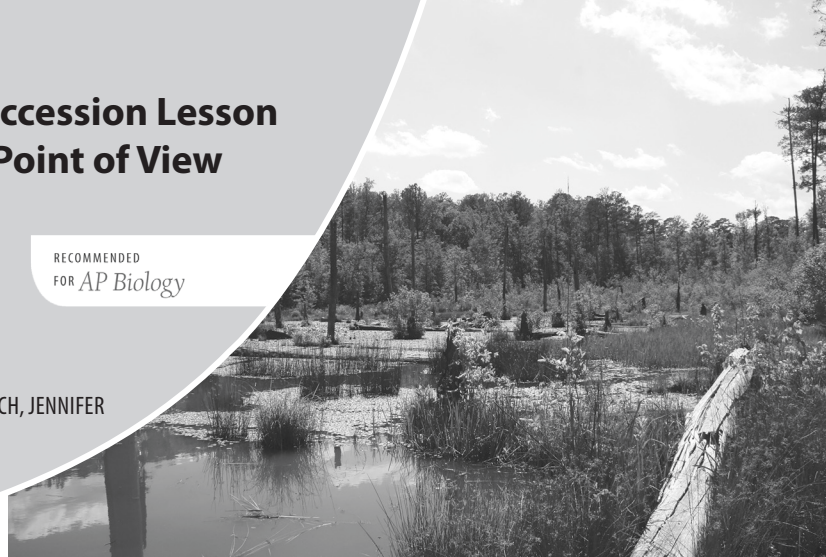


An Ecological Succession Lesson
from a Beaver's Point of ViewRECOMMENDED
FOR AP BiologyHANNAH SCHMIDT, KALEB K. HEINRICH, JENNIFER
REYNOLDS, JENNIFER G. HOWETH**ABSTRACT**

*Ecological succession explored at the secondary and postsecondary level is often limited to terrestrial ecosystems. The emphasis is traditionally placed on how deforestation leads to ecological succession. However, aquatic ecological succession is just as important and allows for many connections to be made with other ecological concepts. Succession initiated by beavers (*Castor canadensis*) in particular links both aquatic and terrestrial ecosystems over time. We present a guide to an inquiry-based lesson for AP Environmental Science and undergraduate ecology courses that explores the effects of aquatic and terrestrial ecological succession initiated by deforestation and beavers. Specifically, the focus is ecological succession and its effects in both terrestrial and aquatic ecosystems. In this lesson, students (1) engage with a preassessment and broad overview of ecological succession, (2) explore authentic research data representing secondary succession in beaver ponds, (3) explain data using detective activities, (4) elaborate with a mystery pond, and (5) evaluate their new understanding by comparing a pre- and postassessment. This lesson plan meets the objectives for AP Environmental Science Biology courses as well as the core concepts and competencies for undergraduate biology education from the Vision and Change report by the American Association for the Advancement of Science in 2011.*

Key Words: ecological succession; inquiry; vision and change; 5E learning cycle; AP environmental science; beaver ponds.

Students will gain a greater understanding of ecological succession, be able to compare and contrast primary versus secondary succession, and be able to differentiate between pioneer, indicator, and keystone species.

Placement (AP) Environmental Science classrooms. Comprehension of ecological succession allows students to grasp the concept of how biological systems influence one another, which is essential to understanding further scientific topics (American Association for the Advancement of Science [AAAS], 2011). Specifically, succession helps students understand that ecosystems are dynamic, so they can better understand predicted changes due to various disturbances, including but not limited to climate change and biodiversity loss. In educational settings, based on our experience, ecological suc-

cession is most often described in terrestrial habitats and is simplified to demonstrate the shift from grass, to shrub, and then to forest after a wildfire or logging event. These traditional examples sometimes overlook or oversimplify aquatic habitat succession, and students may fail to recognize that aquatic and terrestrial ecosystems are linked. Here, we present a lesson plan for an inquiry-based activity that can be applied to both AP Environmental Science and undergraduate ecology courses and that aligns with the AP Environmental Science Course and Exam Description (College Board, 2020), the core concepts and competencies for biology education identified in the *Vision and Change* report (AAAS, 2011), and the Ecological Society of America's (ESA) Four-Dimensional Ecology Education Framework (4DEE) for teaching ecology (Klemow et al., 2019). Students will gain a greater understanding of ecological succession, be able to compare and

contrast primary versus secondary succession, and be able to differentiate between pioneer, indicator, and keystone species. The lesson employs the 5E Learning Cycle, an effective method for teaching students scientific concepts (Bybee et al., 2006), and includes case studies with authentic data of aquatic and terrestrial succession from the Talladega Wetland Ecosystem (TWE) to promote student active learning and critical thinking (Herreid, 2004).

○ Introduction

An understanding of ecological succession is important for the success of students in both undergraduate biology classes and Advanced

○ Background

The TWE is one of the most well-studied and valuable sources of information concerning ecological succession (Cherry et al., 2009). This system, located in Hale County, Alabama (32°55'N, -87°26'W), was formed by beaver (*Castor canadensis*) activity approximately 80 years ago from a second-order stream with surrounding coniferous and deciduous forest areas (Chaubey & Ward, 2006). The entire ecosystem is composed of a multitude of small ponds and stream channels spanning 384 hectares of forested catchment. The TWE has been marked by the appearance and disappearance of ponds since its conception (Cherry et al., 2009). Five major forms of vegetation dominate throughout the TWE and surrounding areas. These include areas of forest with primarily deciduous trees, a mix of coniferous and deciduous trees, a mixture of alder (*Alnus serrulata*) and willow trees (*Salix* spp.), grassland of soft brush (*Juncus effusus*), and six perpetual ponds of differing sizes (Chaubey & Ward, 2006).

In 1996, one pond in the TWE was drained of water due to the failure of a beaver dam. This gave researchers the opportunity to closely analyze succession once a pond has dried up, as well as document the speed with which ecological succession in this ecosystem took place. In 1997, a small grass-like plant known as soft brush (*Juncus effusus*) first appeared where pond water had previously stood. Shrubs subsequently began to establish in 2000, after the soil had dried from the previous wetland habitat, and in 2008 hardwood tree species successfully colonized this area (Figure 1). This case study of the TWE represents an ideal example of aquatic and terrestrial ecological succession—one that is remarkably suitable for teaching and learning opportunities. More information on the TWE can be found at <https://twe.as.ua.edu/research-chronology/>.

○ Content Overview

Ecological succession is the change in species composition over time, the natural replacement of one group of species by another group of species (Morin, 2011). There are two major types of ecological succession: primary succession and secondary succession. In primary succession, a site that is initially absent of species becomes colonized for the very first time. In secondary succession, a site that supports an existing assemblage of species experiences a disturbance that changes the composition of species. Both types of succession can occur in terrestrial and aquatic ecosystems.

Primary succession in terrestrial ecosystems can initiate after rock is newly exposed, such as from glacier retreat or volcanic island formation (Walker & Del Moral, 2003). The first colonizers are microscopic organisms and lichens that can survive on bare rock. Over time, soil begins to develop as the rock weathers and breaks down from precipitation and wind erosion. The formation of soil provides opportunity for the establishment of plants that require substrate to anchor roots and a source of nutrients and water accessible for root uptake. The first species to arrive and colonize the newly formed habitat are pioneer species. These early colonizers contribute nutrients to the soil through organic matter accumulation from decomposition (Chapin et al., 1994). Some early successional plant species can fix atmospheric nitrogen and thereby increase nitrogen availability in the soil for other plants. As soil nutrients increase over succession it allows for the colonization of previously nutrient-limited species that were unable to establish initially (Bishop, 2002). This facilitates the turnover in species composition over time. In terrestrial ecosystems, this compositional shift corresponds to a change in life forms and distinct species assemblages transitioning from small herbaceous plants, to shrubs, and ultimately to stands of trees

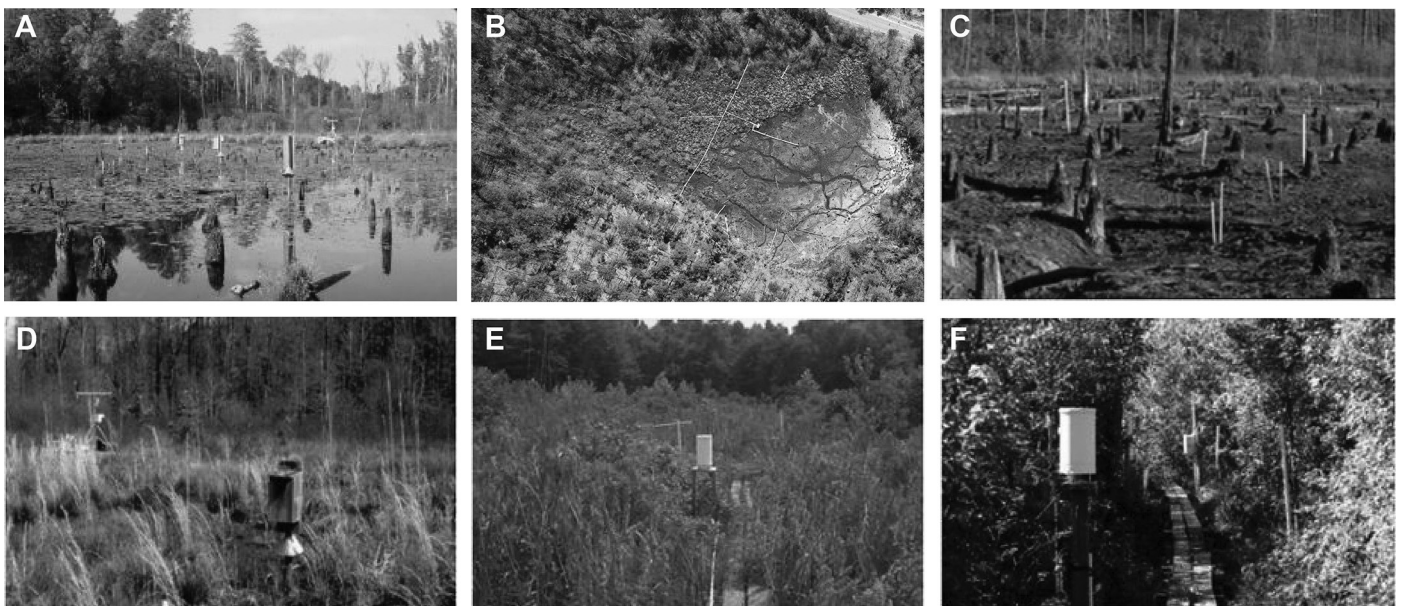


Figure 1. The Talladega Wetland Ecosystem in the Talladega National Forest, Alabama as (A) an active beaver pond in 1992; (B) and (C) abandoned and dewatered (aerial view of former wetland, 1997, and close-up of view, 1996); (D) transitioned to a meadow in 1997; (E) meadow after shrub establishment in 2001; and (F) after hardwood tree establishment and conversion to forest in 2008. Photos by G.M. Ward.

over the course of succession (Morin, 2011). Species that are primarily associated with early, mid, or late stages of succession are considered indicator species of those stages because they are unique to a particular aspect of the ecosystem (in this case, successional stage). Primary succession also occurs in aquatic ecosystems (Walker & Del Moral, 2003). For example, newly formed rock pools (water-filled rock depressions) and newly formed ponds are initially colonized by wind-dispersed algae that facilitates the colonization of aquatic animal species over time yielding distinct species assemblages by successional stage (Louette et al., 2008; Vanschoenwinkel et al., 2010). The limiting resource that was initially absent for species to thrive in these ecosystems was not soil but fresh or saltwater.

Secondary succession in terrestrial ecosystems can begin after fire, tornadoes/hurricanes, or human disturbance of an already established plant community, removing most species but leaving the soil intact (Horn, 1974; Prach & Walker, 2011). The disturbance changes exposure of the habitat to sunlight, wind, and water that alters colonization and the assemblage trajectory of the new plant community (Tilman, 1994). Some plant species may arrive to the disturbed site from dispersal (animal, water, wind) while other species may establish from the existing seed bank (Meiners et al., 2015). Over time, species replacement yields successional stages similar to primary succession (Hart et al., 2008). Secondary succession in aquatic ecosystems can initiate after a habitat dries and refills, after sedimentation occurs, or after a natural or artificial (human-imposed) dam is constructed. For example, beavers (*Castor canadensis*) disturb stream ecosystems and initiate succession by building dams that convert the habitat to pond ecosystems (Naiman et al., 1988). The dams increase aquatic habitat area and depth while reducing stream flow (Rosell et al., 2005). This provides pond habitat for aquatic species with different niche requirements than those that inhabit streams. A new community forms from a combination of existing species that can tolerate the changes in the habitat to pond-adapted species that colonize from nearby pond sites (Olinger et al., 2021). Through the process of dam construction on streams and the corresponding pond formation, beavers have large effects on aquatic community structure and diversity and are therefore considered keystone species and ecosystem engineers (Naiman et al., 1988).

○ Learning Objectives

The concept of ecological succession goes beyond grasslands shifting to shrubs and eventually forests after a wildfire or logging. Ecological succession occurs in both aquatic and terrestrial habitats, often linked together. Here, students are encouraged to explore their own scientific intuition while drawing on AP Environmental Science objectives, *Vision and Change* core concepts and competencies for biological processes, and ESA's 4DEE Framework. These include, for AP Environmental Science (College Board, 2020)

1. ERT-2.I—Describe ecological succession.

Students master this objective by reading the case studies and completing Data Detectives Activities 1 and 2.

2. ERT-2.J—Describe the effect of ecological succession on ecosystems.

Students show mastery of this objective by completing the questions associated with Data Detective Activity 3.

The *Vision and Change* core concepts and competencies (AAAS, 2011) include

1. **Systems:** Students learn this concept by examining how species and environment interact within an ecosystem undergoing ecological succession.
2. **Ability to apply the process of science:** Students acquire competency in this area by examining ponds in various stages of ecological succession and reasoning information from data given.
3. **Ability to use quantitative reasoning:** Students build competency in this area by comparing and using data in Data Detectives Activities 1, 2, and 3.
4. **Ability to understand the relationship between science and society:** Students develop competency in this area by exploring Case Studies 1 and 2, connecting human disturbance to secondary succession in forests and aquatic ecosystems.

ESA's Four-Dimensional Ecology Education Framework (4DEE) for teaching ecology (Klemow et al., 2019) includes

1. **Core ecological concepts:** Students master the concept of succession by reading the case studies and completing Data Detectives Activities 1 and 2.
2. **Ecology practices:** Students practice basic components associated with the scientific process, including making observations and connections, evaluating claims, and generating new hypotheses by examining and comparing ponds in various stages of ecological succession in Data Detectives Activities 1, 2, and 3.
3. **Human-environment interactions:** Students recognize the connections between humans and the environment by exploring Case Studies 1 and 2.
4. **Cross-cutting themes:** Students explore systems and spatial and temporal scales by examining how species and environment interact within an ecosystem undergoing ecological succession through time.

○ Description of Lesson

This activity follows the stages of the 5E Instructional Learning Cycle: engage, explore, explain, elaborate, and evaluate (Bybee et al., 2006). It can be used in the classroom, in-person or virtually, and with slight modification can be converted to a hands-on field exercise.

Engage (~10 minutes)

This lesson will challenge students to think critically about ecological succession and its effects in both terrestrial and aquatic ecosystems. The instructor should first direct students to complete a preassessment assignment to elicit their prior knowledge on the subject of ecological succession by having them write down their answers to the following questions (see rubric, Table 1):

1. Describe ecological succession.
2. Define keystone species and provide one example.
3. Describe the effect of ecological succession on ecosystems.

Instructors should quickly review students' answers to gauge level of competency prior to the exercise. Once the preassessment is completed, introduce the TWE and facilitate discussion that provides a brief overview of ecological succession, primary succession, secondary succession, pioneer species, keystone species,

Table 1. Pre- and postassessment rubric with definitions.

Question	Succession Assessment			
	Exceptional (3)	Mastery (2)	Needs Improvement (1)	Unsatisfactory (0)
1. Describe ecological succession.	Correctly defines ecological succession and includes an explanation of primary and secondary succession.	Correctly defines ecological succession.	Discusses how ecosystems can change over time.	No clear understanding of ecosystems and how species can play a role in changes through time.
2. What is a keystone species?	Correctly defines keystone species and gives an example.	Correctly defines keystone species.	Gives only an example of a keystone species.	Incorrect definition and no example.
3. Describe the effect of ecological succession on ecosystems.	Answer includes disturbance and effects on community structure (richness, diversity) and ecosystem structure/function (biomass, productivity) over time.	Answer includes changes over time but only some of the effects (structure or diversity changes, not both).	Answer includes changes over time but no details on community or ecosystem structure.	No effects described.

and indicator species (information included in previous Content Overview section). The discussion should explicitly address the following (these questions may also be used to further gauge student's previous knowledge of ecological succession):

1. Describe how aquatic and terrestrial ecosystems differ in terms of ecological succession.
2. List examples of species that may be able to first colonize an area following a disturbance.

We developed a PowerPoint, Appendix S1, to aid in the presentation of the Content Overview material (see the Supplemental Material available with the online version of this article).

Example Definitions

ecological succession—The change in species composition over time; that is, the replacement of one group of species by another group of species. There are two major types of ecological succession: primary succession and secondary succession.

primary succession—A site that is initially absent of species becomes colonized for the very first time.

secondary succession—A site that supports an existing assemblage of species experiences a disturbance that changes the composition of species.

keystone species—Organisms that have large effects on community structure and diversity within ecosystems.

pioneer species—The first species to arrive and colonize the newly formed habitat.

indicator species—Species that are associated with a particular community or ecosystem state, or in the case of an ecological experiment, a particular treatment. As an example, an indicator species of succession would be primarily associated (based on incidence and/or abundance) with an early, mid, or late stage of succession and would be an “indicator” of that particular stage.

Explore (~20 minutes)

Students will explore Case Studies 1 and 2 to develop an understanding of secondary succession initiated by animals and human disturbance, respectively in aquatic ecosystems and forests. These case studies explore real-world examples from the TWE previously described in the Background section. (For further exploration, an exhaustive list of research publications citing the TWE can be found at <https://twe.as.ua.edu/publications/>.) A handout is available to give to students encompassing the *explore*, *explain*, and *elaborate* stages (Supplemental Material Appendix S2, available with the online version of this article).

Case Study 1: Aquatic and Terrestrial Secondary Succession Initiated by Beavers

Although beavers can initiate the process of aquatic secondary succession through the construction of dams across streams, they can also indirectly catalyze terrestrial secondary succession from dam failure. When beavers abandon a pond and stop maintaining their constructed dam, the pond transitions back to a stream ecosystem. At this time, terrestrial secondary succession ensues as the desiccated pond site gives way to a terrestrial plant community. Documented examples of aquatic and terrestrial secondary succession initiated by beavers can be found throughout the Talladega National Forest in Alabama (Cherry et al., 2009; Sferra et al., 2017; Olinger et al., 2021). Within the forest there are several beaver-formed ponds of different ages and in different stages of aquatic succession in addition to ponds that have transitioned back to streams and forested habitat. The TWE was constructed by beavers in the 1940s and was abandoned in 1996 (Figure 1).

To students, highlight the dramatic changes in the terrestrial vegetation at the site as a consequence of secondary succession, and emphasize the timeline—as soils dried from pond recession, grasses established after one year, the terrestrial plant community transitioned to shrubs four years after drying, and eventually to hardwood tree species twelve years after drying. For instructors in other geographic regions of the US, expand focus beyond the TWE to include your region. Beavers were historically found in nearly all aquatic habitats in North America prior to European settlement (Rudemann & Schoonmaker, 1938) and have been recolonizing their historic habitats (Naiman et al., 1988).

Explain (~10 minutes)

At this stage, students will move to Data Detectives activities, where they will learn more about some of the specific characteristics of the stages of succession and will begin to apply their understanding of ecological succession accrued from the case studies. Instructors should guide students through the different variables so that

students begin to recognize and evaluate the different stages of succession. Students will need to answer questions related to aquatic ecological succession stages and provide reasoning for their answers.

Data Detectives Activity 1: Previous studies demonstrate that beaver ponds in different stages of secondary succession have contrasting abiotic and biotic characteristics. Notably, older ponds (those in late succession) are deeper than younger ponds (Sferra et al., 2017). Through evaluating the composition of pond zooplankton (crustacean) species, *Daphnia* spp. were determined to be indicator species of old ponds. Let's compare the data in Figure 3, collected from two beaver ponds in the Talladega National Forest, Alabama (data and pond identification numbers from Sferra et al., 2017). Questions for Data Detectives Activity 1 (Figure 3) are

1. What variables do these two ponds differ in most?
2. What other variables could be measured to compare the different successional stages?

Elaborate (~15 minutes)

In this phase students will be given two additional Data Detectives Activities. The second and third Data Detectives Activities will be in the form of mystery ponds, and students will be asked to determine

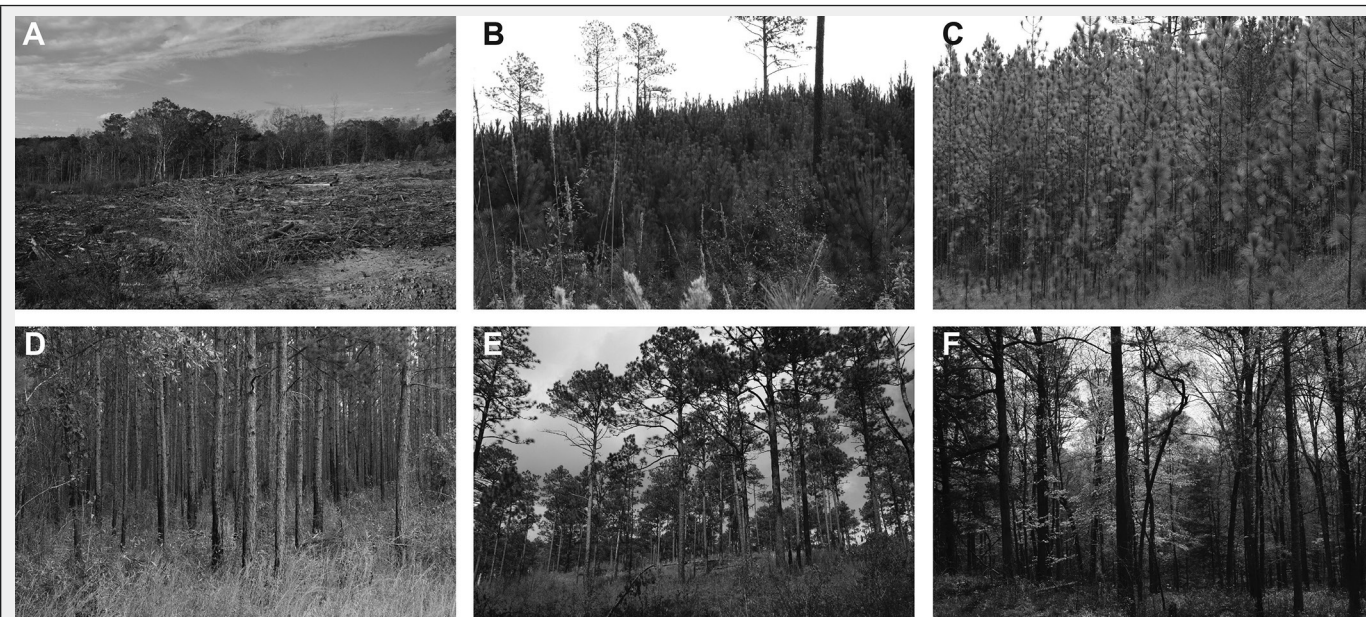


Figure 2. Forest secondary succession in the Talladega National Forest, Alabama. (A) Former forest patch one year after 2018 clear-cut; (B) forest patch 4 years after 2015 clear-cut; (C) forest patch 15 years after 2004 clear-cut; (D) forest patch 27 years after 1992 clear-cut; (E) mature upland forest stand; (F) mature bottomland hardwood forest stand. Photos by J. G. Howeth.

Case Study 2: Forest Secondary Succession Initiated by Human Disturbance

In addition to numerous beaver ponds undergoing secondary succession in the Talladega National Forest, the landscape is composed of forest patches in different stages of secondary succession following intentional human disturbance—tree clearcutting. In these scenarios, the standing trees are mechanically cut and removed for timber harvest and sale (Figure 2). This disturbance removes the standing plant community but leaves the soil and seed bank mostly intact, although erosion does occur from rain and wind after cutting. Early successional herbaceous plant species and fast-growing pine species reestablish first (Emery et al., 2020). After decades of succession, the forest stand is composed of a mix of pine and hardwood species (Cox & Hart, 2015). Because the Talladega National Forest actively manages forest habitat for the endangered red cockaded woodpecker, some cut patches in the forest are replanted with longleaf pine seedlings to improve nesting and foraging habitat (Martin et al., 2021).

Variable	Pond 2	Pond 13
Successional Stage	Early	Late
Year of Origin	1988	1956
Area	0.11 hectares	2.92 hectares
Conductivity	20.12 microsiemens	19.03 microsiemens
<i>Daphnia</i> spp.	Absent	Present
Maximum Depth	0.28 meters	1.63 meters
Total Nitrogen	302 micrograms / L	349 micrograms / L
Photo		

Figure 3. Data Detectives 1: Evaluating Beaver Ponds in Different Stages of Succession. Data and pond number labels from Appendix S2: Table S1 in Sferra and colleagues (2017). Photos by J.G. Howeth.

their stage of ecological succession. Students will draw upon knowledge gained in the previous lessons to answer questions about these mystery ponds. The instructor should ask students to further elaborate and justify their responses to the questions posed by the activity. Further, the Sferra et al. (2017) paper is open access (<https://esajournals.onlinelibrary.wiley.com/doi/full/10.1002/ecs2.1871>) and includes a lot more data about each pond in Appendix S2: Table S1 that instructors could leverage.

Data Detectives Activity 2: Now that you have evaluated data on two beaver ponds in different stages of succession, let's determine the stage of succession of a "mystery" beaver pond (Figure 4). The pond occurs in the same region of the Talladega National Forest as those in the previous exercise. Questions for Data Detectives Activity 2 (Figure 4) are

1. What stage of succession (early, mid, or late) might be represented by Mystery Pond A? Why?
2. What other data might be useful in making your determination?

Data Detectives Activity 3: Here we have Mystery Pond B, where data on beaver pond characteristics were collected for several

Variable	Mystery Pond A
Successional Stage	?
Conductivity	18.98 microsiemens
Maximum Depth	1.09 meters
Total Nitrogen	308 micrograms / L
Photo	

Figure 4. Data Detectives 2: Determining Different Stages of Beaver Pond Succession. Data from Appendix S2, Table S1, in Sferra and colleagues (2017). Photo by J.G. Howeth.

years but are no longer being collected by investigators. Questions for Data Detectives Activity 3 (Figure 5) are

1. Based on these photographs of Mystery Pond B taken in two different years (2014 and 2020), what has likely occurred with this beaver pond?
2. What stages of succession are represented in 2014 and 2020? Carefully explain your answers. (Hint: Review Case Study 1.)

Evaluate (~10 minutes)

Students will be given a postassessment in this stage to evaluate their knowledge of material at the end of the lesson and compare to their knowledge prior to the lesson. Give students the opportunity to rewrite their answers for the same questions from the preassessment:

1. Describe ecological succession.
2. Define keystone species and provide one example.
3. Describe the effect of ecological succession on ecosystems.

As with the preassessment, the attached rubric (Table 1) can be used to evaluate student answers in accordance with the AP Learning Outcomes (College Board, 2020). You may use this as a summative or formative assessment of your students. If there is time, allow for group discussion of these concepts, and of misconceptions. Give students the opportunity to view their preassessment answers and compare them to their postassessment responses. Self-evaluation will empower the students, increase their motivation, and identify strategies to improve learning (McMillan & Hearn, 2008).

○ Broader Application of the Lesson

Based on our experiences from previously delivering this lesson at the high school and undergraduate levels, students are engaged and now able to apply their new knowledge to other regions and ecosystems. Instructors can apply the lesson to their respective geographic regions and ecological settings, allowing for several opportunities of further application and higher level thinking throughout. For example, if there is access to grasslands, instructors might focus on the role of wildfires. Instructors in urban settings can focus on

Variable	Mystery Pond B in 2014	Mystery Pond B in 2020
Successional Stage	?	?
Area	5.19 hectares	?
Conductivity	22.57 microsiemens	?
Maximum Depth	1.18 meters	0
Total Nitrogen	147 micrograms / L	?
Photo		

Figure 5. Data Detectives 3: Determining Different Stages of Beaver Pond Succession. Data from Appendix S2, Table S1, in Sferra and colleagues (2017). Photo by J.G. Howeth.

human initiated succession with a direct focus on time and space. Regardless of whether the focus is on the TWE or a local ecosystem, advanced discussion can focus on the local ecosystem at several spatial (the school, the community, the region, etc.) and temporal scales. We have come up with some guiding advanced discussion questions that are most appropriate for undergraduate ecology:

1. Give examples of ecological succession where you live. Is succession being initiated by beavers, humans, or something else?
2. What indirect impacts can humans have on ecological succession?
3. Compare and contrast keystone species, pioneer species, dominant species, and ecosystem engineers.
4. In what other ways are aquatic and terrestrial ecosystems linked (even beyond ecological succession)?

Lastly, getting students out in the field, taking hands-on measurements, and making observations and predictions will greatly aid in their understanding of the ecological succession concept and the process of science in general (National Research Council, 2000).

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HANNAH SCHMIDT is an undergraduate researcher in the Department of Biological Sciences at the University of Alabama (UA), Tuscaloosa, AL 35487. KALEB K. HEINRICH (kheinrich@ua.edu) is an assistant professor in the Department of Biological Sciences, UA. JENNIFER REYNOLDS is a science teacher at Brookwood High School in Brookwood, AL 35444. JENNIFER G. HOWETH (jghoweth@ua.edu) is an associate professor in the Department of Biological Sciences, UA.