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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 fifth lecture is titled, Communities as Ecological Networks. And now, Dr. Robert Pringle.

[Applause]

[PRINGLE:] So communities can best be represented as networks showing interactions between species. So this is an example of a food web from an African savanna. And it's not a complete one. There are species here-- there are species missing from this graph. But it's an illustrative one. We have plants here at the bottom of the food web, and we have a series of herbivores, ranging from small grasshoppers all the way up to elephants, impala. And then we have some intermediate carnivores, and then our top predators at the very top. And each line in this network represents what we call a direct effect.

So if I were to highlight this particular chain within the interaction, we see that there's a direct effect of the leopard on the impala and a direct effect of impala on the tree or whatever plant species it happens to be eating.

Now, I want to introduce you guys the concept of a trophic cascade. So the impala eats the plant. And that, as I said, is a direct effect. And it's a negative effect on the plant that the impala is exerting. And the leopard eats the impala and exerts a negative direct effect on the impala. And consequently, what you get is a positive indirect effect of the predator on the plants. And that's the famous trophic cascade, and there's a lot of attention to this phenomenon in ecology in the present day.

The original idea of the trophic cascade was conceived and put forward more than 50 years ago now in a classic paper. And the question that they asked really is why is the world green. And what they meant was, why do terrestrial ecosystems look green from above, and why is there still a lot of plant biomass on land. Why haven't the herbivores eaten it all?

And so they proposed an idea that was, at the time, kind of new and controversial and is now widely accepted, which is that predators play a major role in making the world green, in suppressing herbivore populations to levels below which they have a devastating impact on plant populations.

And over the course of the last 15 years, there have been a number of really convincing and just kind of mind-blowing examples of how this works. In Venezuela, the government made a dam. The dam flooded a huge area. And little hills in the Amazonian rain forests there turned into islands, flooded in between. And some of those islands are big, and some of those islands are small. And the big islands had more or less normal predator complement. So here, the apex predators--top predators-- are jaguars and cougars, two kinds of cat. But small islands got isolated that didn't have any predators on them at all. And you can see here what happened on those small islands on the left. The vegetation in the understory is very sparse. And the reason is that the herbivores-- and this means howler monkeys;

it means leafcutter ants and iguanas--just absolutely ran amok. And they devastated the understory vegetation. And that would compare with this sort of normal-looking forest on the right where the understory vegetation is intact.

Another really famous example where trophic cascades are thought to have played a major role in governing the plant community is wolves in Yellowstone. So they were reintroduced in the 1990s. And following their reintroduction, you suddenly got regeneration of aspen, cottonwood, and other such trees along river banks. And the reason they weren't there before, the reason why you don't see those trees in the left-hand picture here, is ostensibly that the herbivores-- elk in this case-- perceive that as a risky environment down by the water because the visibility is low. And so when there were no wolves, they could hang out there and suppress the trees' recovery. But when the wolves were introduced, that suddenly became a very bad place to be because you're very much at risk for predation when you're standing in a low-visibility spot.

But we have to confront the fact-- as somebody who works predominantly in African savannas, I'm very keenly aware of the fact that not all herbivore species are really limited by predators. So in this graph, which is from a 2003 paper in Nature by Tony Sinclair and colleagues, you can see on the y-axis the percent of mortality that is due to predation. And on the x-axis, you have the log of the herbivores' body weight. And what you can see is that our little dik-dik up there at the top basically never dies from anything except for getting eaten. And that is its lot in life, which whether that's a good thing or a bad thing, that's kind of a philosophical question. We can talk about it later.

[Laughter]

[PRINGLE:] The impala is the same thing. And it's the same for the topi, which is this one that's in between impala. And then as you start to get to wildebeest, the percentage mortality from predation starts to decline, and then there's a sudden drop-off.

So there's another threshold--exciting, threshold-- body mass at which predation ceases to become the main limiting factor in population control. And that happens somewhere between zebra and buffalo here. And so what that means is that these five species-- elephant, hippo, rhino, giraffe, and buffalo, are not predominantly predator-controlled. They may--every once in a while, some get taken by predators, and really only by lions. But by and large, they are controlled by the kinds of density-dependent processes that Corina was describing in the previous lecture.

And what that implies, contra the green-world hypothesis, is that the largest herbivores, anyway-- maybe not grasshoppers, but certainly the largest herbivores, should have strong direct and indirect effects within their communities. And to give you just a little taste of that, I want to show you this tree which used to exist in the Serengeti. And I wanted to show you now why I say "used to exist," because it had an unfortunate encounter one day.

[Laughter]

[PRINGLE:] And I want you guys to look at the time. I'm going to go back one. This is--it says 18:16. So within a minute, this elephant comes in and--

[Laughter]

[PRINGLE:] --that tree is no more. And that happened really fast. And I have to tell you sort of what happens next. And this is really interesting. Elephants will do this to a big tree-- huge energy expenditure to push over a tree. Then they'll take, like, one bite and walk, you know?

[Laughter]

[PRINGLE:] And it's, like, really? You knocked down that whole tree to take a bite of one branch? So people actually think that maybe this is partly exercise. They may be partly gardening. They may be--

[Laughter]

[PRINGLE:] No, literally. I mean, people don't know. This is kind of a mystery, and people have various ideas--hypotheses about why it is. Anyway, the point is that, at large scales, it can have a huge effect. And this is our famous Gorongosa National Park now that herbivores, and elephants in particular-- actually just elephants--have started to recover.

And this is a fever tree. It's yellow fever trees. And they grow more densely in Gorongosa than anywhere else, likely because herbivores were gone for a long time. Now that elephants are coming back, the fever trees are getting hammered. And it looks like someone's been in there with a wrecking ball. And this is what it looks like on the ground just driving through it, some photos that I took this past summer.

So that's a direct effect. But what about indirect effects? For that, we really need an experiment. And I should say, we need an experiment to really robustly understand this direct effect, too, because what I just showed you from Gorongosa is observational data. And those changes in tree cover could theoretically have been caused by other things because we didn't have a controlled, manipulative experiment.

So how do we do that? Well, this is an experiment I was involved in setting up in 2008, and we've been running it ever since. And the approach is to selectively exclude different herbivore species based on their body size.

So we have a control plot. We call it control. It's just a plot with no special attributes. And all species are allowed to go there. Then we have what we call megaherbivore exclusion. So this is a kind of fence that just consists of two electrified wires at 2 meters in height, so just a little bit taller than my head. And that's really effective at excluding elephants and giraffes but lets everything else in, so you see those impala and dik-dik are wandering in and out.

Then we have what we call mesoherbivore exclusion over here, and that keeps out the impala and the zebra and the eland and everything bigger than--basically everything bigger than a dik-dik. Dik-dik go in, and everything else comes out--is kept out. So that's mesoherbivore exclusion.

Then lastly, we have what we call total exclusion or minus all-- because it's minus all of the herbivores-- where the largest remaining mammal is a rodent. And here's what it looks like in real life. This is a photo taken with a camera trap that we set up next to the fence line. And you see this is a dik-dik walking along the fence line probably looking for a way to get in there because it looks nice in there, especially for a dik-dik, which needs to hide a lot. There's plenty of dense vegetation.

And here's an impala approaching from the other side. And here's that mesoherbivore exclusion fence. And you can see that right there is a dik-dik bottom. And its head is just sticking in here. There's a green shoot that it's going to browse there, and its partner is over there. Dik-dik are always in two.

And this one--all right, so here's an elephant approaching the mega--actually, it looks like it might get under, but it doesn't.

[Laughter]

[PRINGLE:] Every once in a while, a baby from a herd will kind of take a path that will go inside one of the fences, but the babies don't really do any damage. They leave some droppings behind, but it's no big deal. Here are impala going underneath this fence, and here's the control plot, which is just, again, open.

So you can actually see my experiment on Google Earth if you go to the right place. And I don't know if you guys can see it from there, but it's right there. So those four plots, those four--each one is one hectare. That's 100 by 100 meters. And here are the four treatments as applied in this experimental block. So our total exclusion, the mesoherbivore exclusion at left, our megaherbivore exclusion, and our control. And this is pretty nice because you can actually see the consequences of direct effects.

This imagery is from 2011, which means the experiment had only been running three years at this point. But look at the difference. Look how much denser the vegetation cover is in the place where we've taken out all the animals. And then it's a little less so in the mesoherbivore exclusion. And maybe a bit of a difference there between the elephant exclusion and the others.

So using this kind of experimental approach, we've been doing this for now quite a while. And we studied a number of different things. And we've shown that, again, sort of contra this green-world idea, large, herbivorous mammals have big effects on a whole range of different processes and functions.

So this is bird richness here-- bird species richness; that's just diversity-- bird abundance, beetles, fleas, lizards, insects, rodents, snakes, and ticks. So these animals have big effects-- removing them leads to big changes in the other animals, often leads to them increasing in abundance, which you might think

of as good until you consider that rodents increase in abundance, and rodents carry various kinds of disease vectors.

So I want to now turn this experiment to answering the question of what's going on here. What happened here is that this system has been invaded by toxic shrubs, and specifically a shrub called the Sodom apple, or *Solanum incanum*. First of all, it's the direct ancestor of our native eggplant. But unlike the eggplant, which has been domesticated, and therefore its toxicity bred away, this *Solanum* is still very toxic, as demonstrated by this group of researchers, Kenyan veterinarians, who fed it to a bunch of sheep and then recorded the pretty grotesque things that happened to those sheep.

So it's not--sheep are grazers. They're built for eating grass, and they're not built for digesting these complex glycoalkaloid compounds. And I'll spare you the details, but it's dangerous to the health of the grazers. However, remember the distinction between grazers and browsers. Browsers eat a lot of trees. Trees and other forbs tend to be the things-- shrubs and so forth--tend to be the things with a lot of chemicals. So browsers have digestive machinery that can accommodate some of the more toxic plant species.

And specifically, this plant is eaten by elephants, impala, and dik-dik. And kind of nicely, those fit into our experimental treatments. There's one treatment for each species. And they span three orders of magnitude in body mass.

So what happens, then, to this invasive plant when we remove each set of herbivores? Well, it increases with each set of herbivores that we remove. It increases from the control to the megaherbivore exclusion, and then again from the mega- to the mesoherbivore exclusion, and from the meso exclusion to the total exclusion, where the abundance is greatest. So collectively, these herbivores regulate this plant, and they do it in a way-- the paper we wrote about this is called limited functional redundancy among large savanna browsers, which is a jargony way of saying their effects are nonoverlapping, complementary. So removing each group had an additional effect. There was no redundancy there.

Now, elephants increase the mortality of this plant by a really dramatic amount. So here's where we get really high mortality, 20%, in the presence of elephants, and then you exclude elephants, and the mortality drops off to almost zero. And I want to show you-- and this is based actually on 725 plants that we tagged and followed throughout their lives, revisiting them every once in a while.

And this is why--I want to start that again because you guys need to see. That's a *Solanum* plant right in the middle. And this elephant is going through, and there's a whole bunch of *Solanum* plants around the edge. It is going through and systematically uprooting all of these *Solanum* plants and ignoring everything else. So this is how elephants cause mortality. They are unique among animals. You saw in that camera trap photo how they took down that enormous tree. They have a unique capacity to kill plants.

[Laughter]

[PRINGLE:] Well, not unique. We have herbicide and stuff like that. But they really--they're unique among this set of herbivores. Now, impala do something else entirely, which is that they eat all the fruits, but only the fruits-- well, almost only the fruits. So you find fruits only in plots where impala have been excluded. Everywhere else, all the fruits have been eaten.

And just to prove to you guys that I'm not making that up, you see that fruit down there, impala just going right for it. And yum, yum, yum. Why? Well, these fruits-- I said they contain toxic compounds, glycoalkaloids. That's another one coming in. Yeah, this is again the tomato, potato, eggplant family. But the wild version with these glycoalkaloids that are actually nitrogenous compounds. Nitrogen is a limiting resource in this system. And so if you can detoxify, or if your gut microbiome can detoxify, then you can get a lot of protein from eating these fruits.

Now, what does that mean for the plant? Not necessarily a bad thing. A fruit is just a bribe that a plant pays to an animal to disperse its seeds. And sure enough, these are seeds that we took out of impala dung, put on a petri dish, and they start to grow. And what happens when fruits don't get eaten? Well, this is what happens. They get attacked by a whole host of nasty pests: fungus that rots the fruit and seed predators, like beetles and other things, that drill into the fruit, eat the seeds. And as a result, the fruits in the absence of herbivores-- fruits that don't get eaten have very few surviving seeds because most of them just get attacked.

And what happens to the seeds that manage to survive the fungus--don't get eaten, manage to survive the fungus? Well, then, they have to face yet another problem. This is a pouched mouse, *Saccostomus mearnsi*, and it is feeding on a petri dish full of *Solanum* seeds that we put out. And it is a seed predator. It is killing those seeds. And as it happens, rodent densities increase inside our exclosures. And that is an example of an indirect effect of excluding the large mammals leads to a positive effect on rodents. And that increases the seed predation pressure on the plant.

Now, what I showed you, then, is that there's a whole suite of negative effects of these animals. The elephants are killing it. The other things are consuming tissue. But there's also some positive effects. There's dispersal, and there's suppression of seed predators. So the real question is, what's the net effect? What's the overall effect? And we can't answer this question from our plots alone because seed dispersal is a process that occurs at spatial scales larger than one hectare. That occurs over long distances.

So in order to understand the net effect, we really needed a mathematical model. So I'm going to turn it over to my colleague, Corina Tarnita, who's going to walk us through the mathematical model that we built for this situation.

[TARNITA:] Okay.

[Applause]

[TARNITA:] Ready for some more math? So we'll try to build a model that uses the same ingredients that we learned about, this kind of logistic growth. But it's including everything that's basically

happening to this plant. So it'll be slightly more complicated than our waterbuck model. So it's still a pretty simple model that's trying to integrate all these direct and indirect, these positive and negative effects that Rob just talked about.

So we have a plant population of size N . And we're trying to write the change in this population through time. So what can happen to a plant? Well, the first thing that happens is that it has to make fruit. That's its way of reproducing. Those fruits have seeds, and something will happen to those seeds, and they'll have to turn into more plants. But first, it makes fruit. Then that's why we have--we add a term down here that says there's some reproduction-- let's say at a rate r . That's the production of fruit. And that's proportional to how many individuals there are in that population. And that suspension dots down there is so I keep the suspense up that this is going to be a bigger formula. That's going to fill into that big white rectangle.

So okay, well, once they're on the plant, what can happen to the fruit? The first thing is that they are under a lot of danger from fungus and beetles that may attack the fruit. So we have to take that into account. And so s is a fraction of the fruit-- of the seeds that actually survive fungus and predation by beetles. So a lot of them might get killed, but some of them will end up being on the ground. So we have to multiply however many there are produced by this fraction s . Then what we saw was an important part of the story is rodents. So this first model that we're building here for the plant is actually-- what we're going to do is we're going to focus on the plant alone. Forget about the herbivores for a second. This is exactly what happens to the plant if there were no herbivores in this system. So it reproduces some of the seeds-- some of the fruits get destroyed by fungus and beetles. But some of those seeds get to the ground. And some of those seeds get eaten by the predators, which in this case, is a rodent. And a fraction of those seeds manage to escape. That's a fraction p . We multiplied it down here.

Okay, next thing that happens is that those seeds now have to get established into adults. And this is where carrying capacity starts to play a role again. So not every seed that's on the ground is going to be able to turn into an adult because first of all, not all seeds might be-- some seeds might be desiccated. Not all seeds might be successful to begin with. But at the same time, there's also going to be a lot of competition. So if there are a lot of seeds in a place where there already are a lot of plants, those tiny little seedlings are not going to be able to compete with the big plants. So here, we have an establishment rate e that tells us the likelihood of establishing for a plant. And that has to be multiplied by the carrying capacity. So again, this term $1 - N/K$, that's telling us that if we already have a lot of plants in the system, so N is very high, it's close to K , then no new plants are going to be recruited. So this whole term is going to be 0. But if you are in a place with very few plants, N is small. Then N/K is small, and so a lot of the seeds that manage to survive are going to be established into new plants.

And there's, of course, mortality, so plants also die. This is our model with just plants. And take a second to look at this equation. This is slightly more intricate than what we did before with waterbuck, and that's because we have to take into account all these steps, all these many places where seeds can be lost or plants are not going to be recruited.

Now, we introduce herbivores into the system. So what happens when we have herbivores? Well, some of the fruits get eaten. It doesn't matter whether it's impala or elephant, we'll separate the effects of impala mainly eating the fruits and the elephants mainly increasing the mortality of the plant. But for now, just think that that's the generic herbivore out there. So some fraction of the fruits are going to continue to stay on the parent plant. They're not going to get eaten by the impala. But some fraction are going to get eaten. The fraction that don't get eaten have exactly the same fate as before. They stay on the parent plant. Some of them get attacked by the beetle. Out of those, some survive. They get to the ground. Some of those get attacked by--get eaten by rodents. Of those, some fraction--again, p --is going to survive. And then there's going to be some establishment.

Notice, though, that the moment that we have herbivores in the system, there are all these direct and indirect effects that we have to take into account. So our parameters will change. For example, the one that's most striking is the--well, the one that's most striking is clearly the actual amount of reproduction that exists and the actual amount of deaths because plants are going to have higher mortality when you have herbivores in the system, a lot more-- and they're going to produce fewer fruit.

But an indirect--an important indirect effect is the indirect effect that the herbivores have on the numbers of rodents. So there's going to be a lot more rodents in a system without herbivores, and fewer rodents in a system with herbivores.

So all these parameters have to now account for the fact that there are herbivores in the system. So we take all of them, and we just add a subscript h . That's just so we keep in mind that those parameters actually in our experiments are different from the no-herbivore to the herbivores-present scenarios. Otherwise, the equation hasn't changed, except that now it's multiplied by $1 - f$.

So it's exactly what it was before. Fruit get produced. Of those, a certain fraction don't get eaten. That's $1 - f$. And of that fraction, then it goes in exactly the same path that it had before. Now, what happens to the ones that do get eaten? Well, some of them pass through the gut, or all of them pass through the gut. Some may be affected by going through the gut of animals. So we have to include their viability, rate v . That's the fraction of seeds that are still viable, and they're still able to germinate.

And of those, they have to also get established, and we have this new parameter, e_h , that reflects the fact that it's different from the e below because it reflects the fact that the herbivores are actually dispersing these seeds. So they may have this interesting positive effect of taking them to a place where maybe it's easier for seeds to establish, like a place where there aren't so many plants yet. So that's why we have the different e and e_h . And so when we build the equation, as I said, the $1 - f$ is doing exactly as before.

And now, we have this term here that says the fraction f that get eaten; some of them, a fraction v , are remaining viable after gut passage. And then those establish at a certain rate, e_h . And obviously, now the number of plants has also changed, so we have to take that into account.

So basically, now, if you look at this equation, we start with how many fruits are being produced or how many seeds are being produced, which is the arrow before it splits. That's what the plant does. And then here, we have a split. We have the ones that get eaten, a fraction f of them. And they have their own fate. And the fraction that don't get eaten, and then they have the different kind of fate. And that's multiplied by the carrying capacity, because we have to take that into account, that there's a limited space for these plants to recruit. And there's a mortality that's different when you have herbivores.

So this is as complex of an equation as I ever like to write on a slide. So let's internalize the beauty.

[Laughter]

[TARNITA:] And once we have this, we can say, okay, well, this has a bunch of parameters, clearly more than before. How many of them do we know? Luckily, quite a few.

So from the experiments, a lot of these parameters have been estimated, which is great. So we already have-- we know the reproductive rates. We know the death rates. We know what fraction of fruits get eaten and don't get eaten. And we know about the rodent behavior. We know about the fungus as well. The one that actually we didn't have experiments for is for the viability. But that can be estimated from the literature, and it's around 60% of the seeds remain viable. And the only ones that we didn't actually-- that we don't actually have any kind of estimate for are e and eh .

And so this is a model that's useful in two ways. In one way, it's basically putting together all of these effects, negative and positive, and trying to figure out the balance between them, so what's the net effect. But if we knew all of them, that would be the only thing we would do with this model. If we knew all the parameters, then we would just plug them in, and we would see when do the plant populations do better and when do they do worse. But we actually don't know two of the parameters. So we'll use the model to explore different scenarios. So we plug in the parameters we know, and for the ones we don't know, within a reasonable biological range, we try to vary them and see what kind of scenarios might occur.

So how do we think about these different establishment rates? When they're equal, that means that there's no benefit of this dispersal. That means that they're usually taken to places that are just as competitive, and things are kind of the same for those plants, so there's no benefit to dispersal. If eh is greater than e , that means that there is some benefit to dispersal. And, you know, you can decide on how high of a benefit you'd like to explore. So we again go to simulations here. And this is what we find.

Here's an example where the two parameters are the same, so there's no dispersal benefit. And here's what happens. This is what happens to the plant population when there are no herbivores. This is the familiar logistic growth. So it reaches a certain carrying capacity that's imposed by the available space.

Okay, let's see what happens when you have just the impala-- so only impala in the system. Interestingly, impala are not that bad for the plant because a lot of the seeds that get eaten actually

get saved from the fungus and the beetles and the rodents and all that. And a lot of them remain viable. It's at the lower carrying capacity, so the plants are doing a little bit worse, but not too much worse.

And the third scenario is when both impala and elephants are present, and here we see a dramatically lower carrying capacity. So clearly, adding the elephants in there has a really strong negative effect if there are no dispersal benefits.

Notice also that the other interesting thing that happens here is if you look at the rate at which these curves grow at first, having the herbivores in the system makes the population grow faster. And why is that? It's specifically because they save them from all these other negative effects that are happening, like the fungus and the rodents. And so that's giving it a boost. But overall with the incurred mortality, that still settles at a lower population size. So maybe they could help plants invade a space faster. But they're going to keep it at lower population sizes.

Now, let's look at what happens if we consider a threefold dispersal benefit. So let's assume that these animals are actually taking the plants to areas that haven't been colonized so that there is a release in competitive pressure. If that's the case, first we plot what happens to the plants by themselves. So obviously, this study is the same because this assumes no herbivores at all. And now, we add the herbivores, assuming a threefold dispersal benefit. We'll add them one at a time again.

So first, the impala. And you see now that with this added dispersal benefit, the impala can actually have a strong positive-- or strong-ish positive effect on the plant population. So it's better than before, and it's certainly better than the plant by itself.

And if we now look at what happens when we additionally put elephants into the system, notice now the--compare the two black curves. It's clearly the added dispersal benefits make it such that even though the elephants continue to have a negative effect, it's not as bad as before. So increased-- it's basically balancing between the very positive effects of the impala, the strongly negative effects of the elephants, with some added dispersal benefits from the elephants as well.

So the important point here is that herbivores can have both positive and negative effects. But it looks like elephants within a range that's biologically reasonable of how much dispersal benefit they can actually confer, they seem to still be having a negative effect on the population, so keeping the population under control.

So if we look back, what's the relevance now of this whole study? If we look at what's happening in Africa at the moment, basically there's a huge decline in populations of the world's largest herbivores. So in blue, it's where they used to be before-- elephants, hippos, and black rhinos. And in red, it's basically the small pockets where they can be found now. So it's a very, very dramatic loss of large herbivores. This can have a very strong impact because you'll end up seeing places like this that are basically covered in this noxious, toxic plant.

So the expectation is that now, if elephants come back in a system like this, the direct and indirect effects that they induce can actually transform this really bad-looking place into a place that can be kind of nice as a grassland that's supporting both wildlife and humans. And so there's a constant conflict that you may hear about between humans and wildlife. But this shows that basically wildlife-- in this particular case, herbivores-- can play an extremely important role in facilitating human livelihoods. So that's the main take-home of this.

[Applause]

[TARNITA:] Questions? And we'll try to take some that haven't been--if not, then yours there. Yeah?

[STUDENT:] I had a question for Dr. Pringle about your herbivore exclusion plot. Are the animals just in that area? And if they are, how did you estimate how many animals you needed in the 3 hectares?

[PRINGLE:] Yeah, that's a good question. I should've explained that more clearly. In fact, what they are is just exclusion fences. So we're letting natural abundances of animals roam around, and then we're just building plots that keep certain species out. And the other species are free to wander in and out. So yeah, we're not-- we've thought about doing that kind of experiment where we actually catch some dik-dik and put a fixed density inside and keep them from leaving. But we haven't actually done that yet.

[TARNITA:] There is a question down here.

[STUDENT:] So I was just wondering from a mathematical-model perspective, if you have a system where the herbivore's present or absent, and then you either remove or introduce herbivores to that system, is the rate of change of the toxic shrubs also described with the same logistic equation?

[TARNITA:] When you have the herbivores present or not?

[STUDENT:] If you have-- like, say you have a system with toxic shrubs, and they've reached their carrying capacity, and then you suddenly exclude the herbivores. Is the rate of change now from the old carrying capacity to the new also described by the logistic equation?

[TARNITA:] Yeah. So you'd be able to capture that in the same equation. It's just that you now would have to start at that carrying capacity that you now have with the initial population size and adjust the parameters to account for the new parameters in the absence of herbivores. But the same kind of growth should work in both cases. It would increase or decrease, depending on what the herbivore was doing for that population. Yep, absolutely. Good question there.

[STUDENT:] You had mentioned that, in certain environments, herbivores have a really incredible impact on the plants that grow. And so in environments where we aren't seeing as many herbivores and more dangerous plants are growing, can humans influence their environment by adding herbivores into it?

[TARNITA:] That would be one immediate conclusion from here, that if you have places where it's unmanageable, where you can't really manage invasive species--and sometimes, humans try to manage them with various poisons our own, and that backfires in many, many ways. Sometimes, the best way to do it is to introduce the kinds of animals that used to live there anyway-- so not new animals that you don't know what they're going to the system, but animals that would have been there at some point. And then they'll just retake their roles in that system. But Rob can--

[PRINGLE:] [Interposing] Yeah, no, or it can be as simple as simply not persecuting them. So in this landscape in Kenya, it's pretty remarkable actually because the conservation of wildlife is a major thing, and wildlife populations are doing really well. But it's all private land. And a lot of private landowners who are ranching cattle, a lot of whom still see wildlife as the enemy because the predators will eat the cows, and the herbivores are competitors. Really, it's not so much, especially when-- that metabarcoding diet analysis shows that the amount of resource overlap is low. So if we just stop the persecution of-- or the exclusion of elephants from a lot of these cattle ranches, then it'll happen naturally without needing to import a particular herbivore.

[Applause]

[Music plays]