A New Story for Maize Domestication

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Modern maize has long been a puzzle. Unlike other domesticated grasses, there didn't seem to be any wild species that looked like the modern cereal and from which farmers could have selected better versions. Eventually, the discovery in lowland Mexico of teosinte, a wild and weedy relative of maize, solved the problem. But there was another problem. A lot of the later genetic work to understand the transformation of teosinte into maize found remnants of different types of teosinte. A new research paper by Jeffrey Ross-Ibarra and his colleagues sorts out the story.

We started with the differences between maize and teosinte.

Jeffrey: When they're when they're small, they look very similar. But at maturity they do look pretty different. So teosinte tends to have branches and tends to have many stalks coming from the base. So it looks a bit more bushier than a typical corn plant will. And in teosinte the branches end in a male inflorescence. So that's the tassel that makes pollen. And in maize that that lateral branch has been shortened super super short. And instead of ending in a male inflorescence it ends in an ear, which is why the ears come off the side of the plant. So we've had a switch from a male to a female inflorescence. But the biggest difference is really the ear. So we're familiar with what an ear of corn or maize looks like. And you've got several hundred kernels all together on a single cob. And they're uncovered. So there's no covering of them. And then there's a sort of a husk around them. And in teosinte, the ear, first, you don't have one or two ears per plant like you typically do in maize. You'll have hundreds. And each ear has maybe six to twelve kernels on it in single row. And those kernels first are covered in a hard fruit case. So there's this sort of hardened shell around the kernel. And the kernels aren't attached to a cob. So at maturity they fall off the plant and just sort of scatter to the ground. And when you ... If you manage to open up that kernel, which you can break a tooth doing, it's really rock solid inside, the kernel is much smaller than a kernel you'd see in maize. So those are ... The overall plant structure and the differences in the ear are really the really big differences.

Jeremy: So without going into the kind of genetic differences behind that, what's the standard story of of how teosinte became maize?

Jeffrey: Well, one of the neat things, and it's either embarrassing or exciting, depending on how you look at it, and especially relevant for for thinking about maize as food, is we don't actually know why maize was domesticated. I mean, clearly it was domesticated for food, but it's not clear that it was domesticated as a grain crop. It may have been domesticated for the grains and kernels, but it's hard to imagine or certainly imagining, trying to use teosinte to make flour or to use it as a grain is it's really painful grinding those things, and they're not a particularly efficient way of getting grain. Another possibility is that it was used for popcorn, because you can take the kernels and throw them in the fire, and they'll pop open and you'll get popcorn just very similar to popcorn that you buy in a movie theatre. And the third possibility is that it was actually domesticated or initially used, at least because of the sort of sugar-rich stem, and that you could ferment this stem and make fermented beverages from it.

And certainly some of the evidence from human bone, from archaeological excavations of human skeletons across America suggests that for a long time, maize wasn't an important part of people's diet, and the majority, or quite a bit of the use of maize was as a fermented beverage. That sort of mystery of why it was domesticated, we still don't know. And then there's the question of where it came from and how it was domesticated. And for much of the 20th century, the model was sort of strange, one that suggested, because there was evidence of hybridisation in the archaeological record. If you look at cobs, there seems to be evidence of mixture or hybridisation in the archaeological record. There was this model that you had two different species come together and hybridise, some perennial grass and some extinct maize hybridised together. And that gave rise to both modern maize and teosinte. But the most common model now for the past 20 years or so was one that maize was domesticated a single time from teosinte. So some ancestral plant that looked a lot like modern teosinte gave rise to to modern maize.

Jeremy: And what's wrong with that story, that an ancestral plant like teosinte gave rise to modern maize?

Jeffrey: So it's not wrong. But our current paper suggests it's a bit too simple, in the sense that the genetic data support that idea that maize was originally domesticated from a wild teosinte that grows in the lowlands of southwest Mexico. But over the last ten years, in a number of studies, and when we were looking at how maize is adapted to different environments across the Americas, we kept finding evidence of genetic contributions from a second teosinte. So there are multiple — teosinte is a general term to refer to all of the wild grasses related to maize — and we kept finding evidence of contribution from a second teosinte that grows in the mountains of central Mexico. The really odd thing to us is that we found evidence of contribution from that teosinte, not just in maize from the mountains of Mexico, but in ancient maize from the southwest US, and in maize as far south as the Andes, thousands of kilometers away from any teosinte plant. And so that sort of puzzle of evidence of genetic contributions from a second teosinte made us suspect that maybe this initial model of a single simple domestication was was oversimplified.

Jeremy: So then how did you go about ... You mentioned that you looked in the DNA and found evidence of this other teosinte. But how did you go about investigating the problem for this latest paper?

Jeffrey: The idea actually started almost 13 years ago with the, in reading the literature and seeing the evidence of this simple model of a single domestication, where they pointed out that if you look genetically, the maize that looked most similar to teosinte is maize that grew in the mountains of central Mexico, where this lowland teosinte doesn't grow. And so that didn't make sense with the ecology or the archaeology or anything else. And from there we had a series of papers looking at genetic contributions of the second teosinte in the highlands.

And really what started this paper was a couple of years ago, in thinking about how maize adapted to the Andes, we found that some of the adaptations, some of the way that the genetics that maize used to ... or that indigenous farmers use to sort of breed maize and improve maize to adapt it to the Andes, involved genes from highlands of central Mexico. And so what we did in this paper was say, well, we've always been sort of assuming that this previous model was correct. And so let's take a step back and ask, if we just look at all maize everywhere and as much maize as we can get our hands on, and we do the really sort of simple question of if we treat each maize plant, say how much of its DNA came from this one teosinte, and how much of its DNA came from this other teosinte, which sort of nobody had done that sort of obvious thing before. And we just did that for as much maize as we could get our hands on. And the surprising thing we found was that every single maize plant we looked at, every genome, all the DNA that we looked at, had a meaningful contribution of this second teosinte, which was what really got us started in thinking about our new model and the contributions of the second teosinte.

Jeremy: So you can kind of tell when things happened also, from the number of changes in the DNA. So does this give you a kind of clearer story of what maize domestication might have looked like?

Jeffrey: I think if anything, it complicates the story. We can tell from the genetic and archaeological data that this hybridisation event happened about 6000 years ago. And we know from earlier archaeological data that maize domestication, maize was domesticated as early as 9000 years ago. So we had this initial domestication of maize. And the archaeological data is really clear that it spread across the Americas after that. And so we have these beautiful archaeological samples of maize in Peru that's 6000 years old, and it looks like, you know, a modern corn cob. It doesn't look like teosinte. It's clearly a domesticated corn that was in South America 6000 years ago. And so that must have gotten there before this hybridisation event. And in fact, when we look at its DNA, it doesn't show evidence of contribution from the second teosinte. So we already had something that was a domesticated corn, but then we had this hybridisation event in in the highlands and the mountains of central Mexico, and that somehow made a better corn that spread back across the Americas, mixing with or replacing corn everywhere else. And so I think it actually complicates the story, because it leads to a bunch of questions of why the heck is this second corn, this hybrid, this hybrid corn better? Or what is this second teosinte contributing to the story?

Jeremy: Well, that was that was going to be my next question, is how did the presence of these extra genes from the highland teosinte, how did they benefit the people who were growing the maize?

Jeffrey: Yeah, that's a great question. And the short answer is we still don't know. When we first sort of saw these results suggesting that the contribution of the second highland teosinte to all maize, it seemed really obvious to me that what we would see is that the genes that we know are important for distinguishing, for making maize different from teosinte. So over many, many years, people have done lots of really beautiful genetic work to identify a number of the genes. In some cases, we know the specific change of the DNA that allowed differences in, say, this branching architecture, or we know the genetic basis of the genes that allowed sort of the kernel to be uncovered by this, from this fruit case. And I sort of had the idea that we would look and we would see that these sort of key genes were the ones that were contributed from the second teosinte, and that would be the smoking gun, and that would would show why this was so important. And that's not at all the case. So we don't see any evidence that these sort of obvious key domestication genes were brought in from the second teosinte. And we do some sort of statistical genetic work in the paper and identify a set of genes that look like they were selected by early indigenous farmers, and some of those make some sense, but none of those is a smoking gun.

So we find one example of a gene that is important in photoperiod. So if you take corn from the tropics or teosinte and you try to grow it as far north here as Davis, for example, plant it in March, and it won't flower until November and then gets killed by the frost. Because maize in the tropics requires short day conditions, and if you grow it in long day conditions, it gets confused and won't flower. And this gene sort of modulates that and allows maize to adapt and figure out when to flower, even in long day conditions. So we have some examples like that, of a gene that makes sense, but it's not obvious that that gene alone, or the few that we identify alone, are sufficient to explain the sort of clear advantage that this hybrid seemed to have had. The the other suspicion, or the other explanation, that we have is one of sort of hybrid vigour, that it may be the case that this initial domesticated maize was not particularly reliable, had a bunch of sort of bad alleles that had accumulated because of small population size and going through a bottleneck. And that really that this hybridization with the second teosinte brought in a whole bunch of new genetic variation. And so it may have been that it contributed to allowing early farmers to select a little bit better and more efficiently on a lot of different traits. And we provide some evidence in the paper that that may be the case.

Jeremy: Yeah. It's interesting that you've got this map in your paper of the frequency of genes from teosinte, the highland teosinte, and they seem to be much more common north and south of the original centre of domestication. What do you think that means?

Jeffrey: So some of that I think is latitudinal adaptation. So at higher latitudes you both have shorter days. And so you have to have these this adaptation to short days or ... excuse me not shorter days, shorter growing season. So you have to flower earlier. You also have longer days. So you have to adapt to this photoperiod difference that I talked about. And you also have colder climates. And all of those things are differences between the lowlands and the highlands of central Mexico. So if you look at this highland teosinte, it flowers earlier because it has a shorter growing season and cold, high elevation conditions, and it has to germinate and flower at a different time of the year. So it has a slightly shifted photoperiod and it has a bunch of adaptations for cold. And so I suspect that that those sort of highland lowland differences within Mexico and between those two teosintes are part of the reason why you see that enrichment of highland teosinte alleles at higher latitudes, both north and south.

Jeremy: You mentioned right at the outset a couple of things. One is this huge change from having a male flower, flowers, at the end of every branch to having a single male tassel, and the very reduced stalk on which the ear sits. And am I right that that — I think I remember hearing a lecture that that that only, probably only ever happened once in the history of maize. Is that right?

Jeffrey: Yeah, I think that probably most of those initial changes probably did happen once, but I think it is worth asking maybe what we mean when we say it happened once. I don't think anybody would claim that it happened, you know, on a Tuesday in one particular farmer's backyard, but that it was, you know, one, perhaps one genetic change that was selected in one region. And it wasn't sort of two totally independent things that happened at two totally independent times, but probably lots of different indigenous groups within the same region.

Jeremy: Yeah, but I mean, you said before, at the outset, you said there are these three different ideas of of why teosinte was being grown. You know, that maybe it was for popcorn, maybe it was for grain. Probably unlikely. And this idea that people were growing it for the sweet stalks, a bit like sugarcane almost. It does kind of boggle the imagination that somebody noticed in their teosinte. They must have been ... That they noticed these changes and said, hmm, this is interesting. Maybe we should take more interest in these. I just find it astonishing.

Jeffrey: I totally agree, and I think that's why I say it's both exhilarating — because we don't know. And that, you know, as a scientist, that's fun because it means that there's lots to think about and a lot more work to do. But it's also a little bit embarrassing for a crop that we know so much about, that is such an important crop, that I can't even really tell you why people were growing it initially. I think that there certainly is good evidence that it was being used for fermentation. People ... You can still find today, people that will chew the stalks of teosinte because they're sort of sweet. You can still find maize being used to make fermented beverages. So we know that those things occur today. And we can use isotope data from bones to ask whether maize was being used as a fermented ... Whether the carbon people were getting from maize came from being fermented or from eating the grain. So there's certainly evidence that it was happening. But we don't know that that means that that was why it was initially selected. And even, as you say, even if that's why it's sort of ... It's still hard for me to imagine how somebody had a field of teosinte or was collecting stalks from a field of teosinte, and then how you go from there to developing an ear of modern corn? Yeah. The process still is fascinating and mysterious to me, which is kind of cool.

Jeremy: Can you imagine ever finding an answer to that question? What would it take?

Jeffrey: And I think we can. You know, I don't know if we can get a definitive answer, but for some of this, I think we can, I think we're working towards partial answers. So, for example, for many of the genes that we know are important for distinguishing maize from teosinte, we can look to ask, were those genetic variants already sort of hanging out in teosinte. Were they already segregating in natural populations, or were they things that sort of arose de novo accidentally in some farmer's field after people were selecting on teosinte? And by and large, for essentially almost every variant that we ... All of the genetic variants that we know ... We can show that almost all of them, or maybe all of them were already segregating in teosinte. So you can find teosinte plants that have the maize allele, the maize genetic variant in each of these loci, suggesting that a lot of that genetic variation was already hanging out in teosinte.

And that, I think, means it's a lot more plausible to think, you know ... It's not that early farmers were waiting around for a magical mutation to happen, but that many of those genetic variations were already in the populations. And that makes it a little bit easier. The other thing that's really interesting is that if you grow teosinte in stressed conditions, if you just sort of stress the plant out, it kind of starts to grow like maize. And so you can see examples of stressed teosinte where the fruit case opens a little bit, and in stressed teosinte it tends not to make branches, it'll just have a single central stalk. And so it may be a combination of the right conditions and the right genetic variation in the two populations began to make things that an early farmer, you know, thought were useful or were useful to early farmers.

Jeremy: And talking of stress, a final question: does this research have anything to say to future adaptations of of modern maize so that it can cope with things like the climate emergency?

Jeffrey: Yeah, I think it does. I think I would argue that it sort of highlights the potential useful contributions of wild relatives. We know for many, many different crops that there are close wild relatives that have, over thousands and thousands of years, adapted to different climatic conditions. And I would argue that this is additional evidence, or supports the idea, that genetic variation from those wild relatives can be useful for breeding, and can be useful for breeding for novel environments. How you go about doing that, it's not easy. If you ask a modern day corn breeder to cross in or breed some teosinte into their population, they will not be happy about the idea. Because if you just try crossing a teosinte with maize, you get something that is not going to be as reliable. It won't have as high yield, it will be more variable. It would basically be much, much worse and much lower yielding than a modern hybrid corn. And so really the trick is how do you figure out what are the useful genetic variants, and how do we bring those into modern crops without bringing in sort of all that baggage that breeders over thousands of years, indigenous farmers and breeders, have done such a good job of sort of cleaning up or changing.

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