the weekly anthropocene

dispatches from the wild, weird world of humanity and its biosphere

By Sam Matey

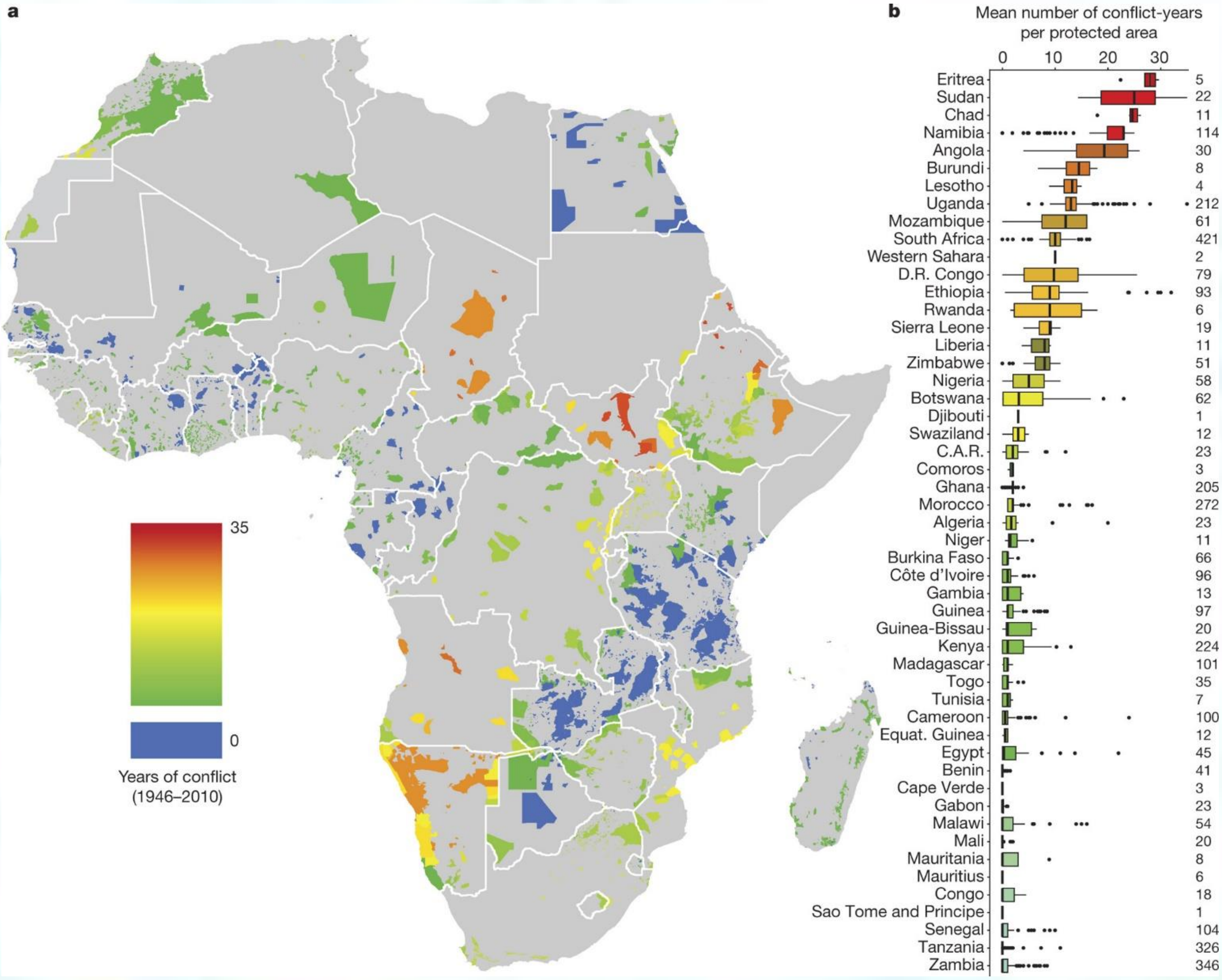
Scientist Spotlight: An Exclusive Interview with Dr. Robert Pringle

Dr. Robert Pringle (pictured) is an associate professor at the Princeton Department of Ecology and Evolutionary Biology. He is a highly cited researcher that has been published multiple times in both *Science* and *Nature*, with diverse and multifarious research interests ranging from the effect of warfare on African national parks to how termite mounds can help protect ecosystems from climate change.

A lightly edited transcript of this exclusive interview follows. This writer's questions and remarks are in **bold**, Dr. Pringle's responses are in regular type. ***Bold italics*** are clarifications and extra information added after the interview. Dr. Pringle's lab website is available at pringle.princeton.edu/. For a page with links to PDFs of some of his most well-known papers, check out eeb.princeton.edu/people/robert-pringle. An awesome documentary about his and his team's work in Mozambique's Gorongosa National Park (including African wild dog reintroduction!) is available at www.pbs.org/wgbh/nova/video/natures-fear-factor/. We encourage you to check it out!

I just saw the NOVA documentary on your Gorongosa research-it's so fascinating, with the elephants being warded off by beehives, the reintroduction of wild dogs, the final arrival of the leopard, and everything! There are so many things I want to talk to you about! Let's start chronologically, if you will-why did you become a scientist? And more specifically, why did you become an ecosystem ecologist, and how did your work come to focus on Africa and the Caribbean?

I was always interested in the outdoors and animals, always trying to catch frogs and snakes and stuff like that, and during college I realized that was something you could do for a career. I didn't actually go straight into science. I really like to write, so as an undergrad I double-majored in biology and history, toyed with the idea of becoming a historian. I was doing environmental history, and reading about really interesting experiences people were having and science they were doing made me feel like I wanted to be doing that instead of reading about the past. I wanted to be out in the field. That's why I ended up doing a Ph.D. in ecology, it's a combination of that innate interest in nature and a triangulation of trying to figure out how my interests and skill set related to that.



Amazing. So, I have a bunch of questions about specific studies. One of your recent papers was an analysis on how African national parks have been affected by and have recovered from war (www.nature.com/articles/nature25194). That's obviously a major issue, with well-known examples from Virunga National Park in the DRC to Gorongosa in Mozambique, where you've done a lot of work. Can you tell me and the readers more about this, and what you wish the general public knew about warfare and conservation in Africa?

(Pictured above: Fig. 1 from that paper, a map of African protected areas, colored by the number of years of conflict they experienced 1946-2010).

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> "Even in a system that's really been heavily damaged by conflict, it's possible to recover. Nature's extremely resilient. We shouldn't give up on these places."

We got interested in that question because we'd been working in Gorongosa, where they lost most of their large wildlife during the Mozambican Civil War in the 80s and 90s. We started wondering how common was that kind of situation, and we realized there was little hard data on the question of how human conflicts affect wild conservation areas. A graduate student, Josh Daskin, started compiling some data on animal populations from the literature, and fortunately the political sciences have come up with some pretty good databases of conflict in Africa in the last 80-odd years. So we were able to basically combine those two data sources to look at the effect of conflict on wildlife. We found that it was not good. Of the factors we were able to test, conflict was the strongest predictor of wildlife trajectories, and it was a negative trend. Populations are variable even under the best of circumstances, so even in peacetime, you got a lot of variance, but on average as you move to sites with more frequent conflict, the wildlife population trajectory became more and more negative. The other interesting thing was that it took only small amount of conflict for that relationship, the expected wildlife trajectory to be negative. When there was zero conflict, the average wildlife was neither increasing nor decreasing, what you'd expect. But just turning up the conflict a little bit causes the average population trajectory to become negative. Populations are declining. So that is some of the first large-scale analysis of its kind. We were struck by how few data there are on that issue. It makes sense when we started to think about it. There were hundreds of data points from places like the Ngorongoro Crater and Kruger National Park, and very few data for places like the Congo, Sudan, Sierra Leone, Liberia, where there had been a lot of conflict. This turns out to be a really general problem, there are a few places that are extremely well studied, and most of the rest of the continent researchers don't visit and there's little local capacity to do that work. The main thing I would want people to know about is obviously that conflict is not a good thing, but also that there's a real need to support research in places that are a bit off the beaten path. We need to know more about these places. There's a need for technology that allows people to gather data in those places. And the last thing I would want people to know, the most important, what Gorongosa shows, is that even in a system that's really been heavily damaged by conflict, it's possible to recover. Nature's extremely resilient. We shouldn't give up on these places.

Speaking of conflict, are you concerned about the rising Islamic terrorism in northern Mozambique, the Cabo Delgado region, spreading southwards, or increasing tension between the political factions and former civil war opponents, FRELIMO and RENAMO? How do politics and current events play into your research?

My research group and I try very hard not to get involved. It's not really something we research. When we visit Gorongosa, we're guests of the Mozambican government, and we try to keep our heads down and do our science. The political dimension is not where our expertise is. The most that it really affects us is, we've had situations where tensions were rising and scary things were happening and we had people we had to evacuate from the park. That's about it. We don't really take an active interest in that, we try to stay safe and not do anything that exacerbates tensions.

How are you staying in contact with your African field sites during the pandemic? Is there Zoom available at Gorongosa?

There is, but the internet connections, they can only marginally sustain Zoom. We mostly email. Quite frankly, a lot of research is on pause right now. We have a lot of GPS-collared animals in Mozambique that are still moving around, their collars are still picking up data. And in Kenya, we have technicians there who are continuing to collect core data. But things have kind of slowed down, we're in touch by email, but things are on autopilot.

You also wrote a paper in which you found that seven African herbivores, from dik-diks to buffaloes to zebras to elephants, were eating very similar diets within their species, but those diets were very different between species (see pringle.princeton.edu/wp-content/uploads/sites/199/2014/01/PNAS-2015-Kartzinel-8019-24-2.pdf). . And you found this out through DNA metabarcoding of the plant DNA in their feces, correct?

Working on ecology in general, and in particular the ecology of wide-ranging, sometimes dangerous animals, it can be really difficult to get insight into their daily lives. One of the reasons we use GPS is to get a better sense of where they go. It's similar problem with diet, amazingly, we don't really have a good idea of what wild animals actually eat. We know zebras eat grass, we know giraffes eat trees, but as far as knowing on a detailed level, what species of grass or trees, we really don't have a very good idea. If you go in as I have done, in the old literature, in the 1950s people used to shoot a bunch of animals and rummage through the guts and try to identify. There's another technique called microhistology, which is extremely laborious and error-prone. There's this gap in our understanding of what animals eat, and that's really important. It's important because we want to understand food webs, we want to understand how the changing abundances, the loss of these species might influence other species, and that’s hard to know if we don’t know what they’re eating. So there’s this big lacuna in what seems like the most fundamental thing, you think surely people must have known what elephants eat for hundreds of years, but in fact it’s pretty difficult to figure out. That was becoming a thorn in my side that I didn’t know what the animals I was studying were eating. And about in 2010, 2011, in the couple years before that, there had been evidence that this technique of DNA metabarcoding could work, proofs of concept were coming out. I thought, this could be a really useful tool. We started to use it in Kenya, there was a postdoc in the lab who’s now a professor at Brown, and we picked those seven because they’re the most abundant species and also because they include a bunch of pairs that are interesting to contrast. ***(Pictured: Figure 1 from the paper)*.** Plains and Grevy’s zebra are very similar, buffalo and cattle are like the wild and domesticated version of each other and we wanted to see how well it would work and what it would tell us about the idea of the dietary niche, that each species eats a slightly different suite of plant species. We found really strong support for that hypothesis, which is fascinating. We used the same method on almost 4000 fecal samples from ten national parks in seven or eight different African countries. It’s a very repeatable pattern Pretty much everywhere you go, the animals are very clearly differentiated in terms of which plant species they’re eating. **This is so fascinating.** What is crazy about it is how fundamental it is, it’s so basic. If you don’t know an animal’s diet, you don’t have much hope of figuring out much else about how these systems work. In some ways, it’s the obvious starting point, but it’s so difficult. We’ve been trying to get the word out, and also lead by example, how we can deepen our insights of community ecology and species interactions using these food webs techniques.

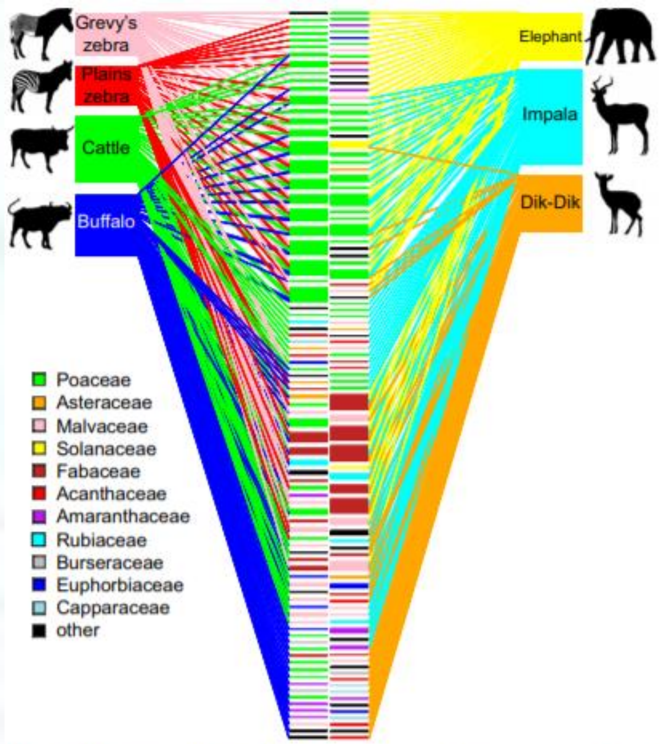

Fig. 1. Bipartite networks depicting diet composition and overlap of grazers (*Left*) and nongrazers (*Right*). Lines connect LMH species (outer boxes) to dietary plant sequences (inner boxes), which are colored by plant family. Widths of inner boxes are scaled to reflect how frequently each sequence was detected across all samples from all LMH species; line widths show how frequently each plant was detected in samples from each LMH species. Plants detected in both grazer and nongrazer diets appear in both networks. Boxes are ordered to minimize overlapping lines.

You coauthored a paper with Paul Ehrlich, among others, warning that we are so far above the normal background extinction rate that we are accelerating into a sixth mass extinction. (See advances.sciencemag.org/content/1/5/e1400253). Can you tell me more about that?

That has turned out to be an enormously influential paper. I didn't expect it to be. I thought we were saying something that everyone pretty much knew, there wasn't any huge trick to what we did there. We were using data from the IUCN, which puts out Red List reports on a regular basis. It wasn't like we were uncovering some huge secret. What we did that was a little unconventional, and maybe drilled the point home a little bit harder, is that a lot of papers about extinction make assumptions about who's going to go extinct based on what threat class they're in or whatever, and we didn't do that, we just looked at how many species had actually gone extinct and plotted that through time. It was very conservative. I think it's always easy…I'm an optimist, personally, despite my association with the trend that I see in the data, I work in places where you can positive things happening conservation-wise. For an optimist, it's easy to see how, if you're reading a paper where there's a lot of conjecture and speculation…remember these IUCN assessments are based on a subjective process, expert assessment. They convene experts on these groups on that basis. The point I'm trying to make is that, if you're reading a paper that says, we assume every species listened as near threatened or worse will go extinct by 2200, you can say to yourself, that's too pessimistic. We just dispensed with that, and went with the actual, literal, data on extinction numbers. I still don't quite know why that paper has been cited as many times as it has. We certainly were not the only paper making this point. It's not a secret, in *Science* and *Nature* magazine there's a paper almost every couple weeks on the extinction crisis. Long story short, it's a problem. But I also, as a personal reflection of my personality and my attitude, I like to work in places where positive things are happening, and I am actually optimistic about the ability of people to bring wilderness to a lot of places where it's been gone for a while. There's very exciting things happening on that front all of the world. That's the frontier for conservation as far as I'm concerned. Biodiversity is in trouble, but there's this increasing grassroots movement of projects that are taking land and helping it go wild again, bringing back species that have been gone for a long time. That to me is very encouraging. **I love rewilding.** I have a friend named Harry Greene who's got a ranch in Texas, he and his neighbors are bringing back prairie

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dogs, they've got cattle that's the closest analog to the Pleistocene herbivores, they're trying to get these critically endangered tortoises back. It's happening on private land, but also Gorongosa's a great example of the rewilding of a national park. This can happen from the scale of people's backyard or an English farm up to a 4000 sq km national park in Africa. There are many other examples, there's American Prairie Reserve out west in the US, there's the rewilding program in Argentina, even in Oostvaardersplassen in the

Netherlands. (Pictured: bison on the American Prairie Reserve, see www.americanprairie.org/project/bison-restoration). These kinds of experiments are growing and the scientific interest in the problem is growing. That's the 21st-century frontier for conservation. We have to try to save what we can, but also go on the offensive, and rewilding some of these places that have been badly damaged.

Another thing I think that's well expressed in your work is the interaction between human communities and conservation.

Conservation is a human decision about what to do, and it has opportunity costs that have to be paid somehow. There's increasing evidence that that's a possible thing to do. Conservation's traditionally been about playing defense, and you never score any points. I do think we need a slightly more balanced game plan as the conservation community.

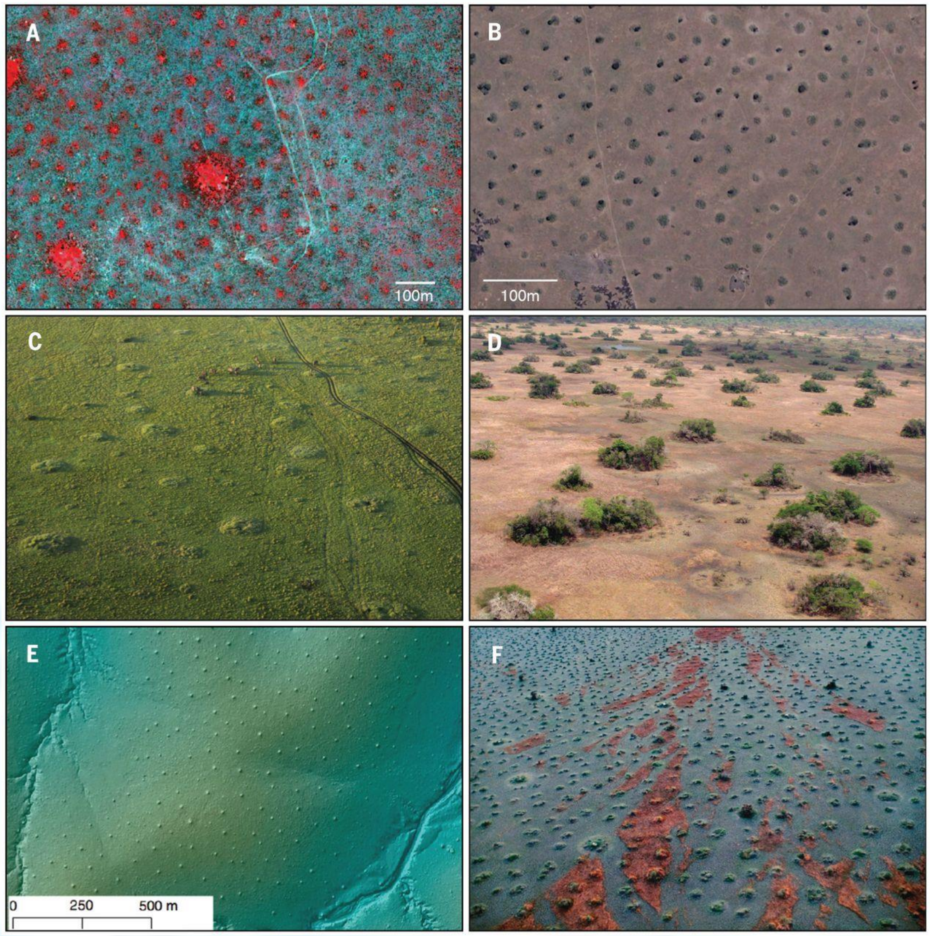
Your paper on upgrading protected areas (www.nature.com/articles/nature22902) was particularly fascinating to me, with its examples of rewilding and community engagement in Guanacaste, Costa Rica and Gorongosa, Mozambique. Let's talk about your eight pillars in action, like "know thy biodiversity," "pay the opportunity costs," and "upsize and interconnect."

(Pictured: Figure 3 from the paper, members of the Nhamatanda Environmental Club meet a lion that was immobilized as part of the Gorongosa Lion Project's conservation programme.).The genesis of that was, I was having this…you see a lot of literature in conservation about finding places for new protected areas, how do you prioritize sites for conservation action. That's important, obviously, but what has struck me in working the places I've worked and visiting the places I've visited, there are already a lot of protected areas that are not doing a very effective job for conservation for one region or another. So the point was really to get the conservation community to think more about investing in existing protected areas and growing them, which may also be easier than establishing a new protected area from scratch. I highlighted these examples because they're two of the best examples of rewilding in a national park-well the ACG [Area Conservation Guanacaste] is multiple national parks, but basically on government lands, where people have restored functional, healthy, regenerating, self-regulating ecosystems but also grown the protected area manyfold in size. I wanted to go deep in showing, these projects have certain things in common. Not the details, northwestern Costa Rica is a very different landscape than central Mozambique, the culture and politics and socioeconomics are totally different. But there are things about the attitude, the philosophy, the general approach, if you want to try to articulate what has made them successful, that was the pillars. What were the shared elements in each of them has made them successful?

You know, it makes sense to me that you wanted to be a writer, because your writing style seemed to me noticeably more engaging than most scientific papers I've read. I appreciate that. What is personality in scientific writing? I think everyone agrees it's more fun to read things that have a voice. The question is, when we're writing actual scientific papers, we're under pretty strong-there's an imperative to say as much as you can with as little as you can, and to be kind of ruthlessly efficient. If I just want to look at your data, I don't want to see a lot of flowery language. I think there's a time and place for different stylistic modes. The review papers and perspective pieces are nice, you have a little more room to be a little bit more inventive with your word choice.

Speaking of inventive, one paper of yours that I was absolutely fascinated by was your team's discovery that termite mounds help protect dryland ecosystems from climate change (science.sciencemag.org/content/347/6222/651.full),

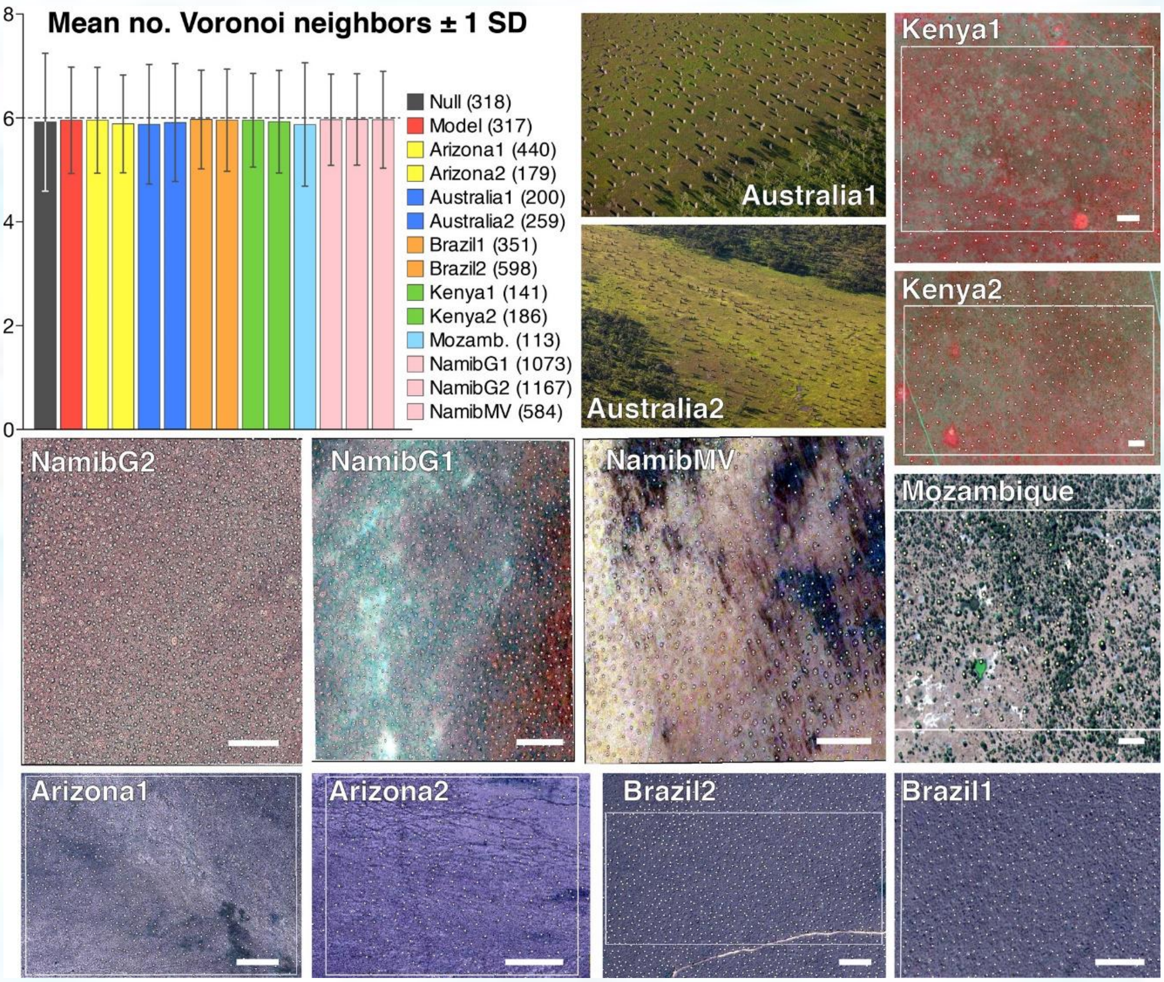
because their aerated soil means rain filters in more and the extra water makes them islands of plants and nutrients. Can you me more about this, and the implications of these refugia!



(Pictured: Figure 1 from the paper, displaying patterned termite mounds from around the world). It's not just the water infiltration, it's also the elevated nutrients. It was my wife's idea, Dr. Corina Tarnita, she's a theoretical biologist who's trained in math but has been doing biology since grad school. She had this idea about how the plant dynamics on termite mounds would help to buffer these dryland ecosystems from climate change. Because the termite mounds are these more productive areas, in a system undergoing desertification, the last place you lose plants is on the termite mounds. The existence of the termite mounds means instead of becoming a complete desert, the vegetation hangs around longer. The level of drought to get complete loss of plants needs to be much more extreme in an ecosystem with these termite mounds. Again, it was really her idea, looking into some of the literature on alternative stable states. That collaboration's fun because the mathematical modeling is not really something I do, but it was great to collaborate with her. Some of the most exciting work I've done in the past eight years has been collaborations with her where we can put experiments with her and take theoretical models and then confront them with data from experiments. That's sort of the epitome of elegance, really, but it's hard to do because it takes a lot of work.

And closely related, let's talk about that one letter you co-wrote to *Nature* (nature.com/articles/nature20801.epdf) about these island-like structures the unified theory of fairy rings, mima mounds, and heuweltjies, if I'm pronouncing that right?

That was the genesis of it. The deep history is, as a grad student, I got interested in the fact that…You start to notice from small planes in Africa that you see these polka dots on the ground, grass that's a different color from the grass around. No two are next to each other, they're very spread out. Everywhere in Africa, you see this thing. Sometimes the circular spots have trees, sometimes different-colored grass, but everywhere you go. It's termite mounds, and this phenomenon that termite mounds are always in this evenly spaced arrangement is fascinating, and has fascinating ecological implications.



(Pictured: Figure 7 from the paper, examples from around the world. Note that all mounds seem to have six neighbors, a constant hexagonal arrangement). An ecosystem with termite mounds spread out like that is going to function better, have higher productivity, than an ecosystem with the same number of termite mounds in a random, jumbled order. The spatial patterning itself is influencing the whole ecosystem. That, I find really, really interesting. The original question to Corina, we're married now but we met in 2010, and the first time we hung out was just to talk about possible collaboration. I was like, there's this phenomenon that termite mounds are always really spread out, and it needs a mathematical model so we can run simulations and see what processes lead to this. I had a sense it was competition, that termite colonies compete with each other and that creates kind of a repulsive force. We actually did a couple other collaborations first, but I just felt it was going to be important. The origins of that whole body of work was me with a simple-minded thing of feeling like there's not really good evidence for how this pattern emerges, no one's talking about termite mounds. In the process, like okay let's write a grant, in the process that's when she had the idea about termite mounds buffering these ecosystems about climate change. The whole is greater than the sum of its parts in terms of creative inspiration and ideas. The *Nature* one you're referring too was the culmination of the original problem. It's not a paper about fairy circles alone, we use them as our main case study to show that our model can reproduce things that no other model can reproduce, not only their even hexagonal arrangement but that our model was generating the spatial patterns of grass in between the fairy circles. The model itself is general. We were including examples of ants and termites. Also in Brazil, they call them *murundu*, it's all over the world this thing happens, and it's not well understood. Wherever you go, there's one or more groups of people arguing about what really causes these things, and it's a fairly simple general explanation: animals that make nests that affect the plants, and compete with each other. If you zoom in on Google Earth on eastern China, you can even see it there, in these human settlements established thousands of years ago, they also are spread out like that. It's not just the social insects, people were also competing with each other. There's still people who are pretty grumpy about that paper, but I think we're right.

That's very E.O. Wilson of you, parallels between civilizational dynamics at the insect and human level.

Yeah, I suppose there is a little bit of an echo of Ed in there.

And you also had a paper that found that large herbivores and soil fertility interact to partition habitat between different species of acacias. (See https://pringle.princeton.edu/wp-content/uploads////sites/199/2014/01/Ecology-2016-Pringle-1.pdf). One more thorny species was on the black cotton soils, one less well defended species was on the red sand soils. But you found that when browsers like elephants and giraffes were excluded, they could grow equally well in each others' habitat, right? So there was an abiotic and biotic filter?

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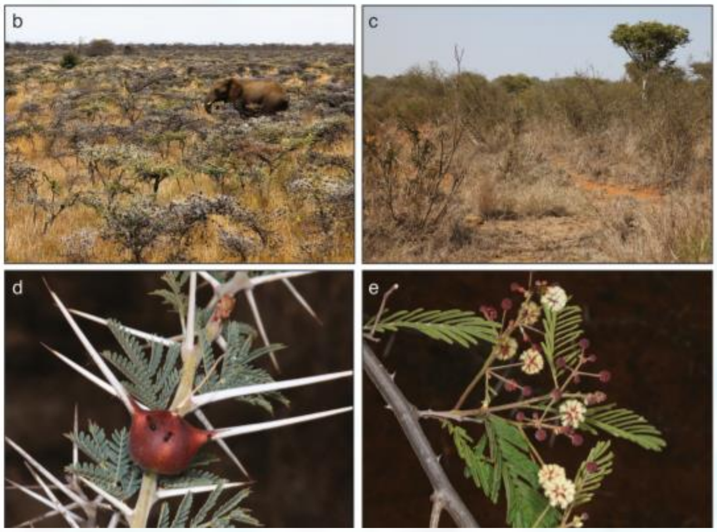

(Pictured, from Fig. 1 of the paper: black cotton soils with their characteristic well-defended acacia species on the left, red sand soils and their less-well defended acacia species on the right). Yeah, so that was another one that, I actually had the idea when I was in grad school, I read a paper from a guy who works in the Amazon. In the Amazon they have these white sand forests, they have very low nutrients, and you get there different kind of plant species that don't occur in the forests, the non white sand forests. White sand is very poor habitat, and trees struggle to survive there, and they basically survive by investing in extremely high levels of defense. It's basically herbivores who create this specialization, looking at the white sand trees. Species from the non-white-sand trees can survive in the white sand trees, provided you protect them from herbivores. You go to these places in Kenya, it's pretty dramatic, you could take one step from one soil type to the other and they have totally different plant species. Thinking back to that paper, maybe herbivores have something to do with this, not just the soil. Maybe they have a preferred soil, and it's the herbivores that do the rest of the work and enforce that habitat preference. That's pretty much what we found. In this case, it was especially elephants, and also other ungulates. The same kind of process plays out in Amazonia where the main herbivores are insects. These things are happening all over the world.

That's awesome! It's fascinating work that you all are doing. I saw that one other amazing project that your lab is working on is Harrison Watson's herbivory and carbon cycling. Could you tell me more about that project?

You should reach out to Harrison yourself, I think you guys would have a lot to talk about. He's in his second year of his Ph.D., and it's pretty early, but he's trying to understand how large herbivores influence carbon cycling in savannahs. Savannahs can be carbon sources or carbon sinks, depending on factors we don't exactly know. He's also working with Carina on some theoretical modeling of the carbon cycle.

Well, Dr. Pringle, thank you so much for sharing your wisdom. Thank you so much for joining this interview. It's been a pleasure talking with you.