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[ANNOUNCER:] Welcome to HHMI's 2016 Holiday Lectures on Science.

[Music plays] This year's lectures--Ecology of Rivers and Coasts: Food Webs and Human Impacts--will be given by Dr. Mary Power of the University of California, Berkeley, and Dr. Brian Silliman of Duke University. The fourth lecture is titled "Climate Stress and Coastal Food Webs." And now, Dr. Brian Silliman.

[Applause]

[SILLIMAN:] Thank you very much. I'm excited to be here in the second lecture to talk to you about solving mysteries of ecosystem decline. And in this talk, I'm going to use the ecological and scientific methods, experimental science, observational studies, and collaboration to try to solve the decline in coastal wetlands that's been occurring over the last 20 or 30 years.

And unfortunately, in marine ecosystems around the world, it's a story that's too common. There's been drastic declines, for example, in oyster reef habitats. Over 90% of the oyster reefs around the world have declined. We've lost those coastal wetlands, including salt marshes and mangroves. It's about 40% decline. And for coral reef, it's 50% to 60%.

So one of the... somebody asked a question about what can scientists do, what can the public do? One of the things scientists have to do is they have to step out of understanding just conceptual ecology and jump into those arenas and help solve those problems. What types of interactions are leading to those declines, and if we change the strength of those interactions, can we help these ecosystems to recover and these systems? And a lot of times, what's going on at the same time we're losing marine ecosystems is that climate change is leading to increased physical stressors. Temperatures are warmer. The oceans are becoming more acidic. And drought becoming more frequent. So we have more frequent, intense droughts.

At the same time, we are altering food webs. We're overhunting. We're overfishing in certain areas. It changes the number of predators and grazers. And there's typically two camps of scientists looking at the declines in these ecosystems, one that says oh, it's climate stress or physical factors. And the other one says oh, it's the change in the food web that's doing the decline. And there's not much looking at how these two factors interact. Could climate and food webs be interacting to either protect or stimulate synergistically the decline in these ecosystems?

And today, I'm going to look at whether or not we have interactions in coastal salt marshes. And over the past 15 years, we've had four 100-year droughts. These droughts last two or three years. They increase salinities in salt marshes, spiking the salt concentration and the salinities 30% to 60%. And that's 350,000 acres of marsh. That's over 10% of the marshes we have in the United States have experienced die-back in just 15 years. So you can imagine people are pretty overwhelmed and upset. The governor of Louisiana started a state of emergency about the die-off of these salt marshes.

Bringing in scientists, we have to solve this mystery, figure out the environmental degradation that's going on, and try to reverse that.

In salt marshes, the prevailing theory is that bottom-up forces or physical factors are the ones you need to worry about. They control the plant growth. The grazers really aren't important in these systems. So what is the physical agent that's changing? And everybody saw this drought and pointed to that. It's the drought stress that's killing these plants. And here's an example of a big area that's been killed off in Louisiana, and the typical area is the size of a football field, double that size. And we have something that's very unique. We have a dying and decaying ecosystem, juxtaposed to a very healthy one. And they seem to be expanding over time.

A lot of theories came about; they sprouted up about what was causing the marsh ecosystem die-off. I was following it, thinking about it, and I got a call from a reporter who was going to put forward a theory based on my work. And he did it in about two or three weeks. He put out there in the newspapers: because blue crabs were declining in these areas at the same time the salt marshes were dying off, he proposed an alternative hypothesis that what I had said in my studies--that blue crabs, by controlling snail densities, indirectly facilitate plants, could be happening at large spatial scales. The loss of blue crabs could be leading to outbreaks of snails and die-off of these marshes. Most of the scientists--almost all the scientists in the Southeast said there's absolutely no way that would happen.

We've looked in our marshes, and we see dying and decaying plants. And we don't see snails in those environments. So I got on the truck, and I wanted to go check out all these areas. And I called up people who didn't believe me. I said, take me to your die-off areas. Let's check them out. Let's see if snails are interacting in these environments. And this is a typical salt marsh die-off that we would come upon. And with Georgia, Louisiana, North Carolina, South Carolina, getting these large football soccer field areas: dying, decaying grass with patches that are left, some doing better than others.

And then this very distinctive line, this demarcation between a dying, matted down ecosystem and one that's starkly opposed to that is pretty healthy. And so if you get out of your truck, and you just don't stop there, and you start to look at the environment and look for potential strength of interactions, this is what we found as we walked across that, is that we went to this line, and we found that there were super concentrations of snails right on that line. And if we walk down that line between the healthy grass and the dead grass, it's about 2 meters wide, and the length of it was between 200 and 500 meters, with 2,000 snails per meter squared in those areas. That's millions of snails. And we term that a consumer front--super concentration of grazers in one area making a front like an army. And it looked like it could be plowing through in those areas.

And we went to Louisiana, Georgia, and we took our quadrats out. We wanted to count the number of snails. So you put it down, and it would take almost an hour in each one of these plots. And one of the scientists who didn't believe me at Louisiana State University, I said take me to your die-off area. We got off the boat, and I said no snails. None whatsoever. I said, let's go over to that other area where it looks like there's a decaying band. Let's see if grazers are there. And lo and behold, we walked over the mud flat--it took us a long time because we got stuck in the mud--got over there and saw lots of snails.

And he said, I believe you; let's get to work. So we did the quadrats, and then we pulled the snails off, and we tried to look for snail grazing effects.

And here's an example, some more... another picture. The plants that were in this die-off area, the ones that were left over, were being... looked to be over-grazed by snails as well. And this is--it looked like the snails were killing them, and this is a big effect for a snail to have to kill a rooted vegetation. But we need to test that experimentally. So based on these observations, we proposed three different questions: do snail fronts generate marsh die-back? Do they contribute to the loss of this ecosystem by overgrazing? Is this front pushing the die-off of the ecosystem further into healthy systems? What factors contribute? Why are these snails piling up?

Something counterintuitive, humans don't necessarily do--we're a little bit claustrophobic. But all these snails are concentrated, and it looks like a powerful edge stress that's out of control in these ecosystems. So what factors could do that, and could snails and drought interact to cause marsh die-off. This is looking at climate stress and food webs. Is there an interaction there, or are they not doing anything to each other? Let's use experiments and modeling to test these ideas, first using one of my favorite tools: the cage.

We go along these snail fronts here, and you set up a control area. So this is a control snails, snail removal, and you come back over time. And this is what we found time and time again at all these die-off areas. We saw that snail fronts were moving through, and in the wake of the snail front, you found an exposed mud flat. They were killing the vegetation. How is the marsh grass doing inside those cages? Well, if you look over the top of the cage, it's doing just fine. And these are the plants that are exposed to the drought stress that's supposed to be killing off and driving death in this ecosystem.

Clearly, physical factors are not killing the marsh in this particular instance. In fact, the drought had subsided, and those physical stresses were now gone. So this experimentally demonstrates that snails... a top-down force is driving die-off in this ecosystem. Ecologically, it's pretty amazing because these plants have small, potato-like storage units called rhizomes. And they have resources to regrow.

A lot of times, grazers go to greener pastures. These snails are sticking on these plants, likely because snails are really after the fungus they facilitate in the plant leaves. And as they graze down those plants, they become better substrates for fungus, so no reason to move off those marshes. So what... we found in all these different sites that the rate of die-off was increasing at different rates. So does the number of snails that you would find in these snail fronts really determine how much ecosystem you're going to lose? And we found a strong correlation there, that with increasing snail density, we saw increasing loss of marsh after three or four months.

And this is in Louisiana, Georgia, and a variety of other places. We also found an interesting, what we thought--it looks like an inflection point. And you see this right here. Below this line is gain, salt marsh gain, so a little bit of recovery in the marsh at the drought, and this was loss, continued die-off of the ecosystem. And about right here, it looks like there's a threshold. And that's a point in an ecosystem, as you're increasing stress, in this instance, it would be stress from grazers. As you increase that stress, is there a point where that plant or animal can no longer take that pressure, and then it collapses? It

disappears spatially from that spot. And we seem to have found that. So it may take 1,000, 1,200 snails per meter squared for this process to generate.

So what factors could change in that ecosystem to lead to a piling up of snails at that density? Could it be blue crabs? The decline in blue crabs... they were falling the same time this was going on. Both drought issues--they don't like drought--and also, there's some overfishing suggestions that were going on.

But let's look at that relationship. And you've seen this graph before. It's the relationship between crab abundance and snail density. Before, you just looked at the relationship. But pay attention to the numbers, the quantitative numbers. In years where you have low blue crab abundance, the snail density does go up, but does it reach that threshold? Per meter squared, in areas where die-off's not going on, the snail numbers double, triple, but they don't go up above 1,000 per meter squared in those areas.

So it suggests that the decline in blue crabs could contribute to increasing snail densities, but not necessarily get them to above 1,000 per meter squared. Could they be interacting with drought stress in the environment? So to do this, we go to experiments. We go to healthy marsh areas that haven't experienced die-off, and we manipulate the amount of snails and the amount of drought stress. And the drought stress is pretty easy to manipulate. You take 50 milliliter centrifuge tubes. You take a drill. You drill holes in the side. You take pantyhose, and you wrap up salt. You stick that in there, and you have a salt shaker--underground salt shaker. And you stick that in the ground, and you can elevate the salt in that muddy environment to levels that mimic what happens in drought. So we have a drought stress. And then the snail stress is easy enough to manipulate.

So this is a picture of a healthy ecosystem right here, of one without drought and without snails. And I'll show you the striking pictorial results there. This is a snail exclusion of very healthy marsh. And if you add salt without snails, you get a strong negative effect: 50% reduction in plant biomass when you increase the amount of salt stress in those ecosystems. So it suggests that drought is having a strong, but nonlethal, effect on this ecosystem. So this experiment predicts that drought alone is not doing it.

And what happens when snails are there, and you have a marsh on snails? Well, you have a control treatment. Again, you can see top-down effects of snails that reduces it 50%. Adding 50% reduction plus 50% reduction is easy math, and it leads to 95% to 100% reduction in biomass. And this shows when you simulate both stressors in the environment, if you increase drought, top-down control is increasing in that environment, and you add those together, and you can experimentally generate die-off in the system. And it shows those climate stressors and the interaction with top-down control could be driving die-off in these systems.

Well, we know from our natural history of the salt marshes that, when drought occurs or lack of water coming into the system, salt doesn't increase equally in all parts of the marsh. It does so more in the high marsh. And so that means that this is going on. What we're having, we're getting pockets of die-off. We're getting mud flat. But what do the snails do when their prey item's gone? You can only guess. They're probably going to go after the prey item. That's we thought, too, but we wanted to test that.

That is the plant. So here's what we did. We went to the mud flat where some of these die-offs had occurred, and we took the snails, and we marked them with little paint, and then we spread them out. And we asked them, which direction do you prefer to go if grass is 2 meters away, and a mud flat's on the other side 2 meters away. They have decent eyes, and they can tell... visual acuity, they can see if something is off in the distance with height, for instance, with shadows. So we put 200 snails out there. Amazingly, after two hours --this is amazing for snail movement. I'm used to working with snails. They don't move more than a meter horizontally in a salt marsh over a year period. They just stay going up and down those stems. They don't move much at all. Two meters in just about two hours--I was amazed. And then 96%--everybody was moving towards the marsh. And then we went back further, and you could do it 4 meters and 6 meters. And they stopped being able to detect the marsh about 10 meters away.

So they're going towards the grass, and they're going fast when they don't have plants. So it's a behavior in which they home to their prey item. And look at this movement, how it changes--16 meters per hour; that's very fast for a snail on mud. And then when they get here, it's 25 centimeters per hour, but it's back and forth. They just stay in one spot once they get to the grass. So this is a visual representation of what happened. You take all those snails, 96%, and they move over to the edge, and then they stop. And because of that behavior and because of the spatial heterogeneity in the system where you have no grasses and grasses, it then creates a wall.

It's like taking the band during a college halftime show, and then everybody moves to the sidelines, and you have a super concentration of individuals right there in a big band. And right there, you go from a situation where you don't have high enough densities to overwhelm the system to one where you're likely to go eclipse a threshold that we've identified before. So if we look at snail front movement, if we hit that threshold, are we going to see movement over time? And let's follow that a little bit more than just with a cage.

So these are in Georgia salt marshes. This is the amount of marsh grass as well as snail density on this axis, and then snail density over a distance is denoted here with this orange line, and then marsh grass with green. Zero meters demarks the differentiation between a dead ecosystem and a live one. So over here, we have green grass, and over here we don't have grass, and we don't have snails. And we can see over time--this is time zero three months later. The snail front's moving across 5 to 10 meters. And in its path, it's killing off the grasses. So it's expanding. And remember, this is happening over a large circle 400 meters long. So you have to multiply that times these distances to get an idea of how much of the ecosystem they're killing off.

Then we get one more time sequence. The front is actually maintaining itself and continuing to go through the system. A little bit scary situation. Importantly, during this period, the drought had subsided. So it looks like we set up a potential catalytic event where you have a wave that's propagating through an ecosystem, despite the fact the original stress is gone that initiated that concentration of grazers in the system... potentially dangerous. So we're interested in what potentially could control those snail fronts. So if we put our die-off sequence together, it looks like we have climate stress and top-down control interacting to cause localized die-off. And we know that from natural history and experiments about... and then once that happens, very importantly, we have the

behavior of the snail comes into play. And because they home into those plants, they all leave the mud flat and go to the sidelines, and then you get this edge stress going on. If they were still spread out, you wouldn't have the threshold eclipse. That eclipses... you get over 1,000, 2,000 snails per meter squared on the sidelines. Then, you've hit the threshold. And then you get this runaway or catalytic effect that, despite the fact that drought has subsided, it continues to mow down this ecosystem.

Very powerful phenomena, interaction between spatial processes and food webs that we haven't really thought about a lot in ecology in these systems, so really big effect. If we can model this--this is fun. You would take your math classes, and you think where are you going to apply the math. It's amazing how much you use math in science. And you can use a lot of calculus when it comes to looking at the functional relationship between cause and effect and x and y . And you can do that in modeling.

And this is a simplification of the model, but we wanted to know, can we actually generate this with math? Can we generate what's going on? And so this simulates--this is distance right here. This point right here is where we have a mud flat die-off. And this area over here, these are snails. So that's snail density in the healthy area. Here's the snail front, and this is the amount of grass in the area. And so we put in there information about how the snails move. They don't do it randomly. They go towards the plants. So the snails in this front, guess what, cannot go backwards in the model. They have to go forward. And as they're going forward, imagine the chaos that's ensuing as you have snails here in a healthy environment. And there's a front of snails rolling over. And they're going to be incorporated in there. Remember, they don't move too fast. So this should expand over time, leading to faster degradation of marshes.

And indeed, when we run the model, that's what we find. It's what we find in nature. It's not a perfect simulation, but we can do that. And we can apply this model to other situations, and we can change things. How important is that behavior? Well, we take the homing out of the model, and the fronts never form. So it's just a localized effect, and you don't get the domino effect. So that behavior becomes really important if we potentially see this in other places. So one of the things people usually ask about is, is this going to kill all the salt marshes. Is this going to stop?

And one of the things that happens is that the winter comes, and these snails will migrate when it gets cold, and they'll leave the fronts, and they go up to the high marsh near the terrestrial borders. So the winter is--the coldness will stop this in action. And there's also a mechanism for recovery that moves faster than the snail fronts in many instances. And that is... we just published this paper. I think it's very exciting results.

And we use models and experiments again in the field. And so what we did is we measured the recovery rate. How fast do these patches of mud fill in with plants? And we did some experiments. We sprinkled seeds out there. And seeds cannot grow. It's so anoxic, without oxygen, they all die. And so the only way these plants can grow back there is vegetatively. The roots go under--it's like a weed, crabgrass growing in your driveway. They send these runners. They're feeling, and they poke up through the surface, and they establish themselves. So then they can go a meter or two meters a year. And the rate of coverage is based on how much perimeter of the marsh is facing that area. And what we found is that if you don't have any of these patches in here, and you just have a mud flat with a

circle, it takes a long time for those places to... years to recovery, 20 to 100 years, depending on the size of the mud flat. But if you have these little patches that are surviving, and we found out that those patches survive if they have mussels, the reason they survive is there's a mussel mound underneath them.

All these ribbed mussels that create what I said earlier was a spa in the marsh. They hold water, so drought doesn't increase salinity there. There are predator crabs that will actually eat the snails. And it's like a tree fertilizer stake. You put it in there, and they're pooping right underneath the *Spartina* plants, the marsh plants, and it increases.

So these plants that are living on top of mussels are very robust, and they can withstand a snail front. They survive, it goes through, and then we get regrowth. It's a nuclei for regrowth resistance. And look how fast regrowth occurs, 10 to 12 years. In some places, it can even be 5 years. So this mutualism underlies the ability of these ecosystems, marsh ecosystems that you have right here on your coasts, to not disappear. It's those mussels that allow it to deal with those consumer fronts--pretty cool interaction.

So let's enter... we talked about climate stress and food webs. Let's put them together. We have a new marsh food web that incorporates bottom-up factors, influencing the plant growth, the conceptual model here, top-down control by snails and blue crabs, and direct facilitation. What is climate stress? What is climate stress doing in these interactions? We know from experiments right here, this is getting stronger, so it's amplifying that. For blue crabs, what drought does is... blue crabs really prefer waters that are about half the salinity of the ocean. It turns out in full ocean salinity waters, they're very susceptible to disease. And they can move.

Before, I told you that they could swim. And they move up rivers. As the ocean moves in in drought, because not as much fresh water's coming down the rivers, they move with it. And so they move off the marshes, and we have less predation in those years. So what happens is we have drought stress that's affecting the interaction strengths here. It's amplifying top-down control by grazers and cutting off the top of the food web, effectively removing this facilitation cascade. So we see a strengthening or a triggering of outbreaks of grazers in this system, two added effects. Very powerful, and it's leading to less of an ecosystem that a lot of people enjoy and depend on. Is this happening in other salt marsh systems?

Asking generality is an important part of ecology. I've been working with collaborators in China, and the same thing is happening. They're having increased frequency of intense droughts, and they're losing one of their prized natural resources: salt marshes that are uninhabited by plants from North America. They have these beautiful native salt marshes that turn maroon in the fall. But they're all dying off, and it's transforming into a lunar landscape. And so they're going after drought that... everybody's pointing their finger; it's just drought, salt stress, and after-drought stress.

They go out there and plant plants, except all those are dying even when drought stress is gone. If we go to a different river basin, we see the same thing going on. Is there a possibility that grazers that we've seen in our last survey, that are in these marshes, are playing a role in this system? So we

started studying it about four or five years ago, and we put cages out to look at before drought, in the anticipation that we would get another one, to see the effect of drought on a system with and without top-down control in the environment. So we used cages again. And this is 2010. This is pre-drought years. And in 2011, there was a big, intense drought. And this is what happened in control cages and exclosures. In control cages, we got nearly a complete die-off. A lunar landscape emerged in those environments. In the caged areas, we saw that there was drought stress. It suppressed the plants' growth, but it didn't kill them. The ecosystem was still intact.

When the drought subsides, you can predict what happens here. You get recovery where you do have plants, and you get continued decline here in those areas. And what we found is that crabs formed fronts just like the snails, and they're more mobile. So when all the plants were done, they would move around and go finish things off. And anything that tried to regrow into the area, even on a mussel mound or anything else, they would clip it down, so having big impacts on those systems. And they've suppressed it from even recovering in those environments. So that suggests that it's a common phenomenon in salt marshes where climate stress is going to amplify top-down control and lead to loss of ecosystems that we really care about. Is this something that we should worry about in other ecosystems that we care about--forests, rivers, coral reefs--or is it something that we can just put to the side and say, it's only in salt marshes, and if you care about salt marshes, you should care about this interaction?

Well, let's go to ecological theory. In ecological theory, we have a very simplistic model that does predict... it's called the environmental stress model. And it's based on work in rocky intertidal systems, where they studied sea stars eating mussels. And what they found was that the stress on the foundation species by the consumer--in this case, the predator, the sea star--decreased predictably as you turned up physical stress. You go up in desiccation stress or wave stress. The sea stars couldn't hold on as well as the mussels, and they couldn't withstand as much desiccation. So they predicted in most situations, as you increase physical stress, consumer pressure would go down. That's not what we're seeing.

But theory suggests that should be a common phenomenon. If that's the case, as physical stress is going up, there's an obvious answer to the amount of stress on the foundation species from physical stress. It just goes up as well. And then you have crisscrossing inverse lines here. If you're measuring total stress, and it's all about grazers or climate, they kind of equal each other out in this conceptual model. It's imperfection. It's not numbers; it's just an idea. And we have total stress in the system is flat. You trade one for the other. So is this happening in other systems? And if it is, in our models for understanding climate stress, we don't have to worry about grazers and food webs. We can just turn it off. Just try to worry about acidification, temperature. But if that's not the case, then we need to bring in food webs, too.

So one of the other examples I was reading in USA Today probably 10 or 12 years ago, looking at this massive loss of forests out on the West Coast of the United States. And it was driven by drought stress and interactions with grazers, these pine bark beetles. They carry fungus with them, and they drill holes in the sides of these trees, and the fungus they carry with them infects those trees. On non-drought years, the plant's immune system will form a wall around that area and keep the fungus from

moving into the plant. On water-deprived years, the plants don't have those resources, and the fungus, hyphae, proliferate in that plant, and they kill it. They kill entire trees like this. And those can have massive consumer cascading effects. You can get big fronts moving that you can see from a helicopter, not when you're hiking, and they move through these forests, killing a lot of these ecosystems. So this suggests that a lot of these are going on.

Here's some numbers behind that. If we increase the intensity of drought frequency, are we going to see more of this? Here's for snail fronts and for pine bark beetles. What we find is that this is a Palmer... these are drought indices. This is very dry, very wet, very dry, very wet, and the area of beetle kill and the number of snail fronts. And there's exponential relationships in both of those. As you get to this--it looks like a threshold here of a minus 2 or minus 3 drought, and the number of snail fronts escalates.

We start to have this process, that we now know about because of models and experiments, is happening on a large spatial scale. And the same thing--it looks like pine bark beetles would get... look at how much area is being killed by pine bark beetles, is proportional to the amount of drought in the area. So how common is this?

We have two examples now. Let's comb the literature, go to the computers, look at the journals. Are people seeing these interactions? And what about these consumer fronts? These are really powerful edge stresses that can devour whole ecosystems. Are these common in other situations? So we looked at grazer outbreaks and consumer fronts. What we found is there was actually 16 examples. That doesn't seem like a big number, but that's 16 different ecosystems in which we found consumer fronts can kill the entire ecosystem. It's not just happening on a small scale. I knew about urchins going into it. An urchin... this happens throughout the world. This happens off the coast of... this is in the North Atlantic, the North Pacific, the South Pacific, and other areas. It's a very common... and they plow over the kelp beds. Locusts can do this in agricultural systems. And this is the one... I teach in coral reefs, but I wasn't even thinking about this. It's not really called that in the literature.

But the disease that's driving a lot of the coral reef die-off in these ecosystems around the world are band diseases, and they're microbial communities that form consumer fronts. And in the back of them, they leave an exposed calcium carbonate skeleton that's colonized by algae. And in front of them is a healthy coral that forms the foundation of those ecosystems. So here's another consumer front. What's potentially setting that off? In 10 of the 16 examples, physical stress--10 out of 16 examples, physical stress was stimulating these consumers to congregate and overwhelm their prey item and then lead a threshold where they could continue that progress without the stress present. And importantly, just like the snails, all of those animals had this characteristic. They always move towards their prey--resource-dependent movement--and they didn't mind being in the closet with other individuals in the same species. They weren't claustrophobic. And so if you put them all together, they don't move faster away from each other. They just kind of slow down.

So the urchins do that, microbes do that, and locusts do that. Here's some more examples. Wildebeests will do this. It's driven by rain deprivation. Gypsy moths and also crown-of-thorns sea stars. This is--no kidding, it's the thorn in the side of coral reef managers throughout the world. These

crown-of-thorns sea stars are outbreaking. And you've all heard the story: you cut them up and divide them up, and they reproduce, and they come back. They're killing entire ecosystems. Hundreds, even thousands, of kilometer squared of coral reef are dying in those areas. So it seems to be a common phenomenon.

What about biotic attack and drought? Drought is a problem. It kills agricultural systems. It kills plant systems that we depend on for resources. And people are studying, they're trying to predict at what level of drought... how much drought can we withstand before we lose the ecosystems we care about? We're trying to predict that. And all those models, none of them include top-down forces in the system. But if you look at the studies where people are noting the natural history, some observations about their studies, almost 80% of them note that there's a biotic attack going on--different players--remember that; we talked about different players--but the same process. These plants that are under stress are being attacked by pathogens.

Nobody's done the experiments to test the relative importance like we've done in salt marshes, so we don't know if they're contributing in a big way. But it could be really, really important. And it suggests--it's a little bit of a smoking gun. So let's revisit theory. So this is the simple environmental stress model. And let's reevaluate this. So in 10 of 16 examples, physical stress was actually increasing consumer pressure. That's the opposite of what that's telling us here. Remember, consumer pressures in this prediction should go down as physical stress goes up. And so if you're over here in a very climate-stressed ecosystem, that's what you have to worry about is dealing with climate stress. But the opposite could be true, and that is, consumer pressure could either be flat, or we have these snails; it could act synergistically. And then look what happens to total stress in the ecosystem. It goes up. And this is a stress on the foundation species. And somewhere along this line, we're going to put a red arrow. And that's the threshold of that ecosystem. That's how much it can withstand before you start to see a decline. And we need to find that. We need to find where that's at.

So this helps inform how we can pose our resistance and our resilience models and recovery models in ecosystems. And let me give you an example. This is... understanding ecosystem resistance, these thresholds, it's in all the science papers and the New York Times, people go, what's the tipping point. How much can these ecosystems handle? Because we'll manage it up to that. We'll find that point, and that'll help us when we have limiting resources and conservation, allocate to the ecosystems that are about ready to go. Find that threshold. Well, okay. Here's a relationship between physical stress and the amount of a foundation species. Marsh grasses, mangroves, coral reefs in those areas--as you turn up climate stress, you could have a relationship that's just linear. So you just turn it up 1 degree; you get a proportional decrease in foundation species of 1%. It could be a 1:1 ratio. That happens a lot of times. You saw that with snails and marsh.

What we're finding in a lot of ecosystems is they have some internal feedbacks that allow them to withstand a little stress, like warm-blooded organisms. They are able to deal with some of those stresses within physiological adaptations. And so you don't see a change in the amount of that species for a while until its eclipse. So we see a flat line as we turn up physical stress. But it gets to a point it's just too much. You have too many exams on one day. You just can't handle it, right? And then boom, you get to that point. We all know about thresholds. That happens in your fifth exam. You're like, I've

just got to get out of here. I can't deal with that fifth exam. And you get this threshold. And that's what we're searching for. So we do experiments with different levels of salt stress, different degrees, and we try to find those in ecosystems. We have one in salt marshes.

But all these models make a basic assumption, or they just forget to include it: as physical stress is going up, they really don't include in these models, quantitative models, what could be happening to the grazers and predators in the system? They're not incorporating that. So we're managing for that. And which way should that threshold go if we have a system where we have additive effects with consumers? Right, to the left. And this is what's likely going to happen. So we're going to have a lower threshold. It can handle less drought in some of these systems, less warming in these systems than we think, or less--for instance, less acidification if the consumers... the grazers are going to say here's a prey item that's weakened. I'm going to attack it in those environments.

So it's important to guard against. So it's a bit overwhelming. You're like, this is a little bit sad to hear all this. They're more vulnerable than we thought. But this is actually empowering, because it tells us, in many of these systems, if they are more susceptible to grazer outbreaks as physical stress increases, we need even more predators around. So we actually have an answer to that, to push their threshold back up. These grazers right here-- if we got rid of those, either through harvesting them or actually having more predators in the system, we may be able to increase the threshold back to where it naturally is with physical.

So here are some key findings. We've talked about trophic cascades. But now, we know by looking, having an open mind and looking at interactions between physical and biological forces, that climate change, just like loss of predators, can also unleash grazers on an ecosystem. I'm calling that a climate cascade in those systems. And it may be happening in a lot more ecosystems than we imagine right now. And so they can also act together.

So if the predators are being lost from these systems--you have less sea otters, or you have less blue crabs --at the same time, the climate's going up, it's going to be even worse, and the threshold's going to come down. It's going to be synergistic, not just additive in those systems. And once you know something, you can take it to a new system. So this puts the alert on. We just didn't stay with salt marshes. You go look for generality. You look at other ecosystems. You talk to other managers. Is this something that you're seeing with urchins? And we start to do generality, and that will help in the conservation of these systems, is the climate for threshold stress is lower, but how do we combat that? We need more otters. We need more blue crabs. In those times of drought, we need more predators in the system.

Or, for instance, if the otters aren't there, we might increase harvesting of urchins for the fishery during those years, because fishery management could compensate for this. And importantly, I think you read a lot about theory, about how systems are supposed to interact. And you've seen that in the lectures here today, that observations that you make yourself in nature may not jive with that. And it's important to trust your instinct and say, okay, let's evaluate that hypothesis. Use experiments, work with other scientists, test those ideas, and confront theory with data. Theory is fantastic because it sets a conceptual idea and a model for your understanding of how that system works. And you may find

something that maybe doesn't jive. You test that. The theory, is it correct. And then you incorporate it in there. So we expand it. We haven't rejected the old bottom-up paradigm in these systems or physical forcing only. It's both. It's not one versus the other. It's both top-down and bottom-up control of these systems. Thank you very much.

[Applause]

[SILLIMAN:] Anybody in the top up here? Maybe in the middle.

[STUDENT:] Are there any successful cases where you introduce, like, a predator, and you help to push the threshold to the right?

[SILLIMAN:] So that's a great question because as these predators... we have conservation for top predators. They were overhunted. They're coming back. And so they're moving into the areas. Wolves: the reintroduction, there's a little debate about this. But the idea is it's changing elk populations, and it's allowing forests to regenerate. So that was an introduction to save the wolves, but there are consequences on that. The sea otters is a good example in salt marshes on the West Coast. The sea otters have been undergoing conservation, their populations are increasing, and they've moved from what we thought was their favorite habitat, kelp beds--very agreeably moving into sea grasses and shallow environments. And they seem to be growing well.

So we may be wrong about what they prefer. They're in salt marshes now, and they're eating the crabs that have been killing the marshes there. And we're seeing a reversal. We're seeing that edge loss that we saw before on the marsh edge, where all the crabs are burrowing crab condominiums. It's not eroding anymore because there's not any crabs there. And the plants are rebounding as the otters come in. So top predators can rescue these systems and these examples, and we need to know how much more often this could be the case. Great question. Top predator rescue: I like that. Back here?

[STUDENT:] I'm wondering if adding mussels to salt marshes could reinstate the natural state of the marshes.

[SILLIMAN:] Right. Love that question. The answer is yes. Here's another paradigm we need to think about: restoration of marshes and protecting... we've taken all the theory from pine forests, where you plant everything away from each other because competition is supposed to be bad. You don't want to be near a neighbor. It's the complete opposite in salt marshes and wetlands. The closer you plant plants, they help each other by shunting oxygen down there. Put mussels in there. They don't compete for space like they do on a rocky shore. They actually increase plant growth.

So we're doing that right now, but it's the scientists working with the conservation organizations, who aren't reading our papers. And we're saying if you just walk a little bit further and get the mussels over here and plant them, it doubles and triples the rate of growth in those areas. And so the generality of that is really important. So these ecosystems are declining, and conservation typically... and the paradigm is that we have to identify a threat and reduce that threat, so get rid of negative interactions. That's really important. The other thing you can do is you can enhance positive interactions, just like in

top predator rescue, another mutualism like that. And so even if you don't have threat reduction, and you increase positive interactions like this, you can overwhelm that stress and shift your threshold out even more.

So that right there is a sort of shining light in all this, finding the species interactions, is we've got to... And we have to do that systematically. When I see the conservation tables, everybody's like, what are the threats? Let's get rid of them. What are the threats? Let's get rid of them. And now, I say, what are the positive interactions? Let's get more of them. And I do it randomly, not just predators, but mussels in those environments, microorganisms, everything. Let's think of every positive interaction that could occur. Great question. In the middle up there at the top.

[STUDENT:] I did a lot of research in the past year on the crown-of-thorns starfish and how it's affecting the Great Barrier Reef. And my question was, there's a recent development that scientists have made in Australia, where they are using the stomach acid of cows to kill the starfish because they're allergic to it. And my question would be, if there's a situation, like with the snails and the crabs, where the crabs do not naturally stay near the snails in a stressful environment, would you condone a path leading to the death of the snails? Would that be a logical way to go? Or would you want to go a different way first?

[SILLIMAN:] It seems like a logical way to go if the method was something similar to like you described. I didn't know about that. That's really fascinating. And the consequences in that method are just the killing of consumers in that front, and there's not consequences on the rest of the ecosystem. And a lot of times, we've gotten that wrong, by introducing other species that we think would just kill that one species, and then they start killing everything in the ecosystem.

So we have to be very careful about that. But yes, we've talked about... with urchins, when they have urchin fronts, they've actually talked to fishermen, and they open the urchin fisheries so they'll consume, they'll take more of those. So managing those consumer fronts, yes. To kill that many snails is difficult because you'd have to spray a molluscicide. And that is not something that's nice to everybody. It kills oyster reefs. It kills the mussels. It kills all kinds of stuff. So we would have to go to snail picking.

[Laughter]

[SILLIMAN:] Right here. Sorry.

[STUDENT:] So are predation relationships and resembling feedback loops, are they necessarily a determinant correspondence phenomenon? Or are they somewhat dynamical chance encounters? And how would that impact the reliability of quantitative models in predicting future events?

[SILLIMAN:] Great question. So the predators finding these prey, like blue crabs finding the snails..

[STUDENT:] Right. Are they...

[SILLIMAN:] Is that random? Or is it actually more likely to find them in these clumps?

[STUDENT:] Is it indeterminate, also considering the spatial heterogeneity among...

[SILLIMAN:] So the blue crabs --they move into the marsh, and they move in there pretty fast. And then in the areas without plants, they actually move faster, and they go towards plants. So there's a little bit of determinism there. And then when they get to the snails, they stop on that patch, and they sit on that patch until they can't feed anymore and another predator shows up. So there are some feedback... as the mud flats appear, the predators will actually find the prey to a greater degree. The problem is there's not as many blue crabs in the environment, so you don't get this feedback, where as snails start to concentrate, predators compensate, and they find them and sit on that.

One of the interesting things we're finding that may be a compensatory feedback is that these snails get infected with parasites. And the parasites stop them from climbing because the parasite's next host is the crab. So they increase their predation rates. But the parasite... the final hosts are birds, migratory birds. And so it goes from birds to snails. And so what happens is birds love mud flats. So as these die-offs increase over time on the snail fronts is that these predators, that aren't snail predators--they're eating worms and crabs--come in, and they fly in, and they parachute, through their poop, a lot of parasites. And we find higher infection rates when they're...and it slows down the front. It actually has a big effect, so very cool question, about that dynamic.

[Applause]

[Music plays]