

## INTEGBI 172 - Coevolution: from genes to ecosystems (4 units)

As your instructor, my ultimate goal for this course is that you find your own scientific identity and voice. Through this course I hope that you discover the aspects of science you enjoy the most and then leverage this excitement to produce an original synthesis of work, collecting existing (published) evidence to explore a species interaction of your choice and determining for yourself if it is the result of coevolution. This class is designed so that everyone can succeed. It's challenging, but there are ample opportunities to gain points towards mastery of the topic, and ultimately to find your own interest in the topic of coevolution – whether it's molecular evolution, chemical ecology, mathematical modeling, phylogenetics, medicine, microbiomes, or something else. I am glad you are here!



**INSTRUCTOR:** Prof Britt Koskella, PhD (she/her)

*Office hours:* In person (Valley Life Sciences Building, room 5099) or on Zoom (<https://berkeley.zoom.us/j/93929606229>) on **Mondays from 10:30-11:30am** or by appointment

*Email:* [bkoskella@berkeley.edu](mailto:bkoskella@berkeley.edu)

*Webpage:* <http://www.naturesmicrocosm.com>

**INSTRUCTOR BACKGROUND:** Prof Koskella has broad training in Ecology and Evolution, with a particular focus on host-pathogen interactions. Her research began as an undergraduate student examining the genetics of a fungal ‘smut’ pathogen that sterilizes flowers, then continued during her PhD where she used a snail-trematode interaction to test for the importance of host-parasite coevolution in driving diversity, and most recently has been focused on how bacteriophage viruses influence their bacterial hosts, and what effects this might have on the eukaryotic hosts in which these bacteria live. Prof Koskella believes in the need for increased diversity in science and works to foster a research and **classroom environment in which all opinions and ideas are valued, and where each student feels empowered to offer new insight to a rapidly developing field.**



**GSI:** Asa Conover (he/him)

*Office hours:* In person (location TBD) or on Zoom

(<https://berkeley.zoom.us/my/asazoomroom>) on Thursdays from 2:00-3:00pm or by appointment.

**GSI BACKGROUND:** Asa is a PhD student in Integrative Biology and Berkeley

Fellow studying plant-associated bacterial and fungal communities. He is a

microbial ecologist with a broad love of natural history. He has worked with a variety of organisms, including cyanobacteria, corals, frogs, and lizards. His current focus is on the use of the insectivorous California pitcher plant as an ideal system to explore the assembly and function of microbiomes.

**CLASS TIME:** Tuesdays and Thursdays, 3:30-5pm

**CLASS LOCATION:** Mulford 230

**bCourses site:** INTEGBI 172 - LEC 001

**DISCUSSION SECTION TIME:** Fridays 1-2pm

**DISCUSSION SECTION LOCATION:** Dwinelle 259

**COURSE FORMAT:** Two 1.5-hour class sessions per week and one hour of discussion section focused on reinforcing class topics and developing your individual case studies. Tuesday classes will consist of a 45-minute lecture, designed to prepare you for the week's reading, followed by an activity to exemplify the key topic. Thursday classes will consist of a 30-minute lecture followed by a class discussion lead by student groups (of 2-3). Every class period will include a short turned-in response to gauge understanding of the previous lecture (completion of which will also act as participation points). Each week, one paper (a piece of peer reviewed literature) will be assigned to read in preparation for discussion. In addition, each week will have a short textbook chapter to help solidify the core concepts and act as a study guide. All students will take a turn at leading discussion in groups of 2-3 students (to be assigned at the first class). Each week also offers an optional reading assignment which was chosen to reinforce ideas introduced in the lectures. It is recommended that these readings be at least skimmed and, if interested, can form the basis for one of your add-on/mastery points. The final project is a two-part assessment: the first involves a poster presentation on the evidence of coevolution from a species interaction of your choice, and the second is a written case study of this system. The discussion section is designed to give you ample opportunity to develop this synthesis and create a truly independent piece of science. Be creative and have fun!

**PREREQUISITES:** Bio 1A and Bio 1B or equivalent required, Genetics or Evolution course suggested.

**FULL COURSE DESCRIPTION AND AIMS:** The biological world is shaped by interactions among species. These inter-specific interactions, such as between predators and prey, plants and pollinators, or hosts and pathogens, have led to an impressive array of adaptations, helping to explain the incredible organismal and genetic diversity on Earth. Our understanding of coevolution (the responses to reciprocal selection acting on two interacting populations) has been greatly facilitated by conceptual advancements, new methods allowing direct tests of theory, next generation sequencing technology, and the advance of 'omics' approaches. But interest in this topic has also increased in light of increasing evidence that human health and happiness is dependent on interactions with other organisms, including the vast array of microbial species that live in and on us (our microbiota), and that climate change is leading to rapid deterioration of our intricate and complex web of life.

The aim of this course is to explore the multitude of ways in which one unit of selection (whether it be a gene, cell, subpopulation, population, or community) reciprocally influences the evolution of other units of selection. **Among the questions we will explore are:** Why do pathogens cause harm to their hosts? How does selection shape elaborate traits associated with plants and pollinators? Why do the phenotypes of sexes across many species differ so dramatically? How much of the diversity we observe on earth is the result of coevolutionary interactions? Why do some predators specialize on prey while others do not? What mechanisms ensure mutualistic interactions remain beneficial to all involved? How is the microbiome formed and how is it influencing the evolution of eukaryotes? And what role might coevolution play in maintaining the stability of an ecosystem? **Not all species interactions lead to and/or are shaped by coevolution, and it requires both a firm knowledge base and ability to think critically about ecology and evolution to discern when coevolution is likely to be occurring.** The development of this understanding is of particular relevance in light of recent human-mediated environmental change, the emergence of new diseases, and the myriad of ways in which humans are engineering organisms in nature. In order to predict the impacts of these changes at the population,

community, and ecosystem levels we need to understand the influence of coevolution across scales. **By the end of the course, you should be able to make such informed predictions and understand how to go about testing them in the future.**

#### INTENDED LEARNING OUTCOMES

- Infer patterns of species interactions by comparing phylogenies, critically examining scientific evidence, and synthesize conclusions from multiple studies.
- Demonstrate a detailed understanding of the traits underlying species interactions and how these traits might evolve through time.
- Formulate and defend hypotheses on how evolution and coevolution might lead to diversification within and among populations, and even lead to new species.
- Apply simple models to untangle the complex nature of ecological interactions.
- Identify practical methods for the study of coevolutionary interactions.
- Interpret relevant information from the primary literature on the evolution and ecology of species interactions.
- Participate in both small (at table) and large (whole class) group discussions.
- Work with others to develop and propose an experiment you could use to test basic coevolutionary theory.
- Lead group discussion on a particular paper topic.
- Write a case study written for a general audience describing a specific coevolutionary interaction.
- Present a scientific poster on the evidence for coevolution between a pair of species.

TEXTBOOK: There isn't a published one.... yet. **Over the course of the semester, you and I are going to continue collaboratively writing the first online, freely accessible textbook on coevolution.** Each week I will provide a (work in progress) chapter that forms the conceptual basis of the textbook. I plan to (finally!) publish this textbook at the end of the semester (Spring 2024). One of the key goals of this course is to develop your ability to think critically about coevolution and use the theory to help determine whether a particular interaction is likely to be coevolving. As such, you will work independently to choose case studies that best illustrate a given concept and to write these up in a textbook format (i.e. accessible to those new to coevolution). This project will form a large part of your final grade, will be presented in the form of a poster to your classmates, and will allow you to think deeply about the coevolutionary process. **These case studies will be revised and collaboratively edited over the course of the semester with the end product being a publicly available online textbook to which each of you (should you wish) will be named as contributors.**

READINGS: The readings are all primary literature from peer-reviewed science journals, and you should therefore expect to be confused and to not understand everything. **Learning to read the literature is a skill that takes time to develop** (as is writing it! And some of the authors you will read are still learning how to communicate their science effectively), so be patient with yourself and give yourself enough time to read the papers. Focus first on the big picture and key results; do you understand the main message from the paper? Can you explain why it's interesting? Then re-read the paper and try to get a bit more from it; where are your points of confusion? What do you find to be most interesting about the paper? If you go through this process each week, you will have no problem

taking part in class discussions. Asking for clarification on points of confusion are just as useful of a contribution as sharing your ideas about what makes the paper strong (or weak)!

**ASSESSMENT:** This semester we are moving towards mastery grading, which means that there are many ways to reach mastery of this topic, and many opportunities to acquire points (i.e. there are far more points available than would be required to get an A – it all depends on where you want to focus your efforts). The primary components of your final grade will be made up from:

- Participation points (approximately 20% of final grade) include: 8 points for your role as Discussion lead and 12 points for in-class activities.
- Discussion activities (approximately 10% of final grade): The discussion section is built to support your success in the class and the expectation is that you attend these regularly (with two automatically excused absences). Your grade from this section (10 points) depends on both active participation in discussion and completion of activities (most of which are to support your continual progress on your final project).
- Exams (approximately 45% of final grade): Each of the two midterms will be worth 10 points, and the cumulative final exam will be worth 25 points. The exams will be made up of short answer (40%) and multiple choice (60%) questions, and the final exam will also include a long answer essay, for which I will provide the possible prompts (one of which will be the verbatim prompt on the exam) the week prior to the exam to help guide your study,
- Case Study (approximately 25% of final grade): The final project consists of both a poster presentation (10 points) and write up (15 points) focusing on the Coevolutionary case study of your choice that you research and write up throughout the semester.

Points associated with the above components can be supplemented by any of the following activities:

- *Optional reading discussion groups* (up to 0.5 point per assignment, depending on level of completion): If you read the optional papers in a given week, please submit 5 questions you had from the readings and come to office hours (mine or Asa's) to discuss these questions (and contribute answers to other's questions) about the reading \*
- *Optional paper suggestions* (up to 1 points per assignment, depending on level of completion): If there is a particular topic you are excited about that is covered in lecture, please find a recent (last 5 years) paper on this topic to read, and write a short (<1 page) essay that explains why you think the paper would be a good addition to the syllabus next year. This should include a clear description of how it relates to the class, why you think students would be interested in it, and how it relates to core concepts taught in the course \*
- *Optional interview questions* (up to 1 point per assignment, depending on level of completion): throughout the course I will be recording interviews with experts in the field to include on the textbook website. I would love to include questions from students in the class. If you are interested in participating, please read a paper from that author that relates to coevolution and submit 3-5 questions that you would like to ask them in light of your reading (although the questions don't have to pertain to the paper, it should be clear that they were motivated from your understanding of the author's work) \*

\* These optional activities must be completed by 4/16/24 to allow us ample time for grading. They can NOT be turned in after 4/16/24. Thank you for your understanding.

**USE OF AI:** ChatGTP and other LLMs can be very useful for finding patterns, collating information and otherwise streamlining efforts. However, this technology is NOT capable of gaining any new insights or synthesizing literature in a novel way. As such, it will do a very poor job of helping you write your poster or case study given the goals of novel synthesis and contribution to the field. More importantly, using AI to complete these assignments stands in direct contrast to how they were designed to help you develop your identity as an independent researcher and scientist. All written components from the class (apart from in-class essays on exams) will require a specific section outlining your use of AI – describing if and how you used it to complete the assignment. This certification must be signed, indicating that it accurately reflects how you used these tools, and any use for the tools beyond what is disclosed will be considered cheating.

**ABSENCES:** We know that this class is just one of many demands on your time and that life often throws unexpected challenges your way. We will make sure that you can succeed despite any unforeseen circumstances you encounter. **All students can miss up to 4 class sessions** and 2 discussion sections without penalty, no need to contact us. Beyond that, please do reach out to discuss how your missed classes can be supplemented to ensure you do not fall behind.

**INCLUSIVE CLASS CULTURE:** This course, at its heart, is a celebration of biological diversity. In my experience, this only works when students are able to bring their genuine selves and viewpoints to the table, and through that openness and vulnerability are then able to develop their own scientific identity. Throughout the semester, we will work together to create a learning community that is inclusive and respectful. A dedication to inclusiveness requires respecting what others say, their right to say it, and the thoughtful consideration of others' communication. Both speaking up and listening are valuable tools for furthering thoughtful, enlightening dialogue. Respecting one another's individual differences is critical in transforming a collection of diverse individuals into an inclusive, collaborative and excellent learning community. When you disagree with someone, be sure that you make a distinction between criticizing an idea and criticizing the person. Expressions or actions that disparage a person's or group's race, ethnicity, nationality, culture, gender, gender identity / expression, religion, sexual orientation, age, veteran status, or disability will not be tolerated (please remember and respect our Principles of Community: <https://diversity.berkeley.edu/principles-community>).

**COURSE ACCESSIBILITY:** UC Berkeley is committed to creating a learning environment that meets the needs of its diverse student body including students with disabilities, as am I. If you anticipate or experience any barriers to learning in this course, please feel welcome to discuss your concerns with me. If you have a disability, or think you may have a disability, you can work with the Disabled Students' Program ('DSP') to request an official accommodation. DSP is the campus office responsible for authorizing disability-related academic accommodations, in cooperation with the students themselves and their instructors. You can find more information about DSP, including contact information and the application process at [dsp.berkeley.edu](https://dsp.berkeley.edu). If you have already been approved for accommodations through DSP, please contact me so we can develop an implementation plan together.

**IF YOU NEED HELP:** We know that sometimes life presents challenges that make learning incredibly difficult. We will always do our best to work with you to develop a plan forward in light of unforeseen challenges, or even at the beginning of the semester if you know ahead of time that there will be an

obstacle to your success. Beyond the course, know that at Berkeley you are part of a community that helps and supports one another. The Supportal is an excellent resource to start finding the help you need: <https://supportal.berkeley.edu/>

## COURSE SCHEDULE:

1/16/24 Introduction to Coevolution

1/18/24 **Lecture 1:** Types of coevolutionary interactions; **Discussion 1** on Janzen paper (instructor lead, but be prepared with thoughts/questions on reading)

Friday: How to lead an active discussion. How to develop discussion questions. How not to dominate the conversation, but rather contribute to and lead it.

*Reading:* Janzen, D. H. (1980). When is it coevolution. *Evolution*, 34(3), 611-612

*Textbook:* I. Introduction to Coevolution

*Optional reading:* Blog post: <https://www.molecular ecologist.com/2023/10/13/when-coevolution-definition-history/>

1/23/24 **Lecture 2:** The basics of competition; **Exercise 1:** Identifying your own niche space and determining when to specialize versus generalize.

1/24/24 **Lecture 3:** When competition leads to character displacement; **Discussion 2:** Grant & Grant (student lead; group 2).

Friday: How to find and read a scientific paper.

*Reading:* Grant, P. R., & Grant, B. R. (2006). Evolution of character displacement in Darwin's finches. *Science*, 313(5784), 224-226.

*Textbook:* II. Competition and ecological character displacement

*Optional:* Stuart, Y. E., & Losos, J. B. (2013). Ecological character displacement: glass half full or half empty? *Trends in ecology & evolution*, 28(7), 402-408.

1/30/24 **Lecture 4:** Host-parasite interactions; **Exercise 3:** Modelling coevolution

2/1/24 **Lecture 5:** The (co)evolution of virulence; **Discussion 3:** Lively & Dybdahl 2000 (student lead; group 3).

Friday: TBD

*Readings:* Lively, C. M., & Dybdahl, M. F. (2000). Parasite adaptation to locally common host genotypes. *Nature*, 405(6787), 679-681.

*Textbook:* III. Host-parasite interactions and the evolution of virulence

*Optional:* Ebert, D., & Hamilton, W. D. (1996). Sex against virulence: the coevolution of parasitic diseases. *Trends in Ecology & Evolution*, 11(2), 79-82.

2/6/24 **Lecture 6:** Predator-prey interactions; **Exercise 4:** Cyclical dynamics of predators and prey; how they happen and why they matter.

2/8/24 **Lecture 7:** Experimental coevolution; **Discussion 4:** Brodie & Brodie 1999 (student lead; group 4).

Friday: How to identify coevolutionary case studies. How to do a literature review.

*Readings:* Blasius, B., Rudolf, L., Weithoff, G., Gaedke, U., & Fussmann, G. F. (2020). Long-term cyclic persistence in an experimental predator-prey system. *Nature*, 577(7789), 226-230.

*Textbook:* IV. Predator-prey interactions

- Optional:* Nair, R. R., Vasse, M., Wielgoss, S., Sun, L., Yuen-Tsu, N. Y., & Velicer, G. J. (2019). Bacterial predator-prey coevolution accelerates genome evolution and selects on virulence-associated prey defences. *Nature communications*, 10(1), 1-10.
- 2/13/24 **Lecture 8:** Introduction to Plant-Herbivore Interactions; **Exercise 5:** Trade-offs in defense
- 2/15/24 **Lecture 9:** Beyond the pair: exploring diffuse coevolution; **Discussion 5:** Iwao and Rausher 1997 (student lead; group 5).
- Friday: Creating an annotated bibliography; Feedback on case study choices
- Readings:* Iwao, K., & Rausher, M. D. (1997). Evolution of plant resistance to multiple herbivores: quantifying diffuse coevolution. *American Naturalist*, 316-335
- Textbook:* V. Herbivory
- Optional:* Agrawal, A. A., Hastings, A. P., Johnson, M. T., Maron, J. L., & Salminen, J. P. (2012). Insect herbivores drive real-time ecological and evolutionary change in plant populations. *Science*, 338(6103), 113-116.
- 2/20/24 MIDTERM 1
- 2/22/24 **Lecture 10:** Antagonistic interactions as drivers of rapid evolutionary change; **Exercise 6:** Time shift experiments as indicators of mode and tempo of coevolution
- Friday: Narrowing down case study options. Identifying overlap and ensuring coverage.
- Readings:* Brockhurst, M. A., & Koskella, B. (2013). Experimental coevolution of species interactions. *Trends in ecology & evolution*, 28(6), 367-375.
- Textbook:* VI. Antagonistic interactions as driver of rapid evolutionary change
- Optional:* Futuyma, D. J., & Agrawal, A. A. (2009). Macroevolution and the biological diversity of plants and herbivores. *Proceedings of the National Academy of Sciences*, 106(43), 18054-18061.
- 2/27/24 **Lecture 11:** Mutualisms and trait loss; **Exercise 7:** The prisoner's dilemma
- 2/29/24 **Lecture 12:** How to prevent a cheat; **Discussion 6:** Ellers et al. 2012 (student lead; group 6).
- Friday: Mini-presentation (2-3 minutes) on identified case study.
- Readings:* Ellers, J., Toby Kiers, E., Currie, C. R., McDonald, B. R., & Visser, B. (2012). Ecological interactions drive evolutionary loss of traits. *Ecology letters*, 15(10), 1071-1082.
- Textbook:* VII. Mutualism
- Optional:* Rand, D. M., Haney, R. A., & Fry, A. J. (2004). Cytonuclear coevolution: the genomics of cooperation. *Trends in ecology & evolution*, 19(12), 645-653.
- 3/5/24 **Lecture 13:** Plant-pollinator interactions; **Exercise 8:** Attracting the right pollinator
- 3/7/24 **Lecture 14:** Chemical ecology underlying species interactions; **Discussion 7:** Hu et al. 2008 (student lead; group 7).
- Friday: Feedback on annotated bibliographies for case study; What makes for a good source?
- Readings:* Hu, S., Dilcher, D. L., Jarzen, D. M., & Taylor, D. W. (2008). Early steps of angiosperm-pollinator coevolution. *Proceedings of the National Academy of Sciences*, 105(1), 240-245.
- Textbook:* VIII. Plant-pollinator interactions
- Optional:* Van Der Kooi, C. J., Vallejo-Marín, M., & Leonhardt, S. D. (2021). Mutualisms and (a) symmetry in plant-pollinator interactions. *Current Biology*, 31(2), R91-R99.

- 3/12/24 **Lecture 15:** Mimicry; **Exercise 8:** Chasing another species through trait space
- 3/14/24 **Lecture 16:** The continuum of coevolutionary interactions from mutualist to antagonist; **Discussion 8:** Kapan 2001 (student lead; group 8).
- Friday: TBD
- Readings:* Kapan, D. D. (2001). Three-butterfly system provides a field test of Müllerian mimicry. *Nature*, 409(6818), 338-340
- Textbook:* IX. Mimicry and the continuum of coevolutionary interactions
- Optional: Lund, J., Dixit, T., Attwood, M. C., Hamama, S., Moya, C., Stevens, M., ... & Spottiswoode, C. N. (2023). When perfection isn't enough: host egg signatures are an effective defence against high-fidelity African cuckoo mimicry. *Proceedings of the Royal Society B*, 290, 20231125.
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- 3/19/24 **Lecture 17:** The Geographic Mosaic Theory of Coevolution; **Exercise 9:** Interpreting variation across space
- 3/21/24 **Lecture 18:** Temporal and spatial scales of coevolution; **Discussion 9:** Anderson and Johnson 2008 (student lead; group 10).
- Friday: TBD
- Readings:* Anderson, B., & Johnson, S. D. (2008). The geographical mosaic of coevolution in a plant–pollinator mutualism. *Evolution*, 62(1), 220-225.
- Textbook:* X. The Geographic Mosaic Theory of Coevolution
- Optional: Gomulkiewicz, R., Thompson, J. N., Holt, R. D., Nuismer, S. L., & Hochberg, M. E. (2000). Hot spots, cold spots, and the geographic mosaic theory of coevolution. *The American Naturalist*, 156(2), 156-174.
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- 3/26/24 **Lecture 19:** Coevolution with and within the microbiome; **Exercise 10:** Competition versus cooperation in microbial communities
- 3/28/24 **Lecture 20:** The great Holobiont controversy – is it worth redefining the unit of selection?; **Discussion 10:** Abdelfattah et al. 2022 (student lead; group 10).
- Friday: TBD
- Readings:* Abdelfattah, A., Tack, A. J., Wasserman, B., Liu, J., Berg, G., Norelli, J., ... & Wisniewski, M. (2022). Evidence for host–microbiome co-evolution in apple. *New Phytologist*, 234(6), 2088-2100.
- Textbook:* XI. Coevolution within communities: from individuals to holobionts to ecosystems
- Optional: Koskella, B., & Bergelson, J. (2020). The study of host–microbiome (co) evolution across levels of selection. *Philosophical Transactions of the Royal Society B*, 375(1808), 20190604.
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- 4/2/24 MIDTERM 2
- 4/4/24 (Britt away) Guest Lecture 21: TBD
- Friday: TBD
- Readings:* None
- Textbook:* None



- Optional:* Wilson, A. C., & Duncan, R. P. (2015). Signatures of host/symbiont genome coevolution in insect nutritional endosymbioses. *Proceedings of the National Academy of Sciences*, 112(33), 10255-10261.
- 4/9/24     **Lecture 22:** Cospeciation and diversification; **Exercise 11:** Interpreting cophylogenies and patterns of phylosymbiosis
- 4/11/24     **Lecture 23:** Phylosymbiosis as an emerging field to understand macroevolutionary patterns of host-microbiome interactions; **Discussion 11:** Currie et al. 2003 (student lead; group 11).
- Friday:     TBD
- Readings:* Currie, C. R., Wong, B., Stuart, A. E., Schultz, T. R., Rehner, S. A., Mueller, U. G., ... & Straus, N. A. (2003). Ancient tripartite coevolution in the attine ant-microbe symbiosis. *Science*, 299(5605), 386-388.
- Textbook:* XII. Cospeciation and phylosymbiosis: Macroevolutionary signatures of coevolution
- Optional:* Moeller, A. H., Sanders, J. G., Sprockett, D. D., & Landers, A. (2023). Assessing co-diversification in host-associated microbiomes. *Journal of Evolutionary Biology*.
- 4/16/24     **Lecture 24:** Applied Coevolution in medicine and agriculture; **Exercise 12:** Coevolving into the future
- 4/18/24     **Lecture 25:** Coevolution and Ecosystem stability; **Discussion 12:** Chan et al. 2016 (student lead; group 12).
- Readings:* Chan, B. K., Siström, M., Wertz, J. E., Kortright, K. E., Narayan, D., & Turner, P. E. (2016). Phage selection restores antibiotic sensitivity in MDR *Pseudomonas aeruginosa*. *Scientific reports*, 6, 26717.
- Textbook:* XIII. Coevolutionary Applications
- Optional:* Jørgensen, P. S., Folke, C., Henriksson, P. J., Malmros, K., Troell, M., & Zorzet, A. (2020). Coevolutionary Governance of Antibiotic and Pesticide Resistance. *Trends in Ecology & Evolution*.
- 4/23/24     POSTER SESSION
- 4/25/24     [Poster awards] **Lecture 26:** Temporal and spatial scales of coevolution (review of key topics)
- Friday:     Final peer feedback on case study
- 4/30/24     RRR Week: NO CLASS
- 5/2/24     RRR Week: (optional) Review session scheduled
- Friday:     RRR Week: NO DISCUSSION SECTION
- 5/10/24     FINAL EXAM