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[NARRATOR:] Welcome to HHMI's 2015 Holiday Lectures on Science. This year's lectures, Patterns and Processes in Ecology, will be given by two leaders in ecological research, Dr. Robert Pringle and Dr. Corina Tarnita of Princeton University. The second lecture is titled, Patterns in Nature. And now, Dr. Corina Tarnita.

[Applause]

[TARNITA:] Thanks, everyone. It's great to be here. It's great to see you all, and I look forward to getting to know you a bit better and getting all your questions.

So this lecture is going to be basically entirely focused on patterns and the very conspicuous kind of patterns that you can spatially see. Once you start looking for patterns, you find them everywhere basically, across many different scales, across a broad range of scales from the tiny diatoms that are basically like the algae, the most important algae in the phytoplankton, to the level of the landscape, where if you use Google Earth, and you look around, you'll find a bunch of these patterns. Those are vegetation patterns that look like gaps of soil in an otherwise sea of vegetation.

So there will be basically two questions that are driving this entire lecture. The first one is, how do patterns form? So what are the mechanisms, what are the processes that lead to pattern? And the second one is, why do patterns matter? In other words, what are their effects on the ecosystem? Are patterns just kind of pretty, or do they have some sort of meaning for the rest of the ecosystem?

So let me give you an example. Here's something that you may see if you use Google Earth, and you were hovering above the Wadden sea, it looks kind of like streaks, but they turn out to be very regular streaks. And if you look carefully, those actually turn out to be mussel beds. And so the question is, how do these tiny mussels organize in such large-scale patterns that you can see them from the satellite. So here are the mussels. And if you put mussels on a concrete substrate, and you're willing to wait for about ten hours, this is what they do. So very small- scale behavior leads to large-scale patterns. So, this is not abiotic. This is not that the substrate was somehow streaky, and the mussels just organized like that. It's the mussels actively organizing themselves on a very local scale that produces that pattern.

So keeping that in mind, we're going to ask the same question about vegetation in this lecture. How do we get these large-scale vegetation patterns that can come in very different shapes? And we'll go through a bunch of them. So here's what happens if you don't have plants in a system. Depending on your soil, water either will pool at the surface, and it will evaporate, or it will go very quickly into the soil to great depths. So it barely ever stays within the region where plants would be able to use it, so kind of close to the surface. But if you manage to get one plant that manages to establish there, that plant, as it grows, its roots are going to retain the water moisture and keep that at the surface, which is great for other plants that might be able to come nearby because they can now use that moisture, and they can also grow. So that's what we call the range of facilitation. So locally, plants facilitate each other.

Now, as these plants grow, their roots are going to get bigger and bigger, especially if they need a lot of water, and the system doesn't have too much water in it. So it's kind of water-limited. Then those roots are going to expand, trying to get the water from everywhere around them. What happens there is that if you now start to get new plants that try to get into the system, the ones that are very close to the roots of the plant that's now big and established are not going to be able to get to compete very successfully for the water, so those are going to wilt. And that's why we call that a range of inhibition. So there's some local facilitation, but then at a distance, there's quite some inhibition. However, the plants that manage to establish at a distance from that actually can do fine.

So in the end, what happens is that you get plants that space each other apart in a way so that they don't interfere with each other's roots. And that's what's going to create this kind of regular patterning or some kind of regular patterning. This is one mechanism, this kind of inhibition and facilitation. The interplay between them can create such patterns.

So we're going to take a look and see what happens in a system as we decrease rainfall. So as we start to put more and more water stress, what kind of patterns are we going to see? So on this plot, you see vegetation biomass on the y-axis and then rainfall. And I'm going to start with very high rainfall, so on the left-hand side of the screen-- or sorry, right-hand side, as you guys are looking. And from a very high rainfall, we're going to have what you guys have at home if you water your lawn. You're going to get homogeneous vegetation.

But as the rainfall decreases, you're going to get less biomass, but not just randomly less biomass. It's going to come in a very patterned kind of way. So you're going to get something that looks like a polka dot of gaps in otherwise what used to be homogeneous vegetation. Then as I decrease the rainfall even more, I start to get-- I get into a different kind of pattern. Those gaps stretch out, and they turn into these mazes, these kind of labyrinthine shapes. So that's my next pattern. As I keep decreasing the rainfall, the final pattern that I see is this clumpy pattern that is, again, very regular, again looks kind of like a polka-dot dress. But now, it's basically clumps of vegetation and otherwise a lot of soil. So those kind of inhibition and facilitation mechanisms play out and produce these patterns depending on rainfall. As you keep decreasing rainfall, you stretch out the soil, you get more and more soil, and you go through these different kinds of patterns.

After this pattern, the very next thing that you see is a dramatic decrease of the biomass and complete loss of that biomass. And we get to see desert. So the point here is that patterns are extremely interesting and important in this system because they actually offer this at least theoretically. We understand that they offer this kind of predictable sequence of what you should see in the system. So you start with homogeneous vegetation, and as you keep decreasing rainfall, you should go through this very predictable sequence of patterns.

At the very end, right before you lose all of your vegetation quite dramatically-- so not in this very smooth-- you get less and less and less biomass. Basically, at around 0.55 or 0.6 millimeters of rainfall, you lose all of it instantaneously. And so one idea would be that maybe the very last pattern could be an important signal that tells us that that vegetation may be in danger, that system may be in danger of collapse.

Now, what happens if precipitation does come back into this system? Well, if precipitation comes back, it turns out-- and that's the blue arrow-- it turns out that you need a lot more water to bring back vegetation than you had when you lost it. So the system needs more effort to restore than it did before complete collapse. This kind of dramatic collapse is called a catastrophic collapse because it doesn't happen smoothly. You basically get no kind of warning other than the pattern. That's why the patterns are considered to be important because they can be early warning signals of what the state of the system may be.

Okay, so now that I explained this, let's take a look at this picture, which you will see over and over and over. This looks like clumps in vegetation. Again, it's taken from Google Earth imagery. And so the question is, is this ecosystem in danger of collapse. We learned that clumps may be an important indicator for collapse, so is this what's happening here? Well, let's take a look at what's under one of these clumps of vegetation.

So as we go down, we see that, in fact, under every clump of vegetation, which is quite a big clump, you see a big mound of dirt. Now, what's inside that mound of dirt? Termites. This is a little termite. So termites build those huge, huge mounds. And inside the mound, there's a great deal of activity that's going on. So termites go out. They forage for plant material, which they find in actual plants or litter or animal dung. They bring back that plant material to the nest. They break it down. They eat it. And in the process of doing that, they produce a lot of nutrients in the form of this nitrogen and phosphorus. Also, as a consequence of their active movement, they churn out the soil a lot, allowing for water to infiltrate much better and for the soil to stay a lot more moist. And so because of both added nutrients and increased water availability, plants are doing really well on the termite mound.

So wherever you have termite mounds, the plants are going to get a boost in that region. So we call the termites ecosystem engineers because tiny, tiny as they are, they can actually transform their environment on scales much larger than their own size.

So we expect that there would be a lot of plants on these mounds. And these are the mounds, everything that's basically bright, bright green in there. But if we look closer, instead of looking from very high up from satellite imagery-- we actually look from a helicopter or even lower sometimes-- we see that in between the mounds of vegetation, there seems to also be something else going on. There seems to also be some maze-like patterns of soil and grasses that appear dark gray here. So the question now is, could there be multiple things happening in the system simultaneously. What happens if we take termites that create their mounds and give boosts to vegetation, and we consider their effects in the context of the models that we looked at previously that were analyzing what happens to vegetation when rainfall decreases.

So basically, exactly the same setup as before: we're going to look at the vegetation biomass as rainfall decreases. But now, we're going to focus on what happens as we also add the termite mound in the center. So in order to see-- because as I showed you here, there is a difference in scale, so termite mounds are very big compared to the patterns that form in between the termite mounds. We're going to focus on one termite mound and the areas right around it.

So if you have a lot of rainfall, there's no surprise. Everything is green. The termite mound will probably be doing a little bit better again because it gets the extra boost of nutrients. But overall, everything is doing fine. As we keep decreasing the rainfall, we expect basically that outside--so outside the termite mounds, we saw what was going to happen. We were starting to get the first type of pattern that were these regular gaps. We still get those. But check out the termite mound. The termite mound is still bright green. It's still doing really, really well. Now, I do the same thing, decrease the rainfall some more. I start to get into the maze-like patterns now, so same as before, but see, the termite mound still persists in being green. So the vegetation there, even though there's decreased rainfall, doesn't seem to be too affected by that.

We keep decreasing; we get very regular clumps of vegetation off the termite mound, so in this matrix vegetation, as we call it. But on the termite mound, we see--now, we finally start to see that it's a little bit less green, so the vegetation starts to be a little bit more affected by the fact that the rainfall is quite so low. But here used to be the point where we have this dramatic, this catastrophic collapse where before, we completely lost the vegetation in the system. But now, what happens is that the very next thing is actually not complete desert, but it's sort of a deserted matrix with termite mounds that although aren't completely covered by vegetation anymore, still retain some vegetation on them. So that's entirely due to these basically ecosystem engineering of the ecosystem termite mounds that retain more moisture. So that means the water is just more efficiently used on the termite mound and have this added bonus of the nutrients.

And finally, if you keep decreasing even more, but now you have to decrease it a whole lot more, you will eventually lose all vegetation in the system. But basically, what termite mounds are doing is they are increasing the ecosystem's resistance to drought. They are somehow offering-- creating these kinds of refugia for the vegetation to persist, even when otherwise it would be lost everywhere else in the system. And of course, eventually, we do get the desert.

Now, if rainfall starts increasing at some point, we start to see again the same succession of patterns. But notice here that the second cycle that I'm showing that has a (ii) in there is a lot narrower than before. So yes, you need more water to restore the system than you had when you lost the vegetation in the system. But because of the termite mound, you only need a bit more. So they're also making the recovery much more likely. So they're increasing the likelihood of the system to recover. You only need a bit more water to bring the vegetation back. So basically, mounds play an extremely important role in this system.

So now, if we compare these side by side, you can see quite dramatically how, in a system that basically was pretty much in danger before at kind of intermediate rainfall, now you need a lot lower rainfall before you completely lose everything. Okay, so clearly, this means that this is not in danger. Now, we look at this pattern, and we see clumps. But this isn't in danger because under every one of those clumps, you see a termite mound. So this system is, in fact, robust-- pretty robust if there are changes in precipitation.

But now, the question is what processes lead to this type of pattern. So we saw that these aren't the kinds of clumps that we were getting. The first mechanism that we talked about was this local facilitation and inhibition at a distance. That's what was creating the gaps between plants, and that's what, at a certain precipitation, was giving us regular clumps. But now, we are in a system where we know that, at a very high scale, we see clumps, but they're not a result of that. They're somehow, because of termites, somehow looking very regular. And in between them, we're going to have the kinds of clumps that we saw before, but just at a much lower scale.

So the question is now if these clumps of vegetation aren't actually--the clumpiness is not the result of vegetation itself, but it must be the result of termites somehow. So somehow, the termites must be doing some sort of self-organization that leads to a clumpiness of the termite mounds. So the termite mounds start to look like polka dots. And because they influence plant growth, then the plants appear as clumps of vegetation.

So the next question we're going to tackle is how do termites organize across the landscape? How can we get this kind of regularity out of termites? So my background is in mathematics actually. And I spend all of my time thinking about ecology and evolution, but I often approach it in this kind of complementary way of coming up with mathematical models that will help me put together the assumptions that I have about a system and try to understand whether those assumptions can actually reproduce the patterns that we see in nature.

So here's a landscape where I thought, let's assume that we have a completely pristine landscape where I have no termites. And somehow, one termite gets introduced there. It's one king and queen pair that start their very first colony. Let's see what happens. So that colony first grows. The way a colony grows is that the king and the queen make a lot of workers that go out and forage. And so they start to have a territory around this colony. It's called their foraging territory. So they have their mound that they form, and then outside of that, they go out to forage. When it reaches--it won't grow forever. Nothing really grows forever. So one thing that limits them is how far a termite can travel. There's only so far that physiologically a termite can reach.

Secondly, they're going to have a certain amount of resources that are needed to support a certain colony size, so they're not going to need to expand infinitely anyway. Once they reach a certain size, they're going to start reproducing. So not only do they create these workers inside the colony that need to go out and forage, but they also want to start new colonies. They want to pass on these colony-making genes of some sort and go out and start baby colonies elsewhere. So at some point, you're going to see colony reproduction.

Now, these colonies, the baby colonies, are actually in a lot of danger. There's a lot of things that can kill tiny termites, especially because they're nutritious, so a lot of things eat them. There's also predation, disease. So focus on this one colony, and you'll see that in a few generations, this colony disappears. And actually, you see that with a lot of them, and you'll keep seeing it. So small colonies have a very high turnover rate. They get produced at a high rate, but they also really die pretty quickly.

Now, as these colonies grow, they're going to start-- their territories are going to start coming into contact with each other.

So focus on those two arrows, and you'll see two-- one small colony you already see. There will be another one appearing on top. And take a look at what happens to them as the simulation keeps playing. So the top one disappeared. It was killed by the parent colony, so this first colony that we started out with. And then the second one actually managed to grow. And when it grew, it put a boundary between itself and the parent colony. So we'll talk a lot about when this happens; how is it possible that some colonies get killed, but some other colonies manage to persist. And so for that, we need some sort of functions that tell us how this conflict and competition resolves.

So colonies, as they try to grow, they want to aggressively get more resources. So if I'm going to look at, "is a colony likely to fight for territory," what I need to know is what the size of that colony is. So if you look at the colony A that's down here, when it's a very small size, it will need to grow big. So it'll be very aggressive in its encounters. It'll really try to push and try to get that extra bit of territory. As it gets bigger, it doesn't really need to expand that much more. So that aggressiveness is completely going down at very, very large sizes. Same thing for colony B: at small sizes, it wants to fight a lot because it needs more resources to grow. At very large sizes, it doesn't really need to grow that much anymore. It's kind of reached its limits, so it's not that aggressive.

But colonies obviously don't exist in a void just by themselves. They typically need to fight when they run into other colonies. So now, the question is what do colonies A and B do when they meet each other. And so each one has their own level of aggression, but in the end, the function that determines whether they're going to fight looks more like this. If they're both small, it's very likely that they're going to fight. If they're both big, it's much more likely that they're going to put a boundary in between them and not really worry about fighting to death. And somewhere in the middle, you can see that even if a colony is quite big, if the other one is small, it can drive the whole conflict because even if I'm big, and I'm not really interested in fighting, if another one just kind of constantly harasses me at the border, I'm going to have to fight back.

Now, there's fighting that's going to happen. But how does that-- who wins this kind of fighting? So if two colonies start to fight, who wins? Well, the probability to win conflict is on the y-axis, and here, we see the relative size of the colonies. So the colony that's bigger always wins basically. If A is bigger than B-- much bigger than B, then it wins. If B is much bigger than A, then it also wins. But if they're somewhere pretty similar in size--let's say within 5%, 10% of each other in size, then what happens is that they actually manage to coexist. So the way these colonies fight is as an actual war. So if there's a colony that's very small and a big one that just comes at it with all it has, it will wipe it off immediately. But if you have colonies of roughly similar size, then they will end up persisting and coexisting.

So these are our assumptions about what colonies do. So let's look at competition again. Focus again on the tips of the arrows. They're going to be two dots that appear there, so two small colonies. And see how the one above started a little bit but didn't expand-- was killed immediately, whereas the one on the bottom actually managed to grow big enough so that when they went into conflict, they were of similar enough sizes that they put a boundary between themselves.

So this is how it all plays out. We have colonies grow. They reproduce. When they reproduce, and they all grow, they start to come into contact with each other. There's competition that plays a very important role. And then of course, large colonies also die, not only because of competition-- so competition is a really important driver of death in the system, especially for small colonies. But even large colonies are not going to live forever. Nothing really lives forever. So at some point, even a very large and well-established colony might die. That might be in about 50, 60 years. These are very long-lived. But it will eventually die. When it dies, it gets replaced by smaller colonies that then fight it out for a little while, and then one of them will manage to take over and fill out that empty space.

So now, I'm going to play for you the whole dynamics, and you'll see that it plays out for quite a while. Gaps appear, they get filled out again, and then they appear later. And so all of this is based on our assumptions of what we've been reading in the literature that termites do. Now, as the model plays out, we can-- basically in the end, we can see does it ever really stabilize, at least for a certain period of time. It may actually end up in a pretty stable state that looks more or less like this. And then we can ask-- so the blue points here that are all surrounded by territories; those are all established termite mounds with their foraging territories. And the point is that we want to compare that with this kind of image, and we want to ask, is the result of our model, with the assumptions that we put into the model, capturing the kinds of patterns that we see in nature.

And so the importance of having a model is that these termite mounds are extremely big and very stable. They're going to be there for a really long time. You can't really do an experiment where you force them to rearrange, like, say, destroying the whole thing and letting them rearrange. Again, it might take longer than our lifetime for that to happen. So a model allows us to take all the assumptions that we have, all the things that we think are happening with termites, putting that into a mathematical framework, letting it run, that gives us a pretty quick assessment of whether the assumptions that we have are correct. If we end up not getting something that looks like nature, because we've put it in this very clear mathematical model, we can go back and revisit the assumptions, and we can say which ones of these isn't right. Maybe we need additional assumptions. Maybe we need to remove or revisit some of these assumptions. So it gives you this kind of clean framework in which to organize these ideas and see. If anything needs to be tweaked, you can go back and reassess everything.

So we're now at this point where we have a bunch of dots on both sides. We need to understand whether these dots are very similar, or similar enough. So we need to have some form of quantifying this spatial distribution of points. There's a tool in spatial statistics that's called a Voronoi diagram. And here's what it does. It uses that set of points-- and I'm going to show you on the right. So it uses the set of points, so every clump of trees here is now for me a point. And it starts to put a boundary in between two points that is equidistant from both of them. It creates that for all the neighbors. So I pick one point, and I do that with every neighboring termite mound around it or every neighboring clump of trees. Then I pick the neighbors of this focal one, and I do the same for them. And I keep doing that, and then I keep doing that. And then I end up with this honeycomb kind of pattern. And so I do this on the right-hand side. I do exactly the same thing on the left-hand side. And now, I can finally analyze them.

And so how do I analyze them? Well, I look at these Voronoi polygons, and I say, let's count the number of neighbors or the number of edges of each one of these polygons. And I create a distribution. So how many pentagons do I have here? How many hexagons? So I count every single one of them. I form a distribution of these polygons and I compare the distribution. So it turns out that in both of these cases, the most represented polygon, the one I encounter the most, is the one that has six edges. So most likely, termite mounds have six neighbors. And I do this on both sides. I also look at the average of these polygons, and I say, okay, there are some with five, some with seven. But overall, they are actually-- the average number of neighbors is six. So it looks like the mathematical modeling that we did was capturing these patterns.

So here's a summary for this lecture. Patterns are basically ubiquitous in nature and are created by both abiotic and biotic processes. Patterns matter. We saw the pattern that is created by vegetation can be a really important indicator. The pattern that's created by termites can stabilize the environment or increase its robustness in the face of drought. But very importantly, mechanisms matter. So we saw very similar patterns, these clump-like patterns, that can arise from very different processes and have completely different implications for the ecosystems. So one was indicating a collapse; whereas the other one was indicating robustness. So it's extremely important to understand patterns because they are everywhere, and they can actually tell us something about the systems. But it's extremely important to really try to get at the mechanisms before we use those patterns as any kind of indicators. That's it. Questions?

[Applause]

[STUDENT:] Do termites only benefit plant populations, or does it also benefit tree populations? And can termites disrupt the tree and grassland equilibrium? Because we kind of talked about how the competition between trees and grasslands--

[TARNITA:] **[Interposing]** That's a great question, and I will do my best impersonation of Rob while answering it. So yes, that's a great question. All plants benefit from termites-- all of them, trees and grasses. But because there's more water, so the termite modification of the soil allows for better water retention and better water use, trees are going to be very likely to grow on termite mounds, so they're going to find a much more favorable habitat. So you are likely to find this kind of savanna that has grassland in between termite mounds and trees on the termite mounds. And that will allow for the coexistence. So maybe where it used to be grassland before, you can actually see savanna that has grassland and trees because of the termite mounds. And of course, then they don't burn because they are covered with trees, and trees aren't flammable. So that creates this feedback that helps the system persist for a long time. Great question.

[STUDENT:] So in terms of restoring a barren area where all of the vegetation's been lost, how would you get a termite mound to come into that area and establish a colony so the vegetation can come back?

[TARNITA:] That's a great question. And so of course, that poses a lot of issues of should you introduce anything, not just termites, into a region. So there are a lot of ethical questions around that. But one thing that we're trying to understand is can humans actually create similar engineering to the termites and basically induce that effect, and maybe termites will come and colonize it later, but without really introducing something. And so we're trying to do that by creating fertilization, so we understand that nutrients are important. So creating this pattern--manmade pattern of fertilization and also trying to see what kind of water treatments one could do to create those effects. But yeah, that's a very good point. There was another question there, Leor?

[STUDENT:] So I was just wondering about the mathematical modeling techniques you're using. Is that just like a cellular automaton that you give it a few simple rules and let it run, or is there some other method?

[TARNITA:] Yeah, this is kind of like a cellular automaton here. We'll see a lot of different kinds of modelings in this system. The first ones that I showed you that showed the predictions about the sequence of the patterns and the catastrophic decline. That was partial differential equations. The second one, with the termites, is like a cellular automaton, so it's basically points that are on a landscape, and they're interacting with each other. But it's not deterministic, meaning that there's some noise in the environment. So there's randomness. Things don't happen in a very well-prescribed manner. We allow for these kind of stochastic effects and randomness and noise to play a role. But yeah, that's a great point. One more question there.

[STUDENT:] I was wondering if there were any other producers that you know of that can form these patterns in ecosystems.

[TARNITA:] Boy, I must have arranged with you to ask all these great questions before my talk. Yes, that's a great point. So we can even find them in North America. You can find gopher mounds that actually are very similar. They don't grow vegetation on them, but they're very, very regular. Also, you can see them from aerial views. A lot of different species of termites do that. Ants can do the same thing-- anything basically that is territorial. We think that this model, which is a very simple model of competition and conflict, can be representative of a lot of different systems. We can imagine that even birds that are territorial and defend their territory or fish that are territorial are going to start to look the same. It's just that we're lucky that the termites are patterning a substrate that's easy to see. They're forming this thing with the feedback on the plants, so it's very easy to see that. But other things are probably creating exactly the same kinds of patterns, and we're trying to come up with creative ways to get at those patterns.

[Applause]

[TARNITA:] All right, thank you.

[Music plays]