Researchers inform ecological theory with findings from decades of coffee farm fieldwork

April 6 2023, by Jim Erickson

University of Michigan ecologists John Vandermeer, left, and Ivette Perfecto at a coffee farm in Mexico. Vandermeer and Perfecto have spent more than 30 years investigating the interrelationships between biodiversity conservation, biological pest control, and food sovereignty at coffee farms in Mexico and

Puerto Rico. Their new study in the *Proceedings of the National Academy of Sciences* examines competition within the ant community at a Puerto Rican coffee farm. Image credit: Levi Stroud

University of Michigan ecologists Ivette Perfecto and John Vandermeer made their initial forays into agrosystems biodiversity research in the late 1980s while teaching an ecology field course in Costa Rica.

They conducted field exercises at local coffee farms and quickly discovered a surprising diversity of insects. Through interactions with local farmers and international students in the course, they gained an appreciation for the role of agriculture in the conservation of biodiversity.

Since then, Perfecto, the James E. Crowfoot Collegiate Professor of Environmental Justice at the School for Environment and Sustainability, and Vandermeer, the Asa Gray Distinguished University Professor of Ecology and Evolutionary Biology, have focused on the interrelationships between biodiversity conservation, biological pest control, and food sovereignty—concepts that they found to be interrelated only through their extensive research at coffee farms in Mexico and Puerto Rico.

In a research article published in *Proceedings of the National Academy of Sciences*, Perfecto and Vandermeer examine competition among the ant community at a Puerto Rican coffee farm and the maintenance of species diversity there.

In general, how does fieldwork like your long-term studies in Mexico and Puerto Rico help inform

ecological theory?

Perfecto: Our work is unusual in that we combine fieldwork and ecological theory in a mutually reinforcing manner. In contemporary research, it is common for ecological studies to be either strictly empirical or strictly theoretical, depending on the researchers and their interests. Our approach is distinct. We take standard ecological theory as a clue for what fieldwork might be interesting and important, do the fieldwork, and then use the field results as a motivation for the development of new theory. Therefore, our fieldwork in Mexico and Puerto Rico is essential for our scientific enterprise as a whole.

In this new *PNAS* paper, you propose merging two concepts in ecological theory, transitive competition and intransitive competition. Explain those terms and describe the organization of the ant community at the Puerto Rican coffee farm.

Vandermeer: The ecological literature now accepts the idea that intransitive competition (like the rock-scissors-paper game, species A beats species B beats species C beats species A) is widespread in nature. We see an example of that in our work on ants as biological control species in the coffee agroecosystem.

But we take that observation further and note that intransitive structures, in turn, may lead to a new type of persistence of other, transitive species in the system. Species not involved in the intransitive structure are generally hierarchically structured (i.e., transitive), wherein the "best" competitor is expected to outcompete all the others and become the only survivor.

Darwin noted, long ago, that when such hierarchies exist, we expect the most dominant to eventually wipe out all the others. However, if some sort of disturbance "resets" the game at periodic intervals, the dominant

may never be able to attain its expected dominance over all other species, and more species could be maintained in the system.

Our theory simply notes that Darwin's idea of a "periodic disturbance" could arise from one of the species in the intransitive structure being a major competitor against the dominant species in the hierarchy. Its cyclical appearance as the intransitive pattern repeats itself (from A to B to C to A again) temporarily knocks down the dominant species in the hierarchy, effectively acting like Darwin's periodic disturbance.

Do your observations at the Puerto Rican farm have broader applications to other ecological communities?

Vandermeer: Ants are ubiquitous in almost all terrestrial ecosystems, including agroecosystems. We have been studying the role of ants in the biological control of insect pests and diseases on coffee farms for many years. Different species of ants have different effects on pests and different life stages of the pests. Understanding the spatial structure of the ant community that emerges from the intransitive competition, and how it changes over time, helps us understand the changes in the pest control service that ants may offer.

For example, in coffee, the coffee berry borer bores into the berries and reproduces inside the berries. Small ants can penetrate the berries and prey on the brood, while large species prey on the CBB while it is outside boring into the berries. Also, arboreal species can prey on the CBBs that are on the plants, while strictly ground foragers may prey on the borers that are found inside old berries that fall to the ground.

Is there a connection between your proposed theoretical structure and the larger topic of biodiversity?

Perfecto: Yes. If transitive competition was universally true, the general expectation would be that the most competitively dominant species would eliminate all the others. Perhaps this result would be variable from site to site, and thus different structures of dominance would permit greater species diversity as environmental heterogeneity increased (each point in space and time would permit the dominance of a different species).

With a central organizing intransitive group, we expect an oscillating framework: Species A gives up to species B gives up to species C gives up to species A and so forth. If each of the species in the intransitive triplet has a distinct competitive relationship with other groups of species—many of which will themselves be transitive—the trend toward the local elimination of all but the most dominant species will be curtailed, promoting species coexistence and therefore higher diversity.

Historically, it's been assumed that many ecological communities exhibit a top-down, hierarchical competition between species. Has that assumption been challenged in recent years?

Vandermeer: Yes, the assumption of hierarchical competition has been vigorously questioned in recent years—especially by theoreticians, many of whom note that we have not looked for intransitivity very vigorously. It just sort of seems natural that if species #1 is bigger and stronger than species #2, and species #2 is bigger and stronger than species #3, it must be true that species #1 is also bigger/stronger than species #3.

This transitive property is certainly true if we consider just a single ecological niche, for example a plant that grows fast and tall and shades everything else. But if other niche elements are involved—let's say that plant also spreads its roots out to get more nitrogen from the soil—that

underlying assumption is simply not true, and intransitivity easily emerges, in theory.

It has been proposed that a number of biotic and abiotic factors—such as predator-prey interactions, rainfall, and temperature—can break a competitive hierarchy and may even lead to intransitivity. Finding such intransitivity under natural circumstances is quite challenging, and our encountering it with these three ant species was largely a matter of luck.

The *PNAS* paper is the latest result of your decades-long ecological field studies at coffee farms in Mexico and Puerto Rico. Briefly, what are some of the key insights you've taken away from that work?

Perfecto: We quickly discovered a surprising diversity of insects living on those farms and soon gained an appreciation of the role of agriculture in the conservation of biodiversity. This contrasted dramatically with the conventional wisdom of the time, that agriculture and biodiversity conservation were antagonistic with one another, and it led to two of our books, "Breakfast of Biodiversity" and "Nature's Matrix."

Over the years, dozens of graduate students, postdocs and undergraduates, both foreign and from the U.S., have helped us in these endeavors. This three-decade-long research effort has taught us humility toward the complexity of nature and patience in the process of trying to understand that complexity.

More information: John Vandermeer et al, Intransitivity as a dynamic assembly engine of competitive communities, *Proceedings of the National Academy of Sciences* (2023). DOI: 10.1073/pnas.2217372120

Provided by University of Michigan