

Coevolution or not? Crossbills, squirrels and pinecones

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Abstract

This case reinforces the concept of coevolution as a reciprocal change in genetic structure between or among two or more populations, by having students analyze and interpret data, build a descriptive model of the system, and use data to make scientific arguments. The case study is designed for a single 50-minute class period after students have completed a brief pre-class reading assignment introducing coevolution. Students analyze evidence for interactions among red squirrels (*Tamiasciurus hudsonicus*), red crossbills (*Loxia curvirostra*), and lodgepole pines (*Pinus contorta* v. *latifolia*). The case describing the interactions among these species invites students to answer three questions: 1) What evidence is required for demonstrating coevolution? 2) What specific evidence supports the conclusion that that red squirrels, red crossbills, and lodgepole pines are coevolving (or not) in this system? 3) Why does the evidence support coevolution (or not)? In this discussion- and jigsaw-based case study, students advance both their core conceptual knowledge and their proficiency with scientific practices.

Learning Goal(s)

- Students will understand that species interact on evolutionary time scales.
- Students will know that other organisms can be powerful agents of selection.

Learning Objective(s)

- Define coevolution.
- Identify types of evidence that would help determine whether two species are currently in a coevolutionary relationship.
- Interpret graphs.
- Evaluate evidence about whether two species are coevolving and use evidence to make a scientific argument.
- Describe what evidence of a coevolutionary relationship might look like.
- Distinguish between coadaptation and coevolution.

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Materials and Supplemental Materials: Table 1. Coevolution or not-Teaching Timeline, Table 2. Coevolution or not-Teaching rubric for exhibits 1-4, Figure 1. Coevolution or not-Distribution of lodgepole pines in the northern Rocky Mountains, Supplemental File S1. Coevolution or not-In-class presentation, Supplemental File S2. Coevolution or not-Pre-class homework, Supplemental File S3. Coevolution or not-Modeling evolutionary relationships handout, Supplemental File S4. Coevolution or not-System map handout and Supplemental File S5. Coevolution or not-Summative assessment question.

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INTRODUCTION

Origin of Lesson

At a national meeting focused on undergraduate biology course curricula, an evolutionary biologist, an ecologist, and a parasitologist found themselves among small group of molecular/cellular biologists. Out of our strong backgrounds

in evolution (Martin) and parasitology (Powers), and the first author's (Hoskinson's) reading of Zimmer's *Parasite Rex* (1) and Ridley's *The Red Queen* (2), we discovered that we had a common interest in coevolution (3). We also recognized how difficult it is to teach coevolution, how few good teaching resources for this topic exist, and how existing lessons and ideas are often constrained by classroom configuration (large

lecture halls with fixed seating) and student background or year in college. We decided to build a lesson on coevolution, but first, we needed an ecological (biological) system in which coevolution had been studied. The University of California – Berkeley’s website Understanding Evolution (4) described a system of crossbills (birds), pinecones, and the more recently introduced red squirrels in the western United States. Using that system description as a starting point, we began researching the primary literature.

Context and Rationale

Coevolution is an important mechanism for producing and maintaining mutualism and parasitism between or among species. Ehrlich and Raven coined the term coevolution to describe the close ecological and evolutionary relationship between butterflies and flowers (3). Coevolution occurs when two (or more) species in a community adapt to one (or more) traits of the other species in a sustained, reciprocal way over time. Coevolution has since been explored by ecologists and evolutionary biologists, and many examples illustrate the richness of the kinds of coevolution that have shaped populations and communities over evolutionary time, including the simultaneous, mutualistic rise of pollinating insects (Lepidoptera, Hymenoptera, Diptera) and flowering plants (Magnoliophyta) in the Jurassic and Triassic periods; host-parasite coevolution (5); and predator-prey relationships such as between cheetahs and gazelles and (possibly!) among crossbills, squirrels, and pinecones. This case study illustrates an example of predator-prey coevolution and asks learners to extend their thinking to diffuse coevolution among more than 2 species (6).

This case is built on the work of Craig Benkman and others (7-9) who studied red squirrels (*Tamiasciurus hudsonicus*), red crossbills (*Loxia curvirostra*), and lodgepole pines (*Pinus contorta* v. *latifolia*) in the northern Rocky Mountains, United States (Figure 1). Both the squirrels and the birds eat lodgepole

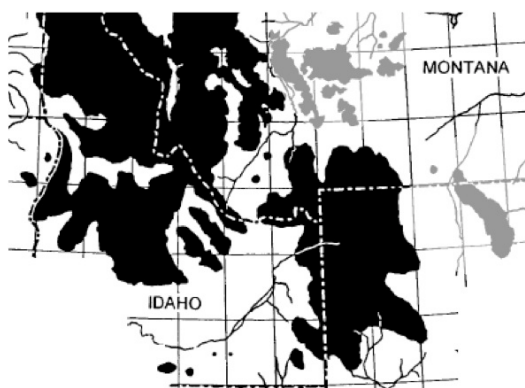


Figure 1. Distribution of lodgepole pines (black) in the northern Rocky Mountains, USA. Crossbills (birds) are present wherever lodgepole pines occur. The range of red squirrels also overlaps with lodgepole pines, but were absent from some areas (gray) until 1950. Figure adapted from Benkman et al. 2003.

pine seeds. However, while crossbills have co-occurred within pine forests for thousands of years, red squirrels were absent from the same forest types for ~10kY, until they were reintroduced in ~1950 (9).

Students' Prior Knowledge

Novice biologists can have many misconceptions or naïve

conceptions about coevolution. One is about the nature of adaptation itself. To many introductory biology students, adaptation sometimes confers an idea of flexibility or choice, i.e. agency, on the part of the species: individuals simply choose to adapt or not to adapt. Students need reminders of the biological definition of adaptation, both as a process, through means of natural and/or sexual selection, and as an outcome, such as a change in a functional trait's allele frequency, or a change in some measure of fitness such as survival or number of offspring. The corollary to this idea is that coadaptation is necessary, but not sufficient, to claim coevolution. Like the broader concept of evolution, coevolution requires a change in allele frequencies (of both or all species), or a change in fitness such as fecundity or survival of offspring. While it is sometimes the case that populations can co-adapt, the evidence of reciprocal changes can be hard to come by. We have found that the misconception that co-adaptation is (equals) coevolution is particularly difficult for students to overcome, and so it is one of the main points of this lesson.

Another naïve conception is that two, and only two, interacting species must necessarily adapt to traits in the other. For example, many students believe some variant of the idea that, if a predator gets faster, its prey will certainly get faster too. This lesson helps students reformulate that conception in three ways: 1) by using a system of three interacting species, in which evidence shows only two of the three species may be co-adapting (crossbills and pinecones) and just one direct piece of evidence shows a change in survivorship necessary to support coevolution (Exhibit 2); (2) by asking students to graphically depict the evolutionary relationship, including its direction and description, and 3) by asking students to make scientific arguments using claims and evidence about whether interacting species are, in fact, coevolving.

Finally, students typically struggle with interpreting graphical data, a scientific practice that is at the heart of this lesson. In order to identify the relationship supported by each piece of evidence, students must 1) identify the dependent and independent variables; 2) determine the effect, if any, of the independent variable on the dependent variable and 3) use the data to determine whether the evidence supports a claim of coevolution. Distinguishing between the dependent and independent variables also serves to emphasize the directional nature of the relationship. Students with less-developed data interpretation skills get the advantage of coaching from peers and/or TAs, learning assistants, or instructors, who have more-developed skills. Students with more-developed data interpretation skills still receive the benefit of reinforcing coevolution concepts through data interpretation, while extending their skills by making predictions and scientific arguments using available evidence.

Intended Audience

The intended audience is students in an introductory biology (majors, non-majors, or mixed) course or a first course in ecology or evolution. It is suitable for any class size up to several hundred, although you will have to think about the logistics of the handouts the same as you must for any other handouts. We have taught the lesson in classes of ~100 – 150 students. The lesson can be completed in a single 50-minute class meeting and includes optional add-ons described in the text and in Table 1. It can be modified for audiences ranging from non-major introductory students to upper division majors. The lesson as written presumes that students know

only what they read from a typical textbook introducing the concept of coevolution.

SCIENTIFIC TEACHING THEMES

Active learning

- Before class: Students begin with a textbook reading about fundamentals of coevolution. Make sure to choose a passage that defines coevolution and gives the two criteria: 1) geographic overlap, and 2) change in allele frequency or measure of fitness. Students complete low-stakes (accountability) homework that prepares them to work with their basic knowledge in class.
- During class: Students engage in small group and whole-class discussions; small-group data analysis, descriptive model construction, argumentation, and collaboration.

Assessment

- Before class: none
- During class: Predict outcome of species interactions; analyze data and use it to construct a scientific argument (claim + evidence); build a box-and-arrow model of the system.
- After class: The given questions (Supplemental File S5: Coevolution or not-Summative Assessment Questions) can be offered either as multiple-choice, higher-order questions, or as open-ended, free-response questions (e.g. interpreting graphs, making arguments, building models).

Inclusive teaching

- The lesson provides multiple ways for students to succeed both with the core concept of evolution, and with a diversity of scientific practices.
- Students represent knowledge and ideas with a variety of means, including language, graphs, diagrams, and a simple model.
- Collaboration is built into the lesson so that students prompt one another to strengthen arguments, explain their thinking, and modify their ideas with feedback.
- The system of birds, pinecones, and squirrels is both familiar to students and invites them to learn more.

LESSON PLAN

This lesson can be adapted to run during a single 50-minute class period, or a longer (70-minute) class period. Table 1 (on page 4) describes a lesson timeline with options for shorter or longer time constraints with suggested time allotments for each of the five (50-minute) or six (70-minute class) lesson activities described below. Based on our teaching of this lesson in our own classrooms, and consistent with student-centered learning, we have built flexibility into the time allotment for each lesson activity. Therefore, we recommend you keep track of how much time your particular class takes for each lesson activity, both to keep your class on track and to adapt the lesson to your own environment in the future.

Before class meeting

What instructors do: We have developed a short set of lesson slides (Supplemental File S1: Coevolution or not-In-class Presentation.pptx) that you are welcome to download and modify at your discretion, depending on your own system of interest and teaching style and goals. You should also print handout copies for each student (Supplemental File S3: Coevolution or not-Modeling Evolutionary Relationships

handout.docx and Supplemental File S4: Coevolution or not-System Map handout.docx) and Exhibits 1-3 (slides 13-15 in Supplemental File S1), one Exhibit for every third group. (If you have 30 groups, you need 10 copies of each Exhibit slide.) If your students do not have existing working groups, it is a good idea to inform them that they'll be working cooperatively during this class meeting. To familiarize yourself with the system on which this lesson is based, you can read any one of the Benkman articles. (7-9)

What students do: Students should read an introduction to coevolution in whatever textbook they are using. Students in most gateway ecology and evolution courses can also read Janzen's article, "When is it coevolution?" a short introduction to the evidence needed for coevolution and common misconceptions about it (6). Give students the accountability homework (Supplemental File S2: Coevolution or not-Pre-class homework.docx) asking them to define coevolution in their own words. They should complete this homework before the target class period.

During class meeting

1. *Lesson introduction (instructor and students, 5-6 minutes).* With student input, you should review two necessary conditions for coevolution to occur: (1) geographical overlap between species, and (2) reciprocal change in heritable traits, i.e. some measure of fitness or survival.

You should prompt the students for the conditions rather than tell students what they are. Depending on your teaching style, you can call randomly on students, or use whatever system you prefer. You can then invite students to view a video of a cheetah chasing a gazelle. Depending on your goals, you can ask students to think-pair-share and consider whether and how coevolution is shown in the video, then predict what would happen if cheetahs were to become faster as a population. The fundamental concepts that students should notice are that speed is under strong directional selection in each species, and that the species themselves (populations of cheetahs and gazelles) are the selective agents for changes in the other species for this trait.

If you have not yet introduced the terms directional selection, selective agents, and fitness, you should spend a few moments having students define these terms in context. You can do this either as a think-write or think-talk activity, again to suit your goals and teaching style. Make sure to emphasize the population-level interaction between cheetahs and gazelles in this and future systems you consider. Introductory biology students often believe that one individual of each species can coevolve with another. Students need reminders that selection acts on traits of individuals, and cumulative changes in a trait occur across a population. A corollary to this reminder is that individuals can change their behavior, but they cannot change the traits they inherit from their parents. Thus, cheetahs and gazelles cannot simply will themselves to run faster.

Note: In our experience, it is a good idea to warn students about what they will see in the video clip of the cheetah chasing, bringing down, and killing a gazelle. You should also be aware that some students, especially introductory students, will not know the word "predate," and are more inclined to think of predation only as one animal eating another animal (not, for example, an animal eating a plant, or invertebrates engulfing bacterial colonies).

Table 1: Coevolution or not-Teaching Timeline

Activity	Description	Approximate Time
Prior to class		
Instructor prep	<ul style="list-style-type: none"> Read one of the Benkman articles (7-9) and skim the others Examine Supplemental File S1. Coevolution or not-In-Class Presentation; modify slides and teaching notes to align with your goals Prepare handouts: <ul style="list-style-type: none"> Supplemental File S3. Coevolution or not-Mapping Evolutionary Relationships – one/student Supplemental File S4. Coevolution or not-System Map – one/student Exhibits 1, 2, & 3 (slides 13, 14, & 15 in the “Supplemental File S1” – each small group will get one Exhibit, so divide your class count by ~12 (assuming ~4 students/team) for an estimate If you plan to do the Optional add-on below, print Exhibit 4 (slide 19), one/team 	60-120 min
Student prep	<ul style="list-style-type: none"> Read an assigned section of text on coevolution Complete homework (can be set up in your CMS) 	20-30 min
Class meeting		
1. Lesson introduction	<p>Begin with Supplemental File S1. Coevolution or not-In-class presentation</p> <ul style="list-style-type: none"> Review conditions for coevolution (think-pair-share) View cheetah-gazelle film clip 	5-6 min 3-4 min 2 min
2. Introducing the system	<p>Introduce the three species</p> <p>Hand out Supplemental File S3. Coevolution or not-Modeling Evolutionary Relationships and Supplemental File S4. Coevolution or not-System Map (1 each/student)</p>	8-9 min (concurrent with system introduction)
3a & b. Group evaluation of evidence	<p>Have students form small groups of 4 (± 1)</p> <p>Hand out Exhibits 1-3 (only one Exhibit per team) and provide directions</p> <p>Circulate among student teams as they work to interpret graphs and craft arguments</p> <p>Project slide 16 with images, or draw the three species (without connections) on board or doc cam</p>	12-14 min Total: 5 min 7-9 min ~1 min (concurrent with students working)
4. Class synthesis and discussion	<p>Call on three teams, one team representing each Exhibit, to draw their relationship arrows and explain conclusion</p> <p>Prompt for questions and discussion</p>	10 min 10 min
5. Wrap-up clicker question	<p>Clicker question</p> <p>Pairwise discussion, if necessary</p>	1-3 min
6. Optional add-on	<p>Hand out and/or display Exhibit 4</p> <p>Ask all students to work with this as they did their own Exhibit</p> <p>Experimental design</p> <p>Generate predictive graph</p>	20 min 6 min 14 min

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2. *Introducing the system (instructor, 8-9 minutes).* You should invite students to consider a more complex system of three species: crossbills, squirrels, and lodgepole pinecones. Briefly describe the natural experiment that exists in the Rocky Mountains: both the squirrels and the birds predate (eat) lodgepole pine seeds. Show the map on your classroom screens. While crossbills have co-occurred within pine forests for thousands of years, red squirrels were absent from the same forest types for approximately 10,000 years, until they were reintroduced around 1950 (9). Our PowerPoint also includes links to movie clips of squirrels and crossbills working on pinecones.

At this point, you should hand out the Modeling Evolutionary Relationships and System Map handouts (Supplemental Files S3 and S4). Don't hand out Exhibits yet. You should step through the handouts with the entire class.

3(a). *Group evaluation of evidence: What students do.* Students should divide into informal small groups; four is an ideal size (10), but some groups of three or five are fine. Each group should get one of the three handouts labeled Exhibits 1-3. Each Exhibit presents data about an interaction between two of the three species. The class needs a minimum of three groups to make sure all datasets are considered. In a large class, multiple groups will receive the same Exhibit.

Ask students to work with the data and consider what the evidence shows. They will work with the Modeling Evolutionary Relationships (Supplemental File S3) and System Map (Supplemental File S4) and decide whether the data set they have been given – Exhibit 1, 2, or 3 – indicates a relationship between any of the species (Table 2 on page 6). On their relationship map, if their Exhibit supports it, each group should draw a directional arrow connecting the two species represented in their Exhibit indicating which species is impacting the traits of the other. Depending on your instructional goals, students can write a scientific claim, which we define as a statement about an observation for which evidence could be collected (Table 2).

3(b). *Group evaluation of evidence: What instructors do.* During this time, you and (if available) TAs/learning assistants should circulate among groups, asking and answering questions and gathering formative feedback about how the process is going. Table 2 provides instructor and TAs/Las guidance about how students are likely to interpret the data, where they might get stuck, and correct claims they can make about their data. Many introductory students will need guidance in interpreting figures, starting with describing the axes, one by one, and then making a statement about the general trend. You should already have a good idea whether you will need to do this with your particular student population. If your students are making wild claims, or leaping ahead of data analysis to their interpretation of the data, probe them to agree in their small groups on a description of each axis, and only then, the overall trend. Since we usually cannot get to all small groups, we typically work on interpreting one of the two axes with small groups as needed or, if an entire classroom is struggling, we pause and do a very short (1-2-minute) mini-lecture on stepwise figure interpretation. However, we have found that even upper-division students often need a reminder to take their time and really look at what the axes are representing. Introductory students will ask for a correct answer or for you to confirm that their guess is correct. We recommend you hold off on providing this opinion and ask them to make a simple

scientific argument using the “claim – because – evidence” framework, where they are to decide what the claim is, and what evidence from the figure supports their claim. Depending on the course and student population, this portion of the lesson can take anywhere from seven to nine minutes, and it is very likely that not all arguments will reference the claim or the evidence correctly. Although you can work with small groups as much as possible, do not worry too much about “correctness” in this part of the lesson; during Class Synthesis and Discussion (next activity), students will synthesize and, where necessary, reformulate their ideas about coevolution among these species. During this lesson activity, you should monitor student progress by checking in on: 1) their figure interpretation, 2) their formation of a scientific argument (claim + evidence), and 3) the beginning of their scientific model (Supplemental File S3: Coevolution or not-Modeling Evolutionary Relationships).

While students are discussing their group's Exhibit, take a moment to project or draw the Model at the front of the classroom, showing only the three species, without interaction arrows. When the groups have their relationship maps completed with a directional arrow, you can proceed to the next activity. If all but one or two groups finish, give a very short (about 1 minute) deadline to the remaining groups.

4. *Class synthesis and discussion (students, with instructor support, 20 minutes).* When the groups have finished examining their Exhibit and determining the relationship and direction of interaction, you should invite a member of a group representing each Exhibit to come to the front of the room and draw an arrow on the map on the board, indicating which relationship their Exhibit supported. While you display each Exhibit in the accompanying PowerPoint slide, a member of each group should share their figure legend (we have left room on the PPT slides for you to type this in, if you desire). The student representative should describe the relationship and what impact was found (e.g., “in areas where squirrels occurred, pinecones became...”). You should guide the conversation as necessary, focusing on what the evidence shows, rather than on what can be assumed or inferred. When the map is complete, the model will most likely show bidirectional arrows between pinecone and crossbill, but only a uni-directional arrow between squirrels and pinecones. Then, you should ask whether the given evidence is sufficient to support the claim that pinecones and crossbills are coevolving.

Introductory biology students typically respond to this prompt in one or both of two ways. First, they are overly skeptical of the evidence, inferring that coevolution is not occurring because they were presented with only one form of data, which is itself not 100% certain. Depending on your teaching goals, you can either take a few moments to talk about the nature of scientific certainty, or you can simply address it momentarily by reminding students that scientific certainty doesn't exist.

The more interesting way students respond really gets to one of the major misconceptions about coevolution: if species are interacting, they must be coevolving. As this assumption emerges, it is a good time for you to remind students that observation of an interaction does not equate to an observation of coevolution. Instead, you can bring them back to the second criterion for coevolution: changes in allele frequencies, or some measure of fitness or survival, over time. Only one of the Exhibits (Exhibit 2) presents data that may

Table 2: Coevolution or not-Teaching rubric for Exhibits 1-4

Exhibit	Data Summary (in typical student language)	Correct Claim (in typical student language)	Possible misconceptions/ misinterpretations of data
1	When squirrels are present, pinecones are more round and contain fewer seeds than pinecones found where squirrels are absent.	Squirrels may be selecting for rounder pinecones with fewer seeds that are harder to eat.	<ul style="list-style-type: none"> Longer cones with more seeds are “better.”* Squirrels are forcing the pinecones to change. Squirrels are just eating fewer seeds per cone. Squirrels prefer* _____.
2	As bill depth increases, average survivorship increases to a maximum of about 0.6, then decreases.	There is an optimal (best) bill depth for bird survival. If birds’ bill depths are too high or too low, they don’t survive as often.	Not understanding that the dots on the figure represent individuals who survived (top) or died.
3	Before crossbills started eating seeds, pinecones were rounder and smaller. After crossbills started eating seeds, pinecones became more oblong and heavier.	Crossbills may be selecting for longer pinecones that are heavier.**	<ul style="list-style-type: none"> Shorter, heavier cones are “better.”* Crossbills are forcing the pinecones to change. Crossbills only eat seeds from larger cones. Crossbills prefer _____.
4	Squirrels that live in areas where there are pine trees have relatively more jaw muscle mass than squirrels who live in areas without pine trees.	Something about the pine trees favors more relative jaw muscle mass in squirrels.	<ul style="list-style-type: none"> Since we do not use this exhibit in our introductory courses, students tend not to make novice interpretation mistakes. They often assume that the selective agent here is pinecones or seeds, but this figure gives no evidence to support that assumption. Students may think (erroneously) that this “explains” why the pinecones in Exhibit 1 are rounder and have more seeds, or the converse: that Exhibit 4 “explains” Exhibit 1.

*Language such as “X is better than Y” or “a tree prefers T” or “a squirrel prefers S” may reflect students’ undeveloped vocabulary in expressing evolutionary concepts, or it may indicate a deeper misconception. This is why it is so important to ask them to explain what they mean; do your best not to assume either that they understand or don’t.

** If students do not observe that squirrels and crossbills have opposite effects on the shape and mass of pinecones, you can point this out, and then ask teams to make a prediction about what will happen to the pinecones in areas where both squirrels and crossbills feed.

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be interpreted as supporting coevolution (Table 2). Although they present real data and actual measurements, the other two Exhibits provide only inferential, not direct, support of coevolution. Depending on your student population, you can bring this limitation up in a couple of different ways. First, you can simply tell your students that only one of the three exhibits presents evidence supporting a coevolutionary relationship, and ask them to discuss in their small groups whether they think it is their evidence or not, and why. This approach may be suitable for introductory students. An alternative for more advanced courses is to have students do an informal jigsaw with other small groups around them about different Exhibits, and see whether they can reach a consensus while practicing their scientific argumentation skills. Even in fixed-seating auditoriums, this discussion is usually possible.

With the prompt that only one of the three studies supports a coevolutionary relationship, students usually need little guidance to see that only Exhibit 2 presents data that shows a direct effect of crossbill (beak) depth on survivorship, thereby supporting a claim of an evolutionary change in crossbills. Exhibits 1 and 3 do not measure allele (trait) frequency, fitness or survivorship, and therefore do not contain data that support the claim of coevolution.

Finally, considering Exhibits 1 and 3 together shows that each animal has an opposite effect of the other on cone shape and mass. You can prompt students to make a prediction about what will happen to cone shape and mass in areas where both crossbills and squirrels co-occur (Figure 1, black areas; see Table 2).

5. Clicker question (students). The instructor should ask the students to consider the completed Modeling Evolutionary Relationships handout (Supplemental File S3) and present the clicker question asking students to conclude which species have a coevolutionary relationship according to the data presented. If there is not agreement about the best answer after polling the students initially, the instructor can ask the students to turn to a neighbor and try to reach a consensus. The instructor should re-poll the students, then ask a volunteer to explain his or her reasoning for the answer (co-evolution requires reciprocal change in traits, or some measurable change in fitness or survivorship).

6. Optional add-on (students, with instructor support). Finally, project Exhibit 4 for the entire class to examine. Have students work in their small groups to answer the same questions as on their Modeling Evolutionary Relationships handout. At this point, you should ask students to write a claim about which species, if any, are in coevolutionary relationships, and what evidence supports their claims. We usually have students work on this as a small group, while being individually responsible for recording the argument in their notes.

If your students are really catching on, you can also have them speculate about experimental design by having them describe some specific data they would collect to test for a change in fitness, and what they predict the data would look like. They can do this on the back of their Modeling Evolutionary Relationships handout (Supplemental File S3). Once they have used plain language to express their predictions (e.g., “We think the squirrel’s [teeth/jaws/mouth etc.] will get [smaller/larger/stronger, etc.]”), prompt them to sketch a predictive figure, labeling both axes. We introduce novices to sketching predictive graphs by having them draw two perpendicular axes,

then label the X-axis “When _____ changes in pinecones...” and the Y-axis “..._____ in squirrels will _____ as a result” (Supplemental File S1: slide 20). After giving students a chance to generate their predictions, the instructor can call on some students to describe their predictions or draw them on chalkboard, whiteboard, or document camera for the class and explain their reasoning.

Several groups will need prompting to return to the specific criterion for coevolution, i.e. a change in survivorship or fitness (# offspring). In order to record their predictions, you should guide students to sketch a graph of the expected trend. You can conclude this add-on with a discussion of similarities and differences among the predictions made by different groups in the class, and a brief discussion of experimental design (see Note).

Note: Students’ experimental designs will be rough and contain many unrealistic elements: too many or too few samples, mass organism capturing and death, species removal or introduction. For the most part, we don’t focus as much on correcting these ideas as we do in helping them constrain reality of experimental design. Next, when we first ask introductory students to perform predictive sketching of graphs, they are often too concerned about the precision of their sketch. It’s a good idea to begin simply with labeling axes (Supplemental File S1, slide 20), then a trendline that “increases, decreases, or stays about the same.” You can add refinements like non-linearity or saturating curves later, as students develop proficiency.

TEACHING DISCUSSION

Our objective was to create a lesson to fill a gap we all observed: developed cases and scenarios on coevolution that were appropriate for undergraduate biology students. Coevolution is relatively easy to identify after species interactions have shaped how species evolved, such as with flowering plants and their pollinators, or parasites and their hosts. However, all of us noticed that students did not connect the outcome with the evidence supporting it or, more problematically, they assumed that any relationship was coevolutionary. We wanted to choose a case where evidence supports coevolution *in vivo*. Therefore, another objective was to create a lesson that specifically linked scientific practices, such as interpreting data and constructing scientific arguments (claim plus evidence), to the concept of coevolution.

Three members of the team of co-authors and one individual outside the team have now taught this case multiple times. Each time, we are impressed with how willing our students are to engage with difficult (for them) figure interpretation, arguing with one another in the best scientific sense, and creating a collaborative product that would be difficult or impossible for many introductory students to complete on their own in the given time. Typically, we get several students who ask, during and after class, whether a system or scenario they are thinking of is coevolutionary. When we ask them what kind of evidence they would need in order to reach a conclusion, we’re impressed at their ability to articulate what they would need to see. In our gateway ecology and evolution courses, we often engage in a student-initiated discussion of the nature of uncertainty and decision-making in science. For many introductory courses, such a discussion may lie outside your objectives and time constraints. However, you should be aware that, for most students, science is a body of facts that are certain and known, and that they think that all it takes for them

to master science is to learn the facts. By engaging in even constrained discussions about ambiguity and uncertainty, you're exposing them to fundamental and important ideas about what science really is and how it is practiced.

One strength of this lesson is that the basic framework can easily be adapted to other systems that interest individual instructors. Other coevolutionary systems that students may have heard of include domestic dogs and humans (11-13), cuckoos laying their eggs in other species' nests (nest parasitism) (14), many systems of wasps and orchids, including an orchid that attracts wasps by mimicking a honeybee alarm pheromone (15), other systems of plants and pollinators, parasites and hosts (16), and even organisms across multiple trophic levels (17-19).

SUPPLEMENTAL MATERIALS

- Table 1. Coevolution or not-Teaching Timeline
- Table 2. Coevolution or not-Teaching rubric for exhibits 1-4
- Figure 1. Coevolution or not-Distribution of lodgepole pines in the northern Rocky Mountains
- Supplemental File S1. Coevolution or not-In-class presentation
- Supplemental File S2. Coevolution or not-Pre-class homework
- Supplemental File S3. Coevolution or not-Modeling evolutionary relationships handout
- Supplemental File S4. Coevolution or not-System map handout
- Supplemental File S5. Coevolution or not-Summative assessment questions

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