Fritz — Tobias Fritz is an expert on the mathematics of entropy and information in both classical and quantum systems. Together with **Baez** and **Leinster**, he is working on abstract characterizations of Shannon and Tsallis entropies which help explain their significance [2]. He is now a Templeton Frontiers Program Postdoctoral Fellow at the Perimeter Institute in Toronto.

Tom Leinster — Leinster is an expert on Shannon and Rényi entropies as measures of biodiversity, and he has proved useful theorems characterizing the best ways to take species similiarity into account in measuring biodiversity [9]. In 2012 he organized a month-long program on The Mathematics of Biodiversity at the Centre de Recerca Matemàtica in Barcelona, which focused on the use of entropy as a measure of biodiversity.

Elisabeth Rieper — Rieper is a promising young biophysicist who has proved bounds on the amount of work that can be obtained from a given amount of information [10], and studied the ways in which cells maintain low internal entropy [11].

Diversity

One of the PIs, John Baez, is Hispanic. We have invited two female postdocs, Matina Donaldson-Matasci and Elisabeth Rieper, and a male one, Tobias Fritz. Annette Ostling is a female assistant professor, and Christina Cobbold is a female senior lecturer. We have also invited a graduate student, Blake Pollard, who is working on applications of information theory to climate science.

Budget

We will invite 5 participants from overseas (Australia, Germany, Singapore, and two from Scotland), 1 from Canada, and 9 from the United States to attend this 3-day workshop.

3. CV: John Baez

Professional Preparation

B.A., Mathematics, Princeton University, 1982.

Ph.D., Mathematics, Massachusetts Institute of Technology, 1986.

Gibbs Instructorship, Department of Mathematics, Yale University, 1986-1988.

Appointments

University of California at Riverside, Department of Mathematics, 1988-present.

On leave, visiting the Centre for Quantum Technologies, 2010-2012 and summer of 2013.

On leave, visiting Wellesley College, 1990-1992.

Books

An Introduction to Algebraic and Constructive Quantum Field Theory, with Irving Segal and Zhengfang Zhou, Princeton University Press, 1992.

Knots and Quantum Gravity, editor, Oxford University Press, 1994.

Gauge Fields, Knots, and Gravity, with Javier Muniain, World Scientific Press, 1994.

Infinite-Dimensional Representations of 2-Groups, with Aristide Baratin, Laurent Freidel and Derek Wise, Memoirs of the American Mathematical Society **1032**, Providence, Rhode Island, 2012.

Selected Papers (out of 85 published papers)

Is life improbable?, *Found. Phys.* **19** (1989), 91–95.

Higher-dimensional algebra and topological quantum field theory, with James Dolan, *Jour. Math. Phys.* **36** (1995), 6073–6105.

Spin networks in gauge theory, *Adv. Math.* **117** (1996), 253–272.

Quantum geometry and black hole entropy, with Abhay Ashtekar, Alejandro Corichi and Kirill Krasnov, *Phys. Rev. Lett.* **80** (1998), 904–907.

Quantum geometry of isolated horizons and black hole entropy, with Abhay Ashtekar and Kirill Krasnov, *Adv. Theor. Math. Phys.* **4** (2001), 1–94.

The algebra of grand unified theories, with John Huerta, *Bull. Amer. Math. Soc.* **47** (2010), 483–552.

Physics, topology, logic and computation: a Rosetta Stone, with Mike Stay, in *New Structures for Physics*, ed. Bob Coecke, Springer, Berlin, 2011, pp. 95-174.

A characterization of entropy in terms of information loss, with Tobias Fritz and Tom Leinster, *Entropy* **13** (2011), 1945–1957.

Algorithmic thermodynamics, with Mike Stay, *Math. Struct. Comp. Sci.* **22** (2012), 771–787.

A Noether theorem for Markov processes, with Brendan Fong, *Jour. Math. Phys.* **54** (2013), 013301.

Synergistic Activities

Author of *This Week's Finds*, expository column, 1993–now. Founding member of the Azimuth Project, an international collaboration of scientists and engineers working on environmental problems. Chair of the Web Editorial Group, American Mathematical Society.

Honors

1982-1985, National Science Foundation Fellowship.

1999, Elected Fellow of the American Association of Science.

2007, Elected Member of the Foundational Questions Institute.

2013, Levi L. Conant Prize for the best expository paper published in the *Notices* or *Bulletin* of the American Mathematical Society.

Research Grants

PI for 'Feynman Diagrams and the Semantics of Quantum Computation', NSF program on Quantum Information and Revolutionary Computing, August 2007 – August 2010. PI for 'Categorifying Fundamental Physics', Foundational Questions Institute, August 2008 – August 2010.

Conferences Organized

Knots and Quantum Gravity workshop, U. C. Riverside, 1993.

Knots and Quantum Gravity session of the Seventh Marcel Grossmann Meeting on General Relativity, Stanford, 1994.

Low-dimensional Topology and Quantum Gravity session of Workshop on Canonical and Quantum Gravity II, Stephan Banach Institute, Warsaw, 1997.

Low-dimensional Topology and Quantum Gravity session of Joint Mathematics Meetings, Baltimore, 1998.

n-Categories: Foundations and Applications, workshop at Institute for Mathematics and its Applications, Minnesota, 2004.

Higher Categories and Their Applications, workshop at the Fields Institute, Toronto, 2007.

4. CV: Marc Harper

Professional Preparation

Ph.D., Mathematics, University of Illinois, Urbana-Champaign, 2009.

B.S., Mathematics and Physics with honors, University of Florida, 2004.

Appointments

Postdoctoral Scholar, University of California at Los Angeles, Department of Genomics and Proteomics, Bioinformatics interdisciplinary group (2009-now). Funded by Office of Science (BER), U.S. Department of Energy.

Papers

Information geometry and evolutionary game theory, arXiv:0911.1383 (2009).

Escort evolutionary game theory, *Physica D* **240** (2011), 1411–1415.

Phenotype sequencing: identifying the genes that cause a phenotype directly from pooled sequencing of independent mutants, with Zugen Chen, Tracy Toy, Lara Machado, Stan Nelson, James Liao, and Chris Lee, *PLoS ONE* **6** (2011).

Basic experiment planning via information metrics: the RoboMendel problem, with Chris Lee, arXiv:1210.4808 (2011).

Stability of evolutionary dynamics on time scales, with Dashiell Fryer, arXiv:1210.5539 (2012).

Inferring fitness in finite, variably-sized, and dynamically-structured populations, arXiv:1303.4566 (2013).

The inherent randomness of evolving populations, arXiv:1303.1890 (2013)

Comprehensive detection of genes causing a phenotype using phenotype sequencing and pathway analysis, with Luisa Gronenberg, James Liao, and Chris Lee., arXiv:1303.0455 (2013).

Phenotype sequencing: high-throughput discovery of the genetic causes of a phenotype, with Chris Lee, *Microbe (Feature)* (2013).

Honors

Five appearances on the list of instructors rated outstanding by students at the University of Illinois.

McLaughlin Scholarship, University of Florida (2003)

National Merit Scholar (2000); National AP Scholar (2000); Valedictorian (2000)

Synergistic Activities

Worked with ALEKS Corporation (Irvine, CA) to develop a next-generation mathematics placement and assessment system used annually by tens of thousands of students in dozens of higher education institutions in the United States. Directly involved in the implementation of mathematics placement programs at dozens of higher education institutions, resulting in a reduction of first-year undergraduate failures in mathematics courses by more than ten thousand over the past five years (conservatively estimated). (2007-)

Organized seminars on Information and Evolution at UCLA; participated in the EvoEco interdisciplinary evolutionary ecology and community genetics seminars at UCLA; organized seminar on Evolutionary Dynamics at the University of Illinois.

Conferences Organized

Graduate Topology Conference, University of Illinois Urbana-Champaign, 2008.

5. CV: John Harte

Professional Preparation

Harvard University, physics, BA, 1961.

University of Wisconsin, theoretical physics, PhD, 1965.

CERN NSF Postdoctoral Fellow in physics, 1965-1966.

Lawrence Berkeley Laboratory AEC Postdoctoral Fellow in physics, 1966-1968.

Appointments

Joint Professorship in the Energy and Resources Group and the Department of Environmental Science, Policy, and Management, University of California, Berkeley Senior Scientist, Lawrence Berkeley Laboratory 1973-1985.

Assistant Professor of Physics, Yale University, 1968-73.

Selected Papers (out of 200+ published papers)

Shifting dominance within a montane vegetation community: results of a climate-warming experiment, with R. Shaw, *Science* **267** (1995), 876–880.

Self-similarity in the distribution and abundance of species, withA. Kinzig and J. Green, *Science* **284** (1999), 334–336.

Self similarity and the relationship between abundance and range size, J. Harte, T. Blackburn and A. Ostling, *American Naturalist* **157** (2001) 374-386.

Carbon-cycle feedbacks to climate change in montane meadows: results from a warming experiment and a natural climate gradient, with S. Saleska, M. Shaw, M. Fischer, J. Dunne, M. Holman, C. Still, *Global Biogeochemical Cycles***16** (2002), 1055.

Integrating experimental and gradient methods in ecological climate change research, with J. Dunne, S. Saleska and M. Fischer, *Ecology* **85** (2004), 904–916.

A theory of spatial structure in ecological communities at multiple spatial scales, with E. Conlisk, A. Ostling, J. Green, and A. Smith, *Ecological Monographs* **75** (2005), 179–197.

Maximum entropy and the state-variable approach to macroecology, with T. Zillio, E. Conlisk and A. Smith, *Ecology* **89** (2008), 2700–2711.

Biodiversity scales from plots to biomes with a universal species-area curve, with A. Smith and D. Storch, *Ecology Letters* **12** (2009), 789797.

Selected Books (out of 8 books)

Consider a Spherical Cow: A Course in Environmental Problem Solving, University Science Books, Sausalito, CA, 1988. (Also in Japanese translation.)

Maximum Entropy and Ecology: A Theory of Abundance, Distribution, and Energetics, Oxford U. Press, Oxford, UK, 2011.

Synergistic Activities

Author of 5 textbooks and 2 books for the lay public on environmental science and ecology. Provided testimony on many occasions to Federal, State and local governing bodies; interviewed on Bill Moyers TV show NOW and the McNeill-Lehrer News Hour; research featured in Mother Jones magazine. Served on 6 National Academy of Sciences Panels dealing with environmental issues. Associate Editor, Annual Review of Energy and Environment (1992-2001). President, Board of Trustees of the Rocky Mountain Biological Laboratory, 1988-92, and Member, Board of Directors of the Point Reyes Bird Observatory, 1991-1998.

Selected Honors

Elected Member, California Academy of Sciences; Elected Member, National Council of the American Federation of Scientists, 1984-88; John Simon Guggenheim Fellow, 1994.

Elected Fellow of the American Physical Society, 1988; PEW Scholars Prize in Conservation and the Environment, 1990; Phi Beta Kappa Distinguished Lecturer for 1998.

Class of 1935 Distinguished Professorship, UC Berkeley; Visiting Distinguished Ecologist, Colorado State University, 1999; 2001 Recipient of the Leo Szilard Award by the American Physical Society; UC Berkeley Distinguished Graduate Mentor Award, 2004, Awarded Miller Foundation Professorship, 2006, Co-recipient of the 2006 George Polk Award in journalism.

Research Grants

Past or present Principal Investigator of research funded by NSF, DOE, DOA, EPA, NIH, EPRI, California Air Resources Board, California Water Resources Center, MacArthur Foundation, The Gordon and Betty Moore Foundation, Man and the Biosphere Program, Pew Charitable Trusts.