So, today we're going to continue with our series of lectures to come to a conclusion from the section on population and community ecology.

At last time, or three lectures ago, we were talking about the regulation of population growth. And this time, we're going to move into, just wanted to make sure the boards are in order, community ecology. And as I said of the first lecture, this is one of the most difficult branches of the ecological sciences to really describe because an ecological community is a bit of an abstract concept. And one definition is that it's a collection of species that are linked together by their feeding relationships.

OK, so it's sort of like the ecosystem without the biogeochemistry in a sense. So really what we're looking at here is the interaction between species in a localized area with respect to how they influence each other's fitness, in a sense.

And these interrelationships between these species govern all of the things that we talked about in the first half of my lectures set.

It's these interactions that shape the biogeochemistry of those systems.

So, this is the structure of the system and the biogeochemistry is the function of the system. And it's also these interactions.

So, they affect the flow of energy, which we talked about. They affect the cycling of elements. They affect the evolution, the very evolution of species within the community.

And these communities self assemble. In other words, if you start with an empty plot of bare land, we talked about this. Remember the example of the glacier retreating and showing the succession of species as the glacier retreated? We started with a bare rock, and you'll start getting lichen growing on the rock.

And then that lichen will create a little bit of soil, allowing plants to come in, and that the plants increase productivity. Some of them bring nitrogen and, allowing shrubs and trees and everything. And that's the self-assembly of the community. Once you have plant there, you can have insects there.

Once you have insects there, you have birds there.

It self assembles. And one of the questions that ecologists ask is, how deterministic is that?

I mean, we know there are some random components to it, and we know that there are some things that will happen because we see it happen over, and over, and over. So the big question is what must happen? What could happen? And what might not ever happen? That's really one of the challenges of ecologists is to understand those assembly rules of community if there are any. Now, we're not going to really get into that. We are just going to start looking at the real fundamentals of community [SOUND OFF/THEN ON] which is, what are the possible interactions between species that shape evolution? OK.

Species interactions: so, when we talk about species interactions and how they structure communities, we have to first define some terms. One is Darwinian fitness.

And the fitness of an individual is the relative ability of an individual in a population to survive and reproduce.

So, it's all relative, OK, within a population.

And we're going to define also, we'll be talking about adaptations, and I know you know what this is, but let's just make sure that we are all operating with the same assumption.

And an adaptation, which is something that affects the fitness, is a heritable trait that increases the fitness of an individual with respect to other individuals in that population.

So, these are just some operating assumptions so that when we talk about species interactions, there are several possibilities.

If we have organism one and organism two, we can have, and we ask how does the presence of organism two and the presence of organism one affect the fitness of the two organisms?

And if the fitness of both organisms is increased by being in the presence of the other, that's called mutualism.

Being together increases the fitness of both relative to when they're alone. If being together decreases the fitness of both, that's called competition. And if you have the situation, what we recall that? It could be parasitism, yeah, parasitism. What else? Was the ultimate form of reduced fitness? Predation, yeah, being dead is the ultimate reduced fitness. So, parasitism and predation.

And then there are some other sort of rather vague interactions where when you put two individuals together, the fitness of one is not influenced but the fitness of the other is either influenced positively or negatively, and we're not going to talk about those. But this one's called commencalism. And this one's called amensalism. And obviously there are gradients.

Actually, an example of commencalism is something that we've talked about. Can anybody think about what that is when we talked about food webs? It's kind of a stretch, but detritivory. An organism eating detritus, in a sense, is commencalism because it doesn't affect the fitness of the dead individual because it's already dead. So, that gets to not having that much meaning. So anyway, these we are not going to spend time on, but they are forms of interaction that do exist. And there are gradients between these. Obviously, it's not all black and white.

So, we're going to start by talking about competition.

And just to remind you, competition comes in two forms.

There is intraspecific competition, which means within a species, OK?

And that's not what we're going to be talking about today, but we've already talked about this without explicitly, remember our logistic equation and the density dependent feedback mechanisms in that population that caused the population to deviate from exponential growth was due to intraspecific competition: individuals within a species competing with each other for resources. We are going to talking about now is more interspecific -- -- which is competition between species, OK? So, I want to show you some slides that are just from your textbook, but just to get you in the mood for competition. So, it comes in all different forms, and I don't care whether you know the names of these.

It doesn't matter. This is just to give you an idea of the different types of competition that we see in nature. This is what's called consumptive competition, and this is just showing the roots of the trees competing for nutrients in the soil. Preemptive competition shows these are barnacles. We're going to talk a little bit more about that later, just totally taking over the substrate. So no other organism could possibly settle there.

Overgrowth competition in plants where this plant would be shading, so other plants that require a lot of light could not grow underneath.

Chemical competition also occurs where one plant will actually excrete certain chemicals that create these corridors of no growth around them so other plants can't get near to compete for the nutrients. The classic form of competition, say, in birds and a lot of higher organisms is competition for territory. So these are displays so that an individual can keep a certain territory, and therefore make that food available to itself, therefore increasing its fitness because it's able to feed its young.

And then this is sort of the classic, really tooth and claw competition where encounter competition where all these species are competing over this zebra carcass, hyena, vultures, etc.

OK, now before we can talk more and more in detail about competition, we need to define the ecological niche.

And this is an interesting concept in ecology that has been around for quite some time, and it kind of went out of popularity for a while. And I was gratified to see that it's made it back into the introductory biology textbooks because I think it's a very profound concept.

In this particular competition, the fundamental ecological niche comes from G. Evelyn Hutchinson, who is one of the founders of modern ecology. He defined as the fundamental niche of an organism as an N-dimensional hypervolume, every point on which a species can survive and reproduce indefinitely in the absence of other species, OK? So, this is an abstract concept, because those species are rarely in the absence of other species, except maybe in a test tube. But it defines the, and also we can't even think about N-dimensions, right? We're able to think about, we can envision three dimensions. But what he's talking about here, is every single dimension in the environment that would have any effect on the fitness of an organism.

So here, just to wrap our brains around this, we're looking at three dimensions. Our organisms here is a ladybug, and this would be food size.

These guys eat little aphids and things. I don't know if you've ever used them under house plants, but it's a good way to keep aphids off your house plants if you want to introduce ladybugs to your dorm room, which maybe you don't. But there's a certain range of size, food size, that they can eat. And so, that's three dimensions.

There are undoubtedly many other dimensions that we don't even know about, elements that they require, etc. So, this would be everywhere, in this space is a space where this organism could survive and reproduce indefinitely. And the reason this concept lost favor is its something you could never ever measure this because we can't know the N-dimensions. Well, you can never say you can't know anything, but it's very difficult to say you could know all the dimensions that influence the fitness of an organism.

But it's still a very important concept for thinking about it.

And the niche is not a physical place, OK? The niche of an organism is not a physical place. In an N-dimensional hypervolume.

It's an abstract concept. So this is the fundamental niche, and here's another closely related species whose niche has some overlap with this one, but has different ranges for temperature, humidity, and food size. And when you have overlapping niches is when you have the possibility, the potential, for competition. And two things can happen.

If they overlap a lot, than those two species cannot coexist in the same environment. One will outcompete the other, and it will move on to some other place where it doesn't have a strong competitor. But if they overlap a little, you can actually have competitive coexistence. And we're going to talk about the results of these degrees of niche overlap as we go on in the lecture.

So, if the species can makes it realized, so this is its fundamental niche, this one's fundamental niche, and what happens if it can make its realized niche small enough so that there's no niche overlap, then you can have coexistence of those two species, or very little niche overlap in the same environment.

So that's the difference between the fundamental and the realized niche. I think this is from your textbook.

This is just one dimension, seed sized, for, say, a bird eating seeds of this size range. We'll be talking about birds a lot in this. And here's partial niche overlap, species to where they eat some seeds of the same size, but by and large the mode is different.

You can have species coexisting. Partial niche overlap can lead to competitive coexistence. And here's the complete overlap in just this one dimension, which would lead to competitive exclusion. But obviously it matters what's happening on all the dimensions. This is just an oversimplification, to give you the idea. OK, so before we go to that, I want to talk about the classic experiment that led to this, they're going to put this screen up. Screen, screen, screen, screen.

Can you see, or do I need to turn the lights on? Thank you. I'm sorry, I always ask my questions that way, where there's no possible answer.

There were some classic competition experiments that's carried out by Gause way back in 1934 -- -- that I'm just going to use to illustrate the concept of competitive exclusion, because these were done with very simple protozoa in a test tube, paramecia, and actually this was back in the days when they were developing these theories for population growth.

And these organisms were growing according to the logistic equation.

So here we are with, and this is the classic experiment actually in your textbook that they talk about in the context of the ecological niche. So this is Paramecia caudatum.

These names aren't important. Don't worry about it, but we have to call them something. P. aurelia, which, when grown alone in a test tube grow according to the logistic equation, they grow up and then they level off at a certain level.

And what Gause did is that he wanted to see, look at this phenomenon of competition and he grew them together, and he found that, actually that no matter what combination he put in, aurelia would always win out in competitive exclusion.

And he learned through a series of experiments, we don't have time to go into the details, but this would always occur if you made two species compete in a very simple environment. In the test tube where he was feeding these guys exactly the same food, some form of bacteria, in a test tube this one would always outcompete the other, and there would be competitive exclusion. If he made the environment more complex, where there were layers in it, or there was sediment in the bottom of the test tube, that allowed more niche dimensions. There were conditions under which the competitive coexistence would be allowed. And he actually developed a set of equations to describe his competition that I'm going to write for you. We're not going to use them; we're not going to analyze them in detail, but I'm just going to show them to you so that you have an appreciation for how population ecologists and community ecologists start to think about these systems.

So, he said we can model this interaction using our logistic equation. So he said dN/dt would be the growth rate of, let's call, the top one, one. It doesn't matter what you call which. The dN/dt equals r1, N1. Now here's our logistic, K1 minus N1 over K. But he said I'm going to modify this equation so that the actual growth of the organism is reduced to some amount that's proportional to the number of the other organisms that are there. So, he called that alpha-N2.

OK, so some amount that's proportional to amount the other species that's here. And then, he said dN2/DT is equal to r2, N2, K2 minus N2 minus beta-N1 over, this should be K1, over K2.

So, the growth rate of species to in the presence of species one is reduced by some amount that's proportional to the abundance of species one. And these, the values of these, these are called competition coefficients. You can actually do experiments and put values on these, and they are a measure of how strong a competitor each of these species are with respect to the other one. So, you're not going to have to deal with these, but I just wanted you to see them, and see how population ecologists began to model these systems. And so, it's the relative values of these relative to the carrying capacities that will ultimately determine whether species will coexist or not when they are competing. OK, so that's more of a theoretical analysis. Now let's look at the real world. Competitive exclusion, that is, the exclusion of one species from an environment because of strong competition in another, is very difficult to study, because if it's not there, you don't know it was excluded, right? I mean, you don't go to some place and say I don't see the species here. It must have been eliminated by competitive exclusion. It might never have been there.

So, the way we learn about this phenomenon is either through inadvertent experiments, and that is the introduction of species to new environments and then see what happens, or actual intentional ecological experiments. So, we're going to talk about both of those.

And the first one -- -- we'll talk about invasions -- -- and competitive exclusion. And one of the classic examples of this is the zebra mussel. I don't know what happened.

Oh, there it is. I didn't realize this was animated.

That's why there was nothing there. So, the zebra mussel is a tiny mussel that was introduced to the United States back in, I guess, 1988. And up here, introduced into the Great Lakes by ships just being attached to ships, or it's possible it might have been the larvae in ships' ballasts.

Ships go into port, they take on water into their ballasts to stabilize, and then they go to another port and let it out.

And they're filled with larvae and species.

So, the entire world oceans are now filled with introduced species from ships ballasts. So here's 1988.

The zebra mussel is there. 1990: here. 92: here. 94, 90 whatever, oh, 2001. It spread amazingly fast.

And it is this tiny little mussel that seems to thrive everywhere: clogs, all kinds of pipes, settles on top of other native shellfish and kills them, and has led to extensive competitive exclusion of native shellfish in a number of ecosystems.

Some of the effects of these: in some ecosystems they cleared up the water. They are able to filter just an amazing amount of water when they're feeding. So they actually have increased the clarity of the water in many ecosystems, filtering out plankton, which allows the light to penetrate deeper in those systems, allowing aquatic plants to grow from the bottom. So the introduction of this one species can completely change the structure of the entire ecosystem.

I just heard a lecture. I was just visiting the Institute for Ecosystem Studies which is out in Millbrook, NY.

By the way, if any of you are looking for summer internships and are interested in ecology, they have a fabulous summer internship program. I've had several students go there that have had great experiences. But there's somebody there studying the zebra mussel invasion in the Hudson River.

And he showed this incredibly depressing graph of over the last ten years of the native mussels in that river going down to basically extinction. And then, this is the weird thing about ecosystems, just last year it started to turn around.

And they haven't done anything to eradicate the zebra mussels, but the native mussels are starting to have a comeback.

And nobody knows why, and nobody knows whether it's a real comeback because it could come back for a couple of years.

So, it's really interesting how unpredictable these complex systems are. But these mussels can cause millions and millions of dollars of damage. And I also learned on that trip that ecologists are trying to get in place policies that if an industry for whatever reasons wants to intentionally introduce, Here's an example of an application of fundamental ecological knowledge. The reason people study the ecology of invasive species, understanding this competitive exclusion and all that, is that you want to use that understanding to be able to predict, if you introduce a new species to a new habitat, whether it will be invasive or not, there are some species you can introduce and they will fit right in and not exclude every other species.

And so, what they're trying to put in place is insurance that a company would have to buy that was either intentionally introducing a species, or whatever practice that they were doing was likely to introduce a species, and the cost of that insurance would be a function of the probability of that species actually causing competitive exclusion.

And this is something that people are trying to put into place in to the economic system basically. So, it puts a new meaning to limited liability company, LLC. So, you have to insure your liability, which I think would go a long way to reduce some of these ecological crises. OK, so that's an inadvertent experiment. Now there are many, many examples of this. There's books written on invasive species. And if I can get this thing to work, I'll show you some clips of invasive species, snakes.

And the biggest impact is on islands because islands have been isolated ecosystems for so long that if you introduce a species, you have dramatic changes. In Australia, a big example was a prickly pear cactus which was introduced many years ago to create living fences for livestock. They completely took over not all of the grasslands, but a lot of the grasslands and turn them into thickets. OK, so invasive species are inadvertent ecological experiments. Let's talk about intentional experiments. And this is also very classic textbook experiment that was one of the first ecological experiments to be done.

And it was done with barnacles. This was Joseph Connell was a professor at the University of California, Santa Barbara.

Barnacles have a larval stage that floats around in the plankton, and then they settle on rocks. So this was a classic barnacle ecosystem in Scotland, actually, in which the upper inner tidal there is a species called Chthamalus.

And then the lower was dominated by a species of mussel called Balanus.

So, he asked the question, is this distribution where the two are exclusive of one another, is it due to competition between them, or is it just that this one tolerates desiccation longer than this one? The inner tidal zone, the tide goes up and down, so this one's going to be exposed to dryness a lot longer.

So, how do you answer that question? Well, you do an experiment and so what he did was he took rocks from the upper, inner tidal that had the Chthamalus on them, and he moved them to the lower one.

And he let the Balanus, the species that dominates down here colonize on those rocks. But then he divided them in half, and removed the Balanus from half of the rock. And then he monitored the survivorship of the Chthamalus. And remember the survivorship curves that we talked about when we created those life tables, he actually measured survivorship curves on these.

If you go to the original paper, you see LX is a function of time.

So that's a tool that we use, to ask the question, is the survivorship of Chthamalus increased in the absence of Balanus?

And this is all from your textbook, showing that the percent of mortality, when a competitor is present is much higher than the competitor is absent. So, he's able to show directly that there was competition between the two. And in fact, this was that kind of aggressive kind of competition where one just plucks the other one off the rock. I mean it's direct: you're on my rock; get out of here, and it pops it off.

He also was able to show that tolerance to desiccation is also a factor in this system. It's not like it's totally competition. But competition was playing a role, and so I've summarized that in this slide using our terminology.

He was able to show that the fundamental niche of Chthamalus, in other words -- -- the region in the inner tidal, where the larvae could actually settle and live in the absence of competitors was much broader than the realized niche.

All right, so let's get this over. This is from your textbook.

And we're going to just use, I'm going to use an example of that.

So, competition can also lead to character displacement -- -- which in turn can lead to actual competitive coexistence. And an example of this, we're going to talk about Darwin's finches in the Galapagos Islands.

And one of the ways that ecologists actually measure, that's a bird, in case you didn't notice it. And this is beak depth. The shape and size of a beak tells you what kinds of seeds a bird can eat, and so they measured beak depth as a niche dimension, basically, because it tells you what size seeds the bird can eat. And a study was done; we're going to make the islands here. What is going to call them A, B, C, D; these are islands. And there are two species of finches, which we are just going to call F. Well, they're fuliginosa. Again, the name's not important, and the other one is called fortis.

So, we'll just call them, on islands that have both of them, and there are some islands that have only one. So, what was done is they measure the beak depth of the different finches on the islands where they were found together versus islands where they were found alone in the Galapagos Islands. And what they found, and this has been shown for many, many different studies. You look at the beak depth distribution.

This is percent in size class. And this is island C, D, and A, and B. And they found that when the species were on islands where they lived alone, they had almost complete niche, oh this is beak depth. They had exactly the same size beak distributions. In other words, they were feeding on the same food. And on the islands where they were together, A and B, I'm just making sure this actually holds together, they found what is called character displacement, and that is that the birds that had longer beaks and smaller beaks, were preferentially selected for such that reducing the amount of niche overlap.

So, and this leads to competitive coexistence.

OK, and that's what we're looking at here. This is from your textbooks.

This is from African seed crackers showing that birds with smaller bills consume soft seeds more efficiently. Birds with larger bills crack hard seeds, and you can see that the width of the bill here is different.