BIOL 691 DL5: Fundamental Concepts in Evolution (3 credits)

Meeting time: Mondays 4:30-7:10 pm
Format: Synchronous (see the course page in Canvas for zoom links)

Instructor
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Office hour: By appointment

Canvas
I will use the learning management system Canvas in this class. Papers, book chapters, slides, announcements, assignment templates, and other relevant course materials will be posted to this site.

Textbook
Losos, J. B., Baum, D. A., Futuyma, D. J., Hoekstra, H. E., Lenski, R. E., Moore, A. J., Peichel, C. L., Schluter, D., & Whitlock, M. C. (Eds.). (2013). *The Princeton Guide to Evolution*. Princeton University Press. https://doi.org/10.1515/9781400848065

Overview
Dobzhansky famously wrote that *"Nothing in biology makes sense except in the light of evolution."* G. Evelyn Hutchinson offered an equally interesting metaphor, describing life as *"the ecological theater and the evolutionary play."* Together, these statements capture a fundamental truth: to understand life, we must view it not only in terms of organismal or molecular functions today, but also through the lens of their histories. Biology is inherently a "vertical" science because one of the defining features of life is heredity—the transmission of information across generations that allows populations and lineages to change through time.

But what exactly do we mean by *evolution*? The term encompasses so many concepts that it might be considered an "accordion" word, expanding to include multiple meanings depending on the context. Evolution can refer to changes in allele frequencies within populations through processes such as natural selection, gene flow and genetic drift. It can also describe the diversification of life over geological epochs, producing the large number of species and ecological communities reconstructed from phylogenies and documented in the fossil record through episodes of adaptive radiation and mass extinction. Evolution can also refer to changes in phenotypes, whether observed over just a few generations, eg, as seen in microbial evolution experiments or Darwin's finches, or inferred from ancestral trait reconstruction. Beyond genetic inheritance through DNA molecules, evolutionary concepts have even been extended to systems involving epigenetic, cultural, and ecological inheritance.

Because evolution spans such a wide range of scales, mechanisms, and disciplines, no single course can cover every aspect of the field. This class will not focus on application areas such as conservation genetics, estimation of the phylogenetic uniqueness of a region's biota or directed evolution applied in medical science. Instead, this seminar concentrates on the fundamental concepts that have shaped evolutionary biology. Instead, this seminar focuses on the fundamental concepts that have shaped evolutionary biology since Darwin proposed natural selection in 1859. Although advances in population genetics, molecular biology, genomics, phylogenetics, developmental biology, ecology, and computational methods have profoundly transformed our understanding of evolutionary processes, many of our current endeavors remain firmly rooted in the field's original conceptual foundations.

Course Description
This graduate seminar examines the historical development of evolutionary biology through landmark papers and their modern counterparts. Rather than functioning as a lecture course, the seminar emphasizes critical analysis of primary literature. Students will read and discuss seminal papers alongside contemporary reviews and empirical studies, anchored by book chapters, allowing them to appreciate both the historical context and modern understanding of major evolutionary concepts, as well as how advances in theory and data have shaped the field.

Weekly Format

- 30 min lecture overview
- 5 min Break
- 45 min discussion of the classic paper
- 5 min Break
- 45 min discussion of the modern paper
- 5 min Break
- 10 min wrap up
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Virtual Class Etiquette and Participation
In our zoom sessions, attentive listening and active participation is crucial for a successful learning experience. Please ensure your **webcam is on**, with a blurred background for privacy (if necessary), and that you're fully engaged in class activities. Respectful communication is essential—listen to others, contribute meaningfully to discussions, and refrain from distractions. Mute your microphone when not speaking to minimize background noise. Your involvement and attention help create a productive virtual learning environment.

Grading

Participation and discussion	15%
Weekly reading critique	30%
Discussion leadership	20%
Final presentation	10%
Final review paper	20%

Grading and late work policy
Unless you have received prior permission, you should not expect to be allowed to turn in assignments after the due date for full credit. Assignment will receive 10% penalty if submitted one day late, and 20% penalty if two days late. Assignments will not be accepted if they are more than 2 days past due.

Full credit for late work will not be accepted except in the case of a documented personal emergency or excused absence. You will not be allowed to make up a piece of graded work unless you have a documented, excused absence. It is your responsibility to provide written documentation from a third party of your emergency or university-excused absence. I do not consider work-related absences, work in other classes, oversleeping, or meetings with other professors a personal emergency. **I do not add points at the end of a semester to “bump up” your letter grade.**

Grading schema
Your final grade will be based on your score out of 100. See below for grading scale. All inquiries about partial credits or potential grading mistakes need to be addressed soon after the graded work is returned, not toward the end of semester.

A+	97-100
A	93-96
A-	90-92
B+	87-89
B	80-86
C	60-79
F	59 or less

Weekly Paper Discussion
Each week, two students will lead the discussion of the assigned papers: one student will lead the **classic paper**, and one student will lead the **modern paper**. Discussion leaders are responsible for guiding the class through the scientific ideas, conceptual development and historical/modern context. The leaders’ goal is not simply to summarize the papers, but to give an overview of each section and generate discussion that critically evaluates how evolutionary concepts were formulated, tested and refined, considering that everyone has already read the papers and the accompanying book chapter.

Discussion guidelines, the leader will provide a short overview of the paper but lead a discussion that critically evaluates the following points. The discussion leader is responsible for ensuring that all students have the opportunity to contribute. The discussion leader shall use powerpoint slides to guide the group through the paper discussion and address the following points:

1. Background and motivation
- What major question or problem was the paper attempting to address?
- What was the prevailing view or limitation in the field?
- Why was this question important for biology?

2. Major conceptual contribution
- What is the central idea or hypothesis proposed by the authors?
- What assumptions (implicit and explicit) underlie this idea?
- How did this paper change the way evolutionary biologists thought about the topic?
- What is its greatest weakness?

3. Evidence and methodical approach
- Were the methods appropriate given the question and the technology?
- What evidence were used to support the conclusions?
- What alternative explanations could account for the observations?

4. Connecting classic and modern perspectives, and closing reflection
For the classic paper:
- What ideas from this paper remain influential today?
- How has our understanding of the concept changed since this paper was published?

- What new tools, data, or approaches have allowed us to revisit this question?

For the modern paper:
- Does the study support, refine, expand, or challenge the original concept?
- What new insights does the modern paper provide?
- What questions remain unresolved? What would you do differently today?

Weekly Reading Critique
For each assigned paper, students will submit a brief critical analysis before class (i.e., submit two critiques per week). The purpose of the critique is to demonstrate engagement and familiarity with the paper and to evaluate its contribution to evolutionary biology. Each critique should be 1.5 pages long (~500-600 words), addressing the above four points. More information is provided in the template.

Final Presentation and Review Paper. Due date to be determined.
Each student will select a topic from the textbook NOT covered by this class, and prepare a presentation during the final week of class. Students should consult with me before selecting a topic to ensure that it's appropriateness.

For each topic, cover the following:
1. **Background and significance**, including how the evolutionary concept connects to the broader concepts covered in class.
2. **Historical development and current advances** in the field.
3. **Critical evaluation and future directions**, including unresolved questions, key assumptions or potential weaknesses, limitations, and future research directions.

The duration of the presentation will depend on the number of students in the class and will include an additional 2 minutes for Q&A. The review paper will be 5 pages (~1,500 words), and you should support your discussion with appropriate literature sources, including a minimum of 12 historical and modern papers. Provide a reference list at the end of your essay and use appropriate in-text citations throughout the text.

Weekly Topics (This reading list is subject to change)

No.	Topic and book chapter	Classic paper	Modern paper	Additional reading
1 8/24	What is evolution? I.1 and I.2	Darwin, C. R. and A. R. Wallace. 1858. On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. [Read 1 July] Journal of the Proceedings of the Linnean Society of London. Zoology 3 (20 August): 45-50.	Reznick, D. N., & Ricklefs, R. E. (2009). Darwin's bridge between microevolution and macroevolution. Nature, 457, 837–842.	Darwin, C. (1859). On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray.
2 8/31	Units of selection III.2	Lewontin, R. C. (1970). The Units of Selection. Annual Review of Ecology and Systematics, 1, 1–18.	Okasha, S. (2006) Chapter 8: Units and levels of Selection.	Mayr, E. (1997). The objects of selection. Proceedings of the National Academy of Sciences, 94(6), 2091–2094.
3 9/14 (9/7 is labor day)	How do populations evolve? III.3	Fisher R. A. (1930). Chapter 3: The Fundamental Theorem of Natural Selection	Okasha, S. (2008) Fisher's Fundamental Theorem of Natural Selection—A Philosophical Analysis | The British Journal for the Philosophy of Science	Travis, J. 1989. The role of optimizing selection in natural populations. Annual Review of Ecology and Systematics 20: 279–296.
4 9/21	Adaptationism III.1	Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. Proceedings of the Royal Society of London. B. Biological Sciences, 205(1161), 581–598.	Barrett, R. D. H., & Hoekstra, H. E. (2011). Molecular spandrels: Tests of adaptation at the genetic level. Nature Reviews. Genetics, 12(11), 767–780.	Nielsen, R. (2009). Adaptionism-30 years after Gould and Lewontin. Evolution; International Journal of Organic Evolution, 63(10), 2487–2490.
5 9/28	Phenotypic Selection on Quantitative Traits III.5	Lande, R. (1976). NATURAL SELECTION AND RANDOM GENETIC DRIFT IN PHENOTYPIC EVOLUTION. Evolution; International Journal of Organic Evolution, 30(2), 314–334.	Walsh, B., & Blows, M. W. (2009). Abundant Genetic Variation + Strong Selection = Multivariate Genetic Constraints: A Geometric View of Adaptation. Annual Review of Ecology, Evolution, and Systematics, 40(Volume 40, 2009), 41–59.	V.12 Genetics of Phenotypic Evolution
6 10/5	Responses of natural populations III.7	Wright, S. (1932). The roles of mutation, inbreeding, crossbreeding and selection in evolution,	Arnold, S. J., Pfrender, M. E., & Jones, A. G. (2001). The adaptive landscape as a conceptual bridge	III.14 Evolution of the Ecological Niche Reznick, D. N., & Ghalambor,

		Proceedings of the Sixth International Congress of Genetics. Proc Sixth Int Congr Genet, 1, 356.	between micro- and macroevolution. Genetica, 112(1), 9–32.	C. K. (2001). The population ecology of contemporary adaptations: What empirical studies reveal about the conditions that promote adaptive evolution. Genetica, 112–113, 183–198.
7 10/19 (10/12 is Fall break)	Evolution at the molecular level V.1	King, J. L., & Jukes, T. H. (1969). Non-Darwinian evolution. Science, 164, 788–798.	Nielsen, R. (2005). Molecular signatures of natural selection. Annu Rev Genet, 39, 197–218. (16285858).	Kern, A. D., & Hahn, M. W. (2018). The neutral theory in light of natural selection. Molecular Biology and Evolution, 35(6), 1366–1371.
8 10/26	Evolution and Development V.11	Alberch, P., Gould, S. J., Oster, G. F., & Wake, D. B. (1979). Size and shape in ontogeny and phylogeny. Paleobiology, 5(3), 296–317.	Carroll, S. B. (2008). Evo-Devo and an Expanding Evolutionary Synthesis: A Genetic Theory of Morphological Evolution. Cell, 134(1), 25–36.	Raff, R. A. (1987). Constraint, flexibility, and phylogenetic history in animal development. Evolution, 41, 737–747.
9 11/2	Species concept VI.1	Mayr, E. (1963) Animal species and evolution. Cambridge. Chp 2.	De Queiroz, K. (2007). Species concepts and species delimitation. Syst Biol, 56(6), 879–886.	Agapow PM, Bininda-Emonds ORP, Crandall KA, Gittleman JL, Mace GM, Marshall JC, Purvis A: The impact of species concept on biodiversity studies. Quart Rev Biol 2004, 79:161-179.
10 11/9	Speciation VI.8	Mayr, E. (1942). Systematics and the origin of species. Columbia University Press. Chp 8	Seehausen, O., et al (2014). Genomics and the origin of species. Nat Rev Genet, 15(3), 176–192.	Roux, C., Fraïsse, C., Romiguier, J., Anciaux, Y., Galtier, N., & Bierne, N. (2016). Shedding Light on the Grey Zone of Speciation along a Continuum of Genomic Divergence. PLOS Biology, 14(12), e2000234.
11 11/16	Is hybridization evolutionary noise or creativity? VI.6	Anderson, E., & Stebbins Jr., G. L. (1954). Hybridization as an Evolutionary Stimulus. Evolution, 8(4), 378–388.	Edelman, N. B., & Mallet, J. (2021). Prevalence and Adaptive Impact of Introgression. Annual Review of Genetics, 55, 265–283.	Marques, D. A., Meier, J. I., & Seehausen, O. (2019). A Combinatorial View on Speciation and Adaptive Radiation. Trends Ecol Evol, 34(6), 531–544.
12	Phylogenetics	Cavalli-Sforza, L. L., & Edwards, A.	Edwards, S. V. (2009). Is a new	Omland, K. E., Cook, L. G., &

11/23	II.2	W. (1967). Phylogenetic analysis. Models and estimation procedures. American Journal of Human Genetics, 19(3 Pt 1), 233–257.	and general theory of molecular systematics emerging? Evolution 63(1), 1–19.	Crisp, M. D. (2008). Tree thinking for all biology: The problem with reading phylogenies as ladders of progress. BioEssays, 30(9), 854–867.
13 11/30	Macroevolution VI.11 and VI.12	Eldredge, N., & Gould, S. (1971). Punctuated Equilibria: An Alternative to Phyletic Gradualism. In Models in Paleobiology (Vol. 82, pp. 82–115).	Uyeda, J. C., Hansen, T. F., Arnold, S. J., & Pienaar, J. (2011). The million-year wait for macroevolutionary bursts. Proceedings of the National Academy of Sciences, 108(38), 15908–15913.	Rabosky, D. L. (2017). Phylogenetic tests for evolutionary innovation: The problematic link between key innovations and exceptional diversification. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 372(1735), 20160417.
14 12/7	Student presentations			