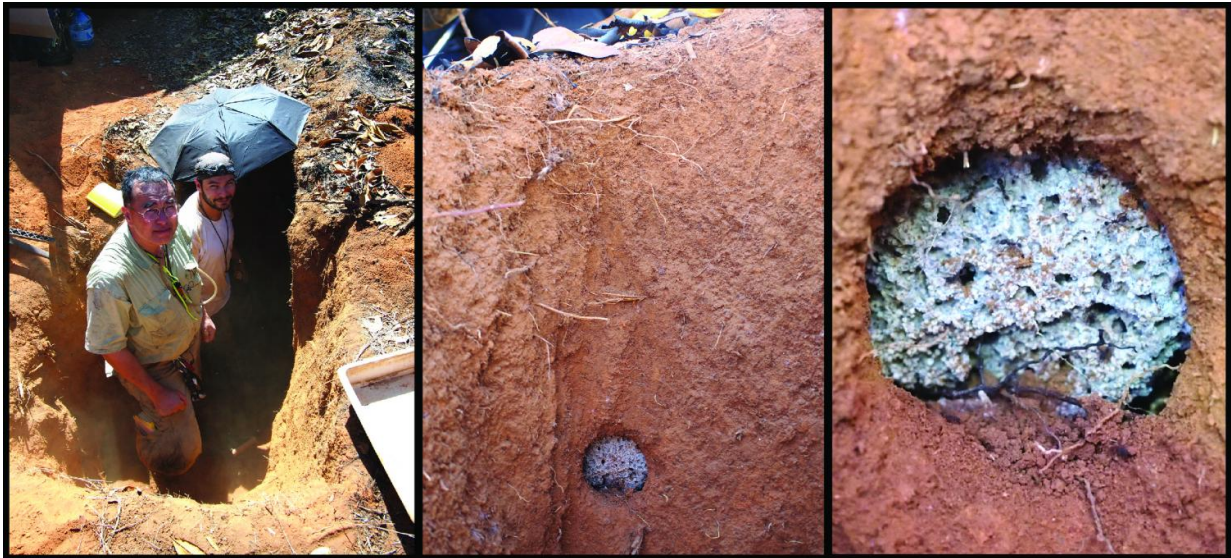


Ant agricultural revolution began 30 million years ago in dry, desert-like climate

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Left panel: Ted Schultz (left) and Jeffrey Sosa-Calvo (right) excavate a primitive, lower fungus-farming ant nest in the seasonally dry Brazilian Cerrado (savanna) near Brasilia in 2009. Photo credit: Cauê Lopes. Center and right panel: The underground garden chamber of a primitive, lower fungus-farming ant colony revealed by excavation. Photo credits: Ted Schultz, Smithsonian. Lower, primitive fungus-farming ant colonies and agricultural behaviors are comparably smaller-scale and simpler than the colonies of higher fungus-farming ants. Credit: Cauê Lopes. Ted Schultz, Smithsonian.

Millions of years before humans discovered agriculture, vast farming systems were thriving beneath the surface of the Earth. The subterranean

farms, which produced various types of fungi, were cultivated and maintained by colonies of ants, whose descendants continue practicing agriculture today.

By tracing the evolutionary history of these fungus-farming ants, scientists at the Smithsonian's National Museum of Natural History have learned about a key transition in the insects' agricultural evolution. This transition allowed the ants to achieve higher levels of complexity in farming, rivaling the agricultural practices of humans: the domestication of crops that became permanently isolated from their wild habitats and thereby grew dependent on their farmers for their evolution and survival.

In the April 12 issue of *Proceedings of Royal Society B*, scientists led by entomologist Ted Schultz, the museum's curator of ants, report that the transition likely occurred when farming ants began living in dry climates, where moisture-loving fungi could not survive on their own. The finding comes from a genetic analysis that charts the evolutionary relationships of farming and non-farming ants from wet and dry habitats throughout the Neotropics.

About 250 [species](#) of fungus-farming ants have been found in tropical forests, deserts and grasslands in the Americas and the Caribbean, and these species fall into two different groups based on the level of complexity of their farming societies: lower and higher agriculture. All farming ants start new fungal gardens when a queen's daughter leaves her mother's nest to go off and found her own nest, taking with her a piece of the original colony's fungus to start the next colony's farm.

In the lower, primitive forms of ant agriculture—which largely occur in wet rain forests—fungal crops occasionally escape from their ant colonies and return to the wild. Lower ants also occasionally regather their farmed fungi from the wild and bring them back to their nests to replace faltering crops. These processes allow wild and cultivated fungi

to interbreed and limit the degree of influence the lower ants have over the evolution of their crops.



Ted Schultz is the curator of ants at the Smithsonian's National Museum of Natural History. He studies ants that began farming millions of years before the evolution of humans. 'These higher agricultural-ant societies have been practicing sustainable, industrial-scale agriculture for millions of years,' Schultz said. 'Studying their dynamics and how their relationships with their fungal partners have evolved may offer important lessons to inform our own challenges with our agricultural practices. Ants have established a form of agriculture that provides all the nourishment needed for their societies using a single crop that is resistant to disease, pests and droughts at a scale and level of efficiency that rivals human agriculture.' Credit: Paul Fetters for the Smithsonian Institution

But, as with certain crops that have been so heavily modified by human breeders that they can no longer reproduce and live on their own in the wild, some fungal species have become so completely dependent on their relationship with farming ants that they are never found living independent of their farmers. These higher agricultural ants cultivate highly "domesticated" crops, enabling them to live in vast communities and to work together through division of labor to fertilize their fungal crops, haul away waste, keep pathogens at bay and maintain ideal growing conditions.

"These higher agricultural-ant societies have been practicing sustainable, industrial-scale agriculture for millions of years," Schultz said. "Studying their dynamics and how their relationships with their fungal partners have evolved may offer important lessons to inform our own challenges with our [agricultural practices](#). Ants have established a form of agriculture that provides all the nourishment needed for their societies using a single crop that is resistant to disease, pests and droughts at a scale and level of efficiency that rivals human agriculture."

Today, many agricultural ant species are threatened by habitat destruction, and as part of his studies, Schultz has been collecting specimens from the field and preserving them in the museum's cryogenic biorepository for future genomic studies. In the current study, he and his colleagues compared the genomes of 119 modern ant species, most of which were collected during his decades of field expeditions.

Using powerful new genomic tools, the scientists compared DNA sequences at each of more than 1,500 genome sites for 78 fungus-farming species and 41 non-fungus-farming species. Their data-rich analysis gave the team a great deal of confidence in the evolutionary relationships they were able to map, Schultz said.

Their analysis clarifies the closest living non-farming relative of today's fungus-growing ants and allows Schultz and his team to begin to look at the geographic backgrounds of these species and deduce when, where and under what conditions particular traits emerged. In this study, the team was interested in learning when ants began practicing higher agriculture—that is, when some fungal [crops](#) came to be dependent on the ant-fungus relationship for survival.



Ted Schultz surveys the gigantic mound of a higher agricultural ant colony in the seasonally dry Brazilian Cerrado (savanna) near Brasilia in 2009. Higher fungus-farming ant colonies and agricultural behaviors are comparably larger-scale and more complex than the colonies of lower fungus-farming ants. Credit: Jeffrey Sosa-Calvo, Smithsonian.

According to the evolutionary tree they constructed, the first ants to transition to higher agriculture likely lived in a dry or seasonally dry climate. The transition appears to have occurred around 30 million years ago—a time when the planet was cooling, and dry areas were becoming more prevalent.

Fungi that had evolved to live in wet forests would have been poorly equipped to survive independently in this changing climate. "But if your

ant farmer evolves to be better at living in a dry habitat, and it brings you along and it sees to all your needs, then you're going to be doing okay," Schultz said.

Just as humans living in a dry or temperate climate might raise tropical plants in a greenhouse, agricultural ants carefully maintain the humidity within their fungal gardens. "If things are getting a little too dry, the ants go out and get water and they add it," Schultz said. "If they're too wet, they do the opposite." So even when conditions above the surface become inhospitable, fungi can thrive inside the underground, climate-controlled chambers of an agricultural ant colony.

In this situation, fungi can become dependent on their ant farmers—unable to escape the nest and return to the wild. "If you've been carried into a dry habitat, your fate is going to match the fate of the colony you're in," Schultz said. "At that point, you're bound in a relationship with those [ants](#) that you were not bound in when you were in a wet forest."

Schultz said the conditions present during this evolutionary transition illustrate how an organism can become domesticated even if its farmers are not consciously selecting for desirable traits as human breeders might do. Ants that moved their fungi into new habitats would have isolated the organism from its wild relatives, just as humans do when they domesticate a crop. This isolation creates an opportunity for the farmed species to evolve independently from species in the wild, adopting new traits.

More information: Dry habitats were crucibles of domestication in the evolution of agriculture in ants, *Proceedings of the Royal Society B*, rspb.royalsocietypublishing.org/doi/10.1098/rspb.2017.0095

Provided by Smithsonian

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