2021-2022

221.4400 – Why Sex? The Mystery of Sexual Recombination
Semester B

Time: Thursdays 12 pm – 2 pm, Room 223 Multipurpose Building

Instructor: Prof. Adi Livnat, **Email:** adi.livnat@sci.haifa.ac.il

Office Hours: Thursdays 10 am – 12 pm, Room 220, 04-664-7989

Teaching Assistants & Office Hours: None

Course Level: Masters and Ph.D. students. The course is also open to undergraduate students of advanced standing and background.

Course Type & Format: Elective, Lecture

Number of Hours/Credits: 2

Prerequisites: General undergraduate level background in evolution and genetics.

Course Overview (Short Abstract):

The problem of what role sex plays in evolution has been called "The Queen of Problems" in evolutionary biology. Defined most generally as the shuffling of genetic material between individuals, sex is nearly universal, occurring in plants and animals via syngamy, in fungi via the fusion of hyphae, and even in bacteria by various means. Species where individuals do not exchange genetic material in any form or manner, called the obligate asexuals, are not only rare, but also appear to occasionally arise from sexual ancestors in the course of evolution and to go extinct over evolutionary time. Even the putative exceptions to this rule have begun to be questioned in recent times. Thus, the empirical facts suggest that the exchange of genetic material between individuals is crucial for evolution. However, from Darwin's time until today, no consensus has been reached among scientists about why this is the case: why sex is needed. As Darwin himself wrote, "We do not even in the least know the final cause of sexuality; why new beings should be produced by the union of the two sexual elements, instead of by a process of parthenogenesis. The whole subject is as yet hidden in darkness."

In this class, we will ask deep questions about sexual recombination and evolution in general: Why does sex exist? role in and influence on evolution? What preserves it? How did it originate? We will examine the diversity of mechanism for genetic exchange between individuals in nature; understand the importance of sexual recombination for the foundations of genetics and evolutionary theory; examine theoretical models of the evolution of recombination and how they fit with empirical evidence; learn about the recently proposed connection between mechanisms of recombination and mutation; and come out with an appreciation of how understanding sex and recombination has always been and continues to be necessary for understanding how evolution happens.

Learning Outcomes (What are the skills, abilities, or major concepts a student is expected to acquire in this course?) – At the end of the course students will be able to:

1. Understand the importance of the problem of sexual recombination for the question of how evolution happens.

2. Understand some of the deepest aspects of the progression of evolutionary theoretical thinking from Darwin's time until today, and the scope of the questions left unanswered.

3. Obtain a historical perspective on revolutions in science and on the open-ended nature of true scientific investigation.

4. Learn to distinguish between facts and opinions and between what is popularly thought and what is truly known about the principles of evolution.

5. Obtain practice in reading primary literature, including both scientific manuscripts and chapters in classic science books.

6. Obtain practice in critical thinking and in reading scientific texts.

7. Obtain practice in reviewing material and in writing a review paper.

8. Practice asking questions and engaging in scientific discussions.

Assessment (Assessment Method and Grade Composition):

Class attendance and class participation – 20%.
Brief weekly summaries of reading material – 20%.
In class presentation – 20%.
Final paper – 40%.

Week-by-Week Content and Assignments:

Week #	Topic	Assignment
1	What is evolution, what is sex? An introduction to the course.	No reading assignment.
2	The problem of the role of sex in evolution and its scientific importance	Darwin, the Origin of Species. Selected readings.
3	The diversity of mechanisms of genetic exchange between individuals in nature I : Mysteries of bacterial genetic exchange.	Stearns SC and Hoekstra RF, Selected readings.

4	The diversity of mechanisms of genetic exchange II : genetic exchange in eukaryotes	Stearns SC and Hoekstra RF, Selected readings.
5	Background to the Darwinism/Mendelism debate I : Darwin vs. Galton	Provine, W. The Origin of Theoretical Population Genetics. Selected readings.
6	Background to the Darwinism/Mendelism debate II: The fundamental, interconnected problems of sexual recombination and the origin of genetic variation, and their consequences for Darwin's views.	Provine, W. The Origin of Theoretical Population Genetics. Selected readings.
7	Mendel's laws of inheritance through sexual reproduction: Students re-build Mendel's model from his empirical observations	No reading assignment.
8	Consequences of Mendel's laws of inheritance through sexual reproduction: How to reconcile Darwinism and Mendelism?	Fisher RA. The Genetical Theory of Natural Selection. Selected readings. Hartl, DL and Clark, AG. The Principles of Population Genetics. Selected readings.
9	Fisher's reconciliation of Darwinism and Mendelism a la Galton's `bean machine'.	Fisher RA. The Genetical Theory of Natural Selection. Selected readings. Hartl, DL and Clark, AG. The Principles of Population Genetics. Selected readings.
10	From Wright's criticism of Fisher's view and the Fisher-Wright debate on biological complexity to the Neutral Theory of evolution : How the difficult problems in evolutionary theory revolve around the problem of sex, and how they have not been resolved.	No reading assignment.
11	Evolution by random mutation and natural selection I : Empirical problems	Dawkins 1976, and Dawkins 1986, Selected readings.
12	Evolution by random mutation and natural selection II :	Dawkins 1976, and Dawkins 1986, Selected readings.

	conceptual problems and Dawkins's model	
13	20th century hypotheses on the role of sex in evolution	Barton NH, Charlesworth B: Why sex and recombination? And other selected readings (Muller, Kondrashov, Hamilton, West et al.)
14	The theory of interaction-based evolution : A new solution to the two fundamental problems intertwined – sexual recombination and the origin of genetic variation.	Livnat, A.: Interaction-based evolution: how natural selection and nonrandom mutation work together. Biology direct 2013, 8(1), 24. Livnat, A., et al. A mixability theory for the role of sex in evolution. Proceedings of the National Academy of Sciences, 2008, 105(50), 19803-19808.

Reading List:

1. Darwin, C. On The Origin of Species by Means of Natural Selection, Or The Preservation of Favoured Races in the Struggle for Life. J. Murray, London, 6th edition, 1876.
2. Stearns SC, Hoekstra RF. Evolution: An Introduction. New York: Oxford University Press; 2005.
3. Fisher RA. The Genetical Theory of Natural Selection. Oxford: The Clarendon Press; 1930.
4. Provine, W. The Origin of Theoretical Population Genetics. University of Chicago Press, Chicago. 1971.
5. Hartl, DL and Clark, AG. The Principles of Population Genetics. Sinauer Associates, 1997.
6. Muller HJ: Some genetic aspects of sex. Am Nat 1932, 66:118–138.
7. Muller HJ: The relation of recombination to mutational advance. Mutation Res 1964, 1:2–9.
8. Kondrashov A: Selection against harmful mutations in large sexual and asexual populations. Genet Res 1982, 40:325–332.
9. Hamilton WD: Sex versus non-sex versus parasite. Oikos 1980, 35(2):282-90.
10. Feldman MW, Otto SP, Christiansen FB: Population genetic perspectives on the evolution of recombination. Annu Rev Genet 1997, 30:261–295.
11. West SA, Lively CM, Read AF: A pluralist approach to sex and recombination. J Evol Biol 1999, 12:1003–1012.
12. Barton NH, Charlesworth B: Why sex and recombination? Science 1998, 281:1986–1990.
13. Glesener, R. R., & Tilman, D.: Sexuality and the components of environmental uncertainty: clues from geographic parthenogenesis in terrestrial animals. American Naturalist, 1978, 659-673.
14. Dawkins, R. The Selfish Gene. Oxford University Press. 1976.
15. Dawkins, R. The Blind Watchmaker. Norton & Company. 1986.

16. Livnat, A., Papadimitriou, C., Dushoff, J., & Feldman, M. W.: A mixability theory for the role of sex in evolution. Proceedings of the National Academy of Sciences, 2008, 105(50), 19803-19808.
17. Chastain, E., Livnat, A., Papadimitriou, C., & Vazirani, U.: Algorithms, games, and evolution. Proceedings of the National Academy of Sciences 2014, 111(29), 10620-10623.
18. Livnat, A.: Interaction-based evolution: how natural selection and nonrandom mutation work together. Biology direct 2013, 8(1), 24.