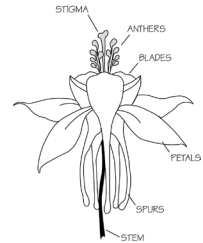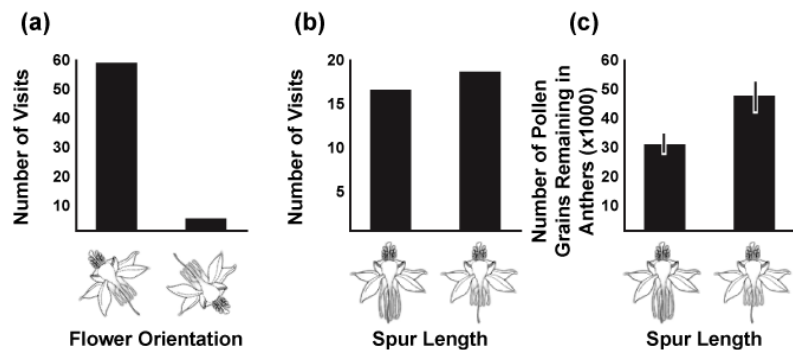# Flowers and Trees

Columbines are a diverse group of wildflowers that live in the mountains of North America, Europe, and Asia. Among their most striking traits are nectar spurs. Nectar spurs are tube-shaped modified petals, topped by structures called blades, that offer a sweet prize at the bottom for the hummingbirds, hawkmoths, and bees that pollinate the flowers.

Also striking about columbines is that there are so many different kinds. Some seventy species have been described and given Latin names. The species vary in color, spur length and shape, and flower orientation. Scott Hodges suspected that there is a connection between the nectar spurs of columbines and the number and diversity of species.

Because nectar spurs offer an enticing reward that is nonetheless hard to access, small changes in floral traits can have big effects on pollination success. The graphs above (reprinted with permission of the New Phytologist Trust from Hodges, et al.) summarize research by Hodges, in collaboration with Michelle Fulton, on the Sierra columbine (*Aquilegia pubescens*). This species is pollinated by hawkmoths. It has white or yellow upward-facing flowers with long thin nectar spurs. When Fulton and Hodges tipped Sierra columbine flowers downward, hawkmoths visited the downward-facing flowers only 10% as frequently as upward-facing flowers (graph a). When the researchers shortened the nectar spurs of flowers, by tying them off with thread, the short-spurred flowers were just as attractive to hawkmoths as long-spurred flowers (graph b). But because the moths could sip the nectar without getting as close to the flower, the moths left more of each flower's pollen behind (graph c).

When small changes in floral traits have big effects on pollination success, populations of plants may rapidly evolve flowers that allow them to specialize on particular species of pollinators. Flowers that are especially attractive to a particular pollinator but unattractive to others may disperse more

pollen to compatible recipients and receive more pollen from compatible donors. They may also diverge dramatically from populations that specialize on different pollinators. Columbines pollinated by hawkmoths tend to resemble the Sierra columbine: they have light coloration, upward-facing flowers, and long spurs. Columbines pollinated by hummingbirds, in contrast, have bright red and yellow downward-facing flowers with short nectar spurs.

To test his hypothesis that the evolution of nectar spurs led to a rapid diversification of columbine species, Hodges needed a tool that would enable him to summarize and analyze the evolutionary history of the columbines and their closest relatives. That tool is the evolutionary tree. Evolutionary trees have many applications. Evolutionary trees have been used to test the hypothesis that birds evolved from dinosaurs, to determine where the HIV virus originated, and even to prosecute a Louisiana doctor for attempted murder.

This lab will help you learn to read and use evolutionary trees by experimenting with simulated columbine populations. After you have honed your skills, we will return to Hodges' analysis of columbines and see whether his hypothesis is correct.

Exercise 1: Columbine Flower Traits

[1]   Launch **SIMBIO VIRTUAL LABS**. Select **FLOWERS AND TREES** from the **EvoBeaker** Labs options.

The model columbine populations you will experiment with live on a series of peaks in the Rocky Mountains in western North America. These peaks are shown as squares on the right side of the lab window. Because our model columbines thrive only at high elevations, the mountain peaks are effectively islands of good habitat floating in an uninhabitable sea of poor habitat.

Columbine seeds typically do not travel far. Instead, they drop to the ground near their parents. The mountain peaks in our model are far apart, so columbine seeds rarely move from one peak to another. A seed can make such a trip only if it gets picked up by an extraordinarily strong wind or if it gets stuck to the hoof of an elk or the boot of a hiker.

[2]   There are 8 flower traits that you will look for in the model columbines. To see the traits, double click or CTRL-click (⌘ click on a Mac) on one of the tiny flowers, such as the one on Peak 1. You will see a **Trait Editor** window appear. This window contains an enlarged profile view of the flower, plus the 8 variable traits listed in pull-down menus.

In the center of the window, you'll find an enlarged profile view of a columbine flower, with each of the structures labeled. Use this large-scale view as a guide when working with the Trait Editor.

[3]   Find the trait listed as **"Anthers"**. Anthers are the male parts of the flower; they are the structures that make pollen. The anthers sit atop hair-like filaments that poke up from the middle of the flower. The columbine you found on Peak 1 has white anthers. To mutate the flower so it has yellow anthers, select **Yellow** from the pull-down menu next to the word **Anthers**.

[4]   Go to each of the other traits and mutate them back and forth between their two states. As you do so, examine the changes in the enlarged cartoon flowers until you are familiar with what each of the traits looks like. When you are done, close the **Trait Editor** window.

    ★   *Note: Don't worry that flower icons, as shown on mountain peaks in the landscape panel, do not visually match flowers in the Trait Editor. For clarity, icons on peaks simply distinguish one flower type from one another rather than represent specific flower traits.*

Exercise 2: Watching Evolutionary Trees Grow

[1]   Imagine that only one of our seven peaks is inhabited by columbines, and that as this population evolves over time, seeds occasionally make the long trip from one peak to another to establish a new population. If you could watch this happen over hundreds of generations, what would you see? EvoBeaker can show you, and can summarize the events you would witness in a diagram called an **evolutionary tree** (also known as a **phylogenetic tree** or a **phylogeny**). To see this, go to the **Select An Exercise** menu and select **GROWING TREE**.

[2]   The ancestors of the columbines in our mountain range blew in as seeds several years ago and landed on one of the peaks. You can see the population of flowers now living there. Click on the **GO** button to let time advance until the original population splits into two populations. Then stop the model by clicking on the **STOP** button.

★   *Population: A population is a group of individuals that live in the same place at the same time. Because travel among peaks is difficult, the columbines on any one of our peaks interbreed with each other, but not with individuals from other peaks. This isolation means that each of our seven populations can evolve independently of the others.*

[3]   Each year as the model runs, all the old flowers set seed and then die. The following spring, the seeds sprout, grow up, and flower. Normally seeds stay on the mountain peak of their parents, but once in a long while, a fierce storm comes through and carries a seed from one peak to another, establishing a new population, which you just watched happen. Look at the evolutionary tree in the **Lab Notebook** panel.

[3.1]   **Describe how the division of one population into two is represented in the tree diagram.**

[4]   Every so often, a mutation happens in an individual flower in one of the populations. The program indicates this by changing the color and design of the tiny icon that represents the individual flower. The model is rigged so that new mutations quickly spread through the population in which they arise. Continue running the model with the **GO** button until you see the color of the flowers on one of the peaks change. When the change has spread through all flowers on that peak, **STOP** the model.

[4.1]   **In addition to the change in color of the little flowers in the peaks, describe how the change in a trait is represented on the evolutionary tree diagram.**

Hint: it is shown in two places on the tree diagram—look at both the tree itself and at the pictures of the flowers at the branch tips.

★   *Traits and Mutations: The model in this lab is rigged to make all changes be advantageous, and, therefore, spread quickly throughout the populations in which they arise. The model is further rigged so that any given trait changes only once. This way a trait once changed never reverts to its original state. This is much simpler than real life. In real life, most mutations are disadvantageous, and thus usually disappear before they become fixed in the population. In real life, new traits can arise independently in different populations, and traits can appear and disappear over time. The simplifications we have made are intended to help you see the main points of this lab.*

[4.2]   **As the changes were happening in Step 4, time was moving forward. Aside from the time scale on the left, how is the movement of time represented in the evolutionary tree? (Start the model running again if you want to remind yourself).**

[5]   Each time a seed blows from one peak to another, we say that the tree diagram **bifurcates**, or splits. The tips of the two resulting branches are the two new populations, drawn at the top of the tree to show that they are currently alive. The base of the two branches come together to show that both new populations came from the same parent population. This parent is the **most recent common ancestor** of the two new populations. Continue running the model until populations have become established on a couple of other peaks, and then stop the model.

[6]   Time is shown at the bottom of the main window. Run the model until 800 years have gone by. Be patient…evolution takes time. Watch the action both on the mountain peaks and on the evolutionary tree. At the end, look at the pictures of the flowers at the tips of the tree branches.

[6.1]   **Pick a flower picture at the tip of the tree diagram (representing one of the living mountain peak populations). Follow its branch all the way to the base of the tree. Does the flower picture at the tip reflect all the trait changes that occurred among its ancestors?**
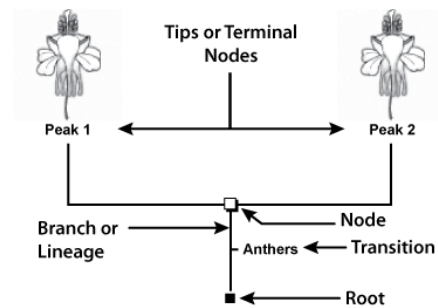
Exercise 3: Building and Reading Trees

[1]   In the **Select An Exercise** menu, select **SIMPLE EVOLVING FLOWERS**.

[2]   The setup here is the same as last time, except that there are only 4 mountain peaks and 5 traits for each flower. The **Lab Notebook** on the left will still show the evolutionary tree as it grows, but now no changes will occur unless you make them happen.

[3]   Start the model running by clicking on the **GO** button. Let time advance for 20-40 years so there is a little trunk at the bottom of the tree. Then stop the model by clicking on the **STOP** button.

[4]   In Exercise 2, you watched as mutations appeared on their own in the columbine populations. In this experiment, you will play mutator, changing the traits of flowers at your whim. Start by changing the anthers of one of your flowers from white to yellow. To do that, double-click or CTRL-click (⌘ click on a Mac) on one of the flowers in the Peak 1 population. A **Trait Editor** window will appear.

[5]   Change this flower to have yellow anthers by selecting **Yellow** from the **Anthers** pull-down menu. Don't change any other traits right now.

[6]   Close the **Trait Editor** window by clicking on its close button at the top left of the window. (As noted earlier, ignore the literal color and design of the icons on the peaks in the Landscape panel.)

[7]   Run the model again for 20-40 years by clicking on the **GO** button. Look at the evolutionary tree. Notice that, as in the last experiment, there is a label showing when the new trait appeared. Note also that the picture at the top shows the current living population with the new trait.

[8]   Your evolutionary tree should now look like the one shown at right (without the arrows). The evolutionary tree traces the 80 or so previous generations that are ancestors of your current Peak 1 population.

Peak 1

Anthers

[8.1]   **The more recent ancestors are indicated by the dark arrow. What color were their anthers?**

[8.2]   **The earlier ancestors are indicated by the white arrow. What color were their anthers?**

[9]   There are no storms modeled in this experiment. Instead, you will establish new flower populations on the other peaks yourself, by traveling with seeds stuck to your hiking boots.

[9.1]   **Before doing this, draw a diagram of what you think the evolutionary tree will look like when you carry a seed from Peak 1 to establish a new population on Peak 2. You don't have to draw pictures of the flowers at the tips, just use the names of the populations.**

[10]   Now go ahead and carry a seed from Peak 1 to Peak 2 by clicking on a flower in Peak 1, holding your mouse button down, and dragging the flower to Peak 2.

[11]   **START** the model running again and run it for 20-40 years.

[12]   **STOP** the model and look at the tree.

[12.1]   **Was your prediction in Question 9 correct?**
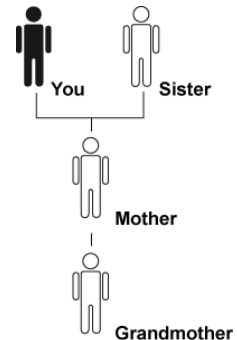
What is your evolutionary tree showing?

At right is a picture of the tree that you now have, with some of its parts labeled. Each point along a branch represents a population that lived at a particular point in time. The small black squares mark particularly significant populations. The root is the population you started with. The node marks the population that split to produce two daughter populations. The tips represent the populations that are currently living on Peak 1 and Peak 2.

[13]   Think about your own family for a moment. Imagine that you have a sister (right).

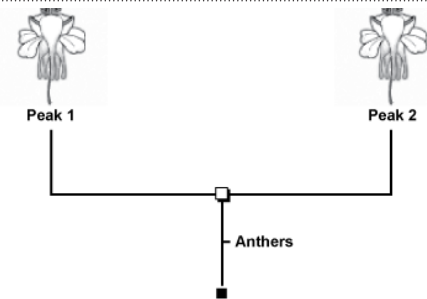[13.1]   **Why are you and your sister said to be closely related?**

[14]   In your answer to Question 13.1, you probably said something to the effect that you and your sister are considered kin, because the two of you share ancestors—namely, your mother and father. You and your sister share lots of other ancestors too, of course. These include your father's parents, their parents, and so on. Evolutionary biologists refer to the ancestors two individuals share as **common ancestors**. Note that **common**, in this context, means "held in common" or "shared." It does not mean "ordinary."

[14.1]   **Who are you and your sister's *most recent* common ancestors?**

★   *Evolutionary biologists think about the relationships among populations and species in a way that is similar to how we think about our relationships with our kin. Two populations (or species) are related to each other if the individuals living in one of the populations are kin to the individuals living in the other. Likewise, a past population is an ancestor of a present population if individuals that lived in the past population were ancestors of the individuals living in the present population.*

[14.2] **In the diagram at right, draw an arrow pointing to the most recent common ancestor of the populations currently living at Peak 1 and Peak 2. Label the arrow "most recent common ancestor."**

[14.3] **Over time, new traits could arise in the population on either mountain peak that make the flowers on the two peaks look different. Draw what the tree diagram will look like if the flowers on Peak 1 mutate to have pointy petal tips.**

[15]   Change the petal tips of a flower on Peak 1 to "pointy" (using the **Trait Editor**).

[16]   Close the **Trait Editor** and run the model for another 20–40 years.

[16.1] **Compare the evolutionary tree on the screen to the one you drew in Question 14.3 above. Was your prediction correct?**
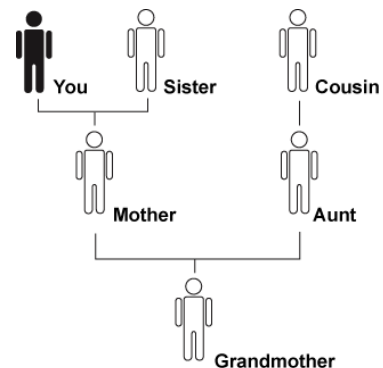
[16.2] **Draw what the tree will look like if you transfer a seed from Peak 1 to Peak 3:**

[17] Now click and drag one of the flowers to transplant it from Peak 1 to Peak 3.

[18] Run the model for 20-40 years.

[18.1] **Was your prediction in Question 16.2 correct?**

[18.2] **Think about your own family again. Imagine that in addition to a sister, you have a cousin (right.) You are related to both your sister and your cousin. To which of these relatives are you more closely related? Why?**
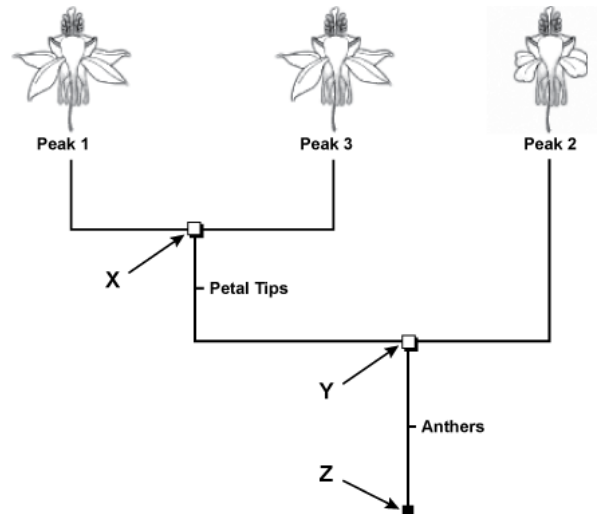
[18.3] **Although you might not have used this language, one way to answer the previous question is to think about your most recent common ancestors with your sister versus your cousin. Who are you and your cousin's most recent common ancestors?**

[18.4] **Who lived more recently (came later): your most recent common ancestors with your sister, or your most recent common ancestors with your cousin?**

You are more closely related to your sister than to your cousin, because your most recent common ancestors with your sister (your mom and dad) lived more recently than your most recent common ancestors with your cousin (your grandparents). We can use similar reasoning in thinking about the evolutionary relationships among populations and species.

[18.5] **In the diagram below, which arrow (X, Y, or Z) points to the most recent common ancestor of the populations currently living on Peak 1 and Peak 3?**

[18.6] **Which arrow points to the most recent common ancestor of the populations currently living at Peak 1 and Peak 2?**

[18.7] **Which lived most recently, the most recent common ancestor of the Peak 1 and Peak 3 populations, or the most recent common ancestor of the Peak 1 and Peak 2 populations?**

[18.8] **Which is more closely related to the current Peak 1 population–the population currently living at Peak 2, or the population currently living at Peak 3?**

[19] Make the following changes happen, being sure to run the model for 20-40 years between each one.
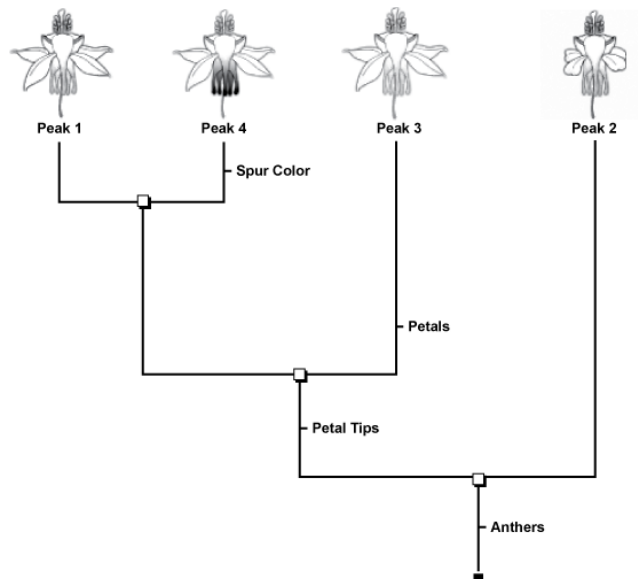
– The population on Peak 3 acquires dark petals

– 20-40 years go by

– A hiker carries a seed from Peak 1 to Peak 4

– 20-40 years go by

– The population on Peak 4 acquires blue spur bottoms

– 20-40 years go by

The diagram below is what the evolutionary tree on your screen should look like now.

[19.1] **On the diagram to the right, label the most recent common ancestor of the populations on Peak 1 and Peak 3 with the letter B.**

[19.2] **Label the most recent common ancestor of the populations on Peak 1 and Peak 2 with the letter C.**

[19.3] **Label the most recent common ancestor of the populations on Peak 3 and Peak 2 with the letter D.**

[20] Now look at the time scale on the screen. Measure approximately the amounts of time from:

[20.1] **Peak 1 population to B: _____**

   Peak 1 population to C: _____

   Peak 3 population to B: _____

   Peak 3 population to D: _____

[20.2] **Have more years passed since the Peak 3 population split from Peak 1 at B, or since the Peak 3 population split from the Peak 2 population at D?**

[20.3] **Have more years passed since the Peak 1 population split from Peak 3 at B, or since the Peak 1 population split from Peak 2 at C?**

[20.4] **Is the population at B an ancestor of C or is the population at C an ancestor of B?**

[20.5] Given how much time has passed from each ancestral population to the current populations on the mountain peaks, write down the order of relationships (which population is most closely related to which other) among the four currently living populations.

[20.6] Explain why they have that relationship based on the amount of time that has passed from each common ancestor.

★ *When thinking about who is more related to whom, the number of differences in traits between the populations does NOT matter. What counts is how much time (i.e., height on the tree diagram) has passed since they shared a common ancestor. Species whose common ancestors were farther in the past are less closely related than species whose ancestors were more recent.*

Exercise 4: Flipping Out

[1]   Right now, the populations are drawn left to right as Peak 1, Peak 4, Peak 3, and Peak 2. Now consider what would happen if you were to flip the Peak 1/Peak 4 branch of the tree with the Peak 3 branch.

[1.1]   **Would this switch make any difference to any of the information given on the tree? (To answer this question, drag the Peak 3 picture on the tree to the left, so it switches places with the Peak 1/Peak 4 branch. Then drag it back to its original position.)**

[1.2]   **As you flip the tree back and forth, does the most recent common ancestor between Peak 1 and Peak 3 change?**

[1.3]   **As you flip the tree back and forth, does the branch of the tree on which dark petals arose change?**

[1.4]   **How about the time at which dark petals arose?**

[1.5]   **Does the time when the ancestor of the populations on Peak 1 and Peak 3 split into those separate lineages change?**

[1.6]   **According to the tree diagram, does moving Peak 3 to the left make it older than the Peak 1 population, or do they stay the same age?**
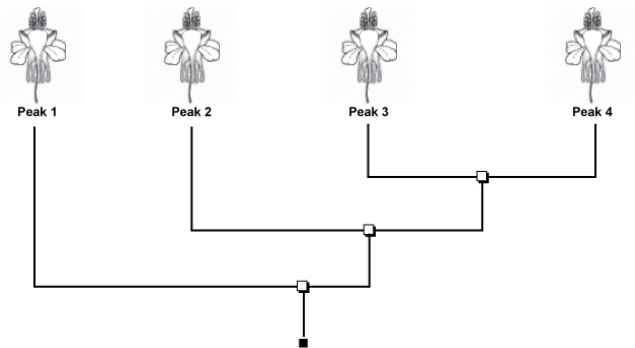
[1.7]   **Did any of the information shown in the evolutionary tree change when you flipped branches around?**

[1.8]   **Based on your answers in 1.1 through 1.7, what, if anything, does the left to right order of the populations in the tree tell you?**

Exercise 5: Tree Building Challenge

[1]   Examine the tree at the right. Consider
          the following questions regarding this
          tree:

          [1.1]   **Does the tree tell us which
                      peak was occupied by
                      columbines at the start? If
                      so, which peak was it?**

          [1.2]   **Does the tree tell us the order in which the remaining peaks were colonized? If so,
                      what is the order?**

          [1.3]   **Does the tree tell us which pair of peaks were involved in the most recent colonization
                      event? If so, which peaks were they?**

[2]   In the **Select an Exercise** menu, select **TREE BUILDING CHALLENGE**.

[3]   You will see a flower population on one of the peaks. If the starting population is on Peak 1, click
          the **RESET** button until the starting population appears on Peak 2, 3 or 4.

          [3.1]   **Try to build a tree starting from this population that looks <u>exactly</u> like the tree shown
                      above. Record the steps required below.**

[3.2] On the tree you have made, Peak 1 seems to branch off from the trunk before any of the others. Based on what you did above, does that mean that Peak 1 is more closely related to the original ancestor than the others? Why or why not?

[3.3] How much time has passed between the original ancestor and the current populations on...

...Peak 1?

...Peak 2?

...Peak 3?

...Peak 4?

[3.4] Does your answer to Question 3.3 change your answer to Question 3.2?

[3.5] Think back to the tree you just built. Is the current Peak 1 population (shown at the tip of the tree) the ancestor of the other three populations? Why or why not?

[3.6] Look back at your answers to Questions 1.1–1.3 above, in this exercise. Would you change any of them now? Why or why not? (Hint: If your answers were not NO, NO, and YES, you should change them.)

★ *As you saw here, no currently living population is an ancestor of another currently living population. They are all equal to each other, just like your cousin is not your ancestor, even if he looks exactly like your grandfather.*

In this example, none of the flower traits changed as the populations split, so there are no trait changes marked on any of the branches. But this doesn't mean that nothing has changed. There may be changes in other parts of these plants, such as the stalk, roots, seeds, and even changes in the genetic sequence that are not shown on this tree, because this tree is only about the flowers.
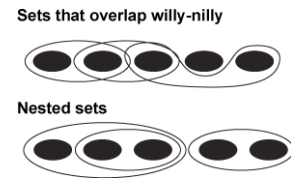
Exercise 6: Reconstructing Trees

In all of the simulations we have run so far, we have known the true evolutionary history of all our populations. This is because the computer has drawn an evolutionary tree for us as our populations have evolved. In the real world, we virtually never know the true evolutionary history for a set of populations, because we weren't there to watch the populations evolve. Instead of having the evolutionary tree drawn for us, we have to reconstruct it based on available evidence.

The available evidence is found in the traits of the currently living populations. When populations or species arise by descent with modification from common ancestors, they show a special pattern of similarities and differences. This pattern is often enough to allow us to develop a reasonable hypothesis about their evolutionary history.

[1]   In the **Select An Exercise** menu, select **GROWING TREE**.

[2]   Run the model until there are 4 mountain peaks with populations of flowers and at least three novel traits, then click the **STOP** button.

[3]   To reconstruct a tree by looking at the traits of currently living populations, you need to look for shared evolutionary innovations. These are novel characters, also known as derived traits that were absent in the earliest common ancestor but are present in some of the extant populations.

[4]   Find the **PENCIL** tool. Click on the down arrow to get a menu of different color pencils. Select a color.

[5]   Now pick one of the novel traits you see on the tree (for instance yellow anthers, pointy petal tips, dark petal colors, yellow blade colors, etc.). Use your mouse to draw a circle around all living flower populations on the tree that have that trait.

   ★   *NOTE: If you make a mistake, you can delete a line as follows: Click on the* **DELETE** *tool and then click on the line you want to delete. To resume drawing lines, click on the* **PENCIL** *tool.*

[6]   Pick a different color from the **COLOR** menu and draw another circle around the populations with another of the novel traits.

[7]   Keep circling populations with shared derived traits until you have a circle for each trait.

[8]   Note that in each case, you have been circling populations that share evolutionary innovations. The beginning population did not have yellow anthers, pointy petal tips, or the rest. The populations that share these evolutionary innovations inherited their shared traits from their common ancestors.

[8.1]   Note that your circles do not overlap willy-nilly (haphazardly). Instead, they form nested sets of circles (right). Why is this? (Use the words "common ancestor" in your answer.)
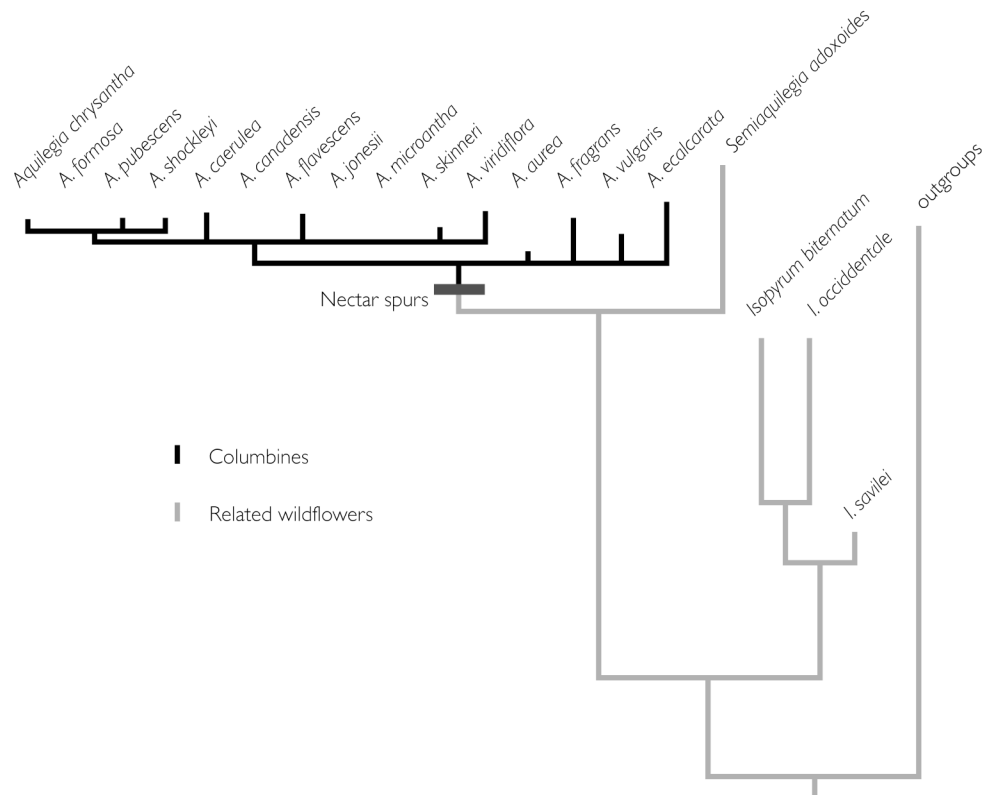

Sets that overlap willy-nilly

Nested sets

[9]   Now go the **Select An Exercise** menu and select the **FLOWER CHALLENGE 1** experiment.

[10]   When you run this model, the program will move flowers from peak to peak and change their traits, without you doing anything. However, the flower populations will be hidden for the first 400 years. You will only be able to see them once all the movement and trait changes have happened. Start the model running and wait 401 years until the flowers appear on the peaks. Then use the **STOP** button to stop the simulation.

[11]   Your task is to reconstruct a tree representing the evolutionary history of the flower populations on the four peaks. To start, put flower samples into your notebook by clicking on a flower from each mountain peak, holding down your mouse button and dragging the flower to the **Lab Notebook**. Repeat this with a flower from each of the peaks so you have four flower samples in your **Notebook**.

You can **CLOSE** the **Landscape** panel so that you have more room to work with your columbines in the **Notebook**.

[12]   Move the flowers around so that flowers sharing evolutionary innovations (new traits that weren't in the earliest ancestral population) are near each other.

[13]   Based on what you have done so far, think about where on the screen these flower pictures should be sitting. Should they be at the bottom? The top? Lined up in a row or a column? Bunched together? (Remember that you just took these pictures from currently living flower populations on the four mountain peaks).

[14]   As you did above, use different colors to circle all the flowers that have yellow anthers, all the flowers that have pointy petal tips, all with long spur lengths, dark petal colors, and blue spur colors.

[15]   All of your columbines share an evolutionary innovation that makes them columbines. This novel trait is nectar spurs. Draw one big circle around all of your flowers to indicate that they share this key derived trait, which they have all inherited from their common ancestor.

[15.1]   **From your circles, find two flowers that must represent sister populations (that is, they share a more recent common ancestor with each other than either does with any other population). Explain why you think these two are sister populations, based on your multicolored circles.**

[16]   To connect the two sister populations together with a tree branch, click on the **TREE** tool (the tree shaped button).

[17]   Click on one of the flower populations you want to connect and then, holding the mouse button down, drag the mouse to the other one and let go. You will see a tree branch connect the two. The most recent common ancestor of the two populations you have connected will be shown as a small square at the base of the new branch.

[18]   Are there any other circles you drew that have exactly two flower populations inside of them? If so, those two must also be sisters. Use the **TREE** tool to connect them as well.

★   *NOTE: Depending on the evolutionary history of your populations, there might not be another sister pair.*

[19]   Now look for the next largest circle you have. The populations within that circle must share a most recent common ancestor just a little older than the ones you've already identified. Connect the populations within this circle together using the **TREE** tool. This may involve connecting a common ancestor to an extant population, or it might involve connecting two common ancestors to each other.

★   *NOTE: If you make a mistake, you can delete a branch as follows: Click on the **DELETE** tool. Click on the square at the base of the branch you want to delete. The branch will disappear. Finally, click back on the **TREE** tool so you don't accidentally delete anything else.*

[20]   Continue looking for larger circles and connecting populations together until you have all the extant populations connected to the tree.

[21]   There are labels for each of the possible flower traits at the top edge of the **Lab Notebook**. Click on the **SELECT** tool (the arrow button). Then drag the trait labels to the appropriate branch of the tree to show where each trait changed.

[22]   Now check whether your reconstruction matches the true evolutionary history of your populations. Click **CLOSE** on the **Landscape** panel to minimize it, if you haven't done so already. Then click **REVEAL** on the top right corner of the **Solution** panel. A new window will appear below the **Lab Notebook** that shows the real tree. Compare your reconstruction with the real tree. (You may want to drag branches around in the real tree so the flower populations are in the same order in both). To see the four populations again, click **OPEN** on the Landscape tab at the bottom right.

[22.1]   **Did you get your reconstruction correct? Are your flowers connected correctly? Are they positioned at the proper time? If not, explain the mistakes you made.**

[23]   If you did not reconstruct the tree correctly, **RESET** the **FLOWER CHALLENGE** 1 experiment, and repeat steps 10-21. See if this time you can reconstruct the tree accurately.

[24]   As a final challenge to yourself, load the **FLOWER CHALLENGE 2** experiment from the **Select An Exercise** menu. This experiment has 7 mountain peaks and the full set of traits that you saw at the beginning of this lab. Run this model for 701 years until the flowers all appear. Then see if you can reconstruct the evolutionary history of all 7 populations.

Why Are There So Many Species of Columbines?

Now that you have honed your tree-thinking skills, we can return to Scott Hodges' hypothesis about why there are so many species of columbines. Hodges suspected that the evolution of nectar spurs created an opportunity for rapid evolutionary diversification. He tested this hypothesis with the evolutionary tree shown here (adapted from Hodges and Arnold, 1995).

The tree shows the evolutionary history of 15 species of columbines (Latin name *Aquilegia*, abbreviated as *A.*), plus several of their kin, as reconstructed by Scott Hodges and Michael Arnold (1995) based on genetic data. (Other EvoBeaker labs explore how this kind of reconstruction works.) The extant (currently living) species don't all line up horizontally at the top, because on this tree branch, length indicates not time, *per se*, but accumulated genetic differences in regions of the genome not subject to natural selection. To qualitatively estimate how closely related two species are, assess the distance from one branch tip to the other, traversing the tree through the most recent common ancestor of the two species. The shorter this distance is, the more closely related are the two species at the tips.

Find the most recent common ancestor of all 15 columbines. Find, also, the point on the tree at which nectar spurs appeared. The two match up. As we have said before, nectar spurs are the shared evolutionary innovation that defines the columbines.

Note that branches on the tree are more densely packed and branch lengths are shorter among columbines than elsewhere on the tree. This is not because Hodges and Arnold went looking for columbines that were closely related. Instead, it appears that *all* columbines are closely related. As Hodges had hypothesized, the evolution of nectar spurs apparently resulted in rapid evolution and diversification among columbine populations. Quite likely, it is because they have nectar spurs that columbine species are so numerous.

Bibliography

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