

THE **Current**

March 14, 2011

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Rock-Paper-Scissors Tournaments Explain Ecological Diversity

The mystery of biodiversity -- how thousands of similar species can coexist in a single ecosystem -- might best be understood as the result of a massive rock-paper-scissors tournament, a new study has revealed.

According to classical ecology, when two species compete for the same resource, eventually the more successful species will win out while the other will go extinct. But that rule cannot explain systems such as the Amazon, where thousands of tree species occupy similar ecological niches.

The childhood game of rock-paper-scissors provides one solution to this puzzle, report researchers at UC Santa Barbara and The University of Chicago in *Proceedings of the National Academy of Sciences*. A mathematical model designed around the game's dynamics produced the potential for limitless biodiversity, and suggested some surprising new ecological rules.

"If you have two competitors and one is better, eventually one of the two will be driven extinct," said co-author Stefano Allesina, assistant professor of ecology and evolution at the University of Chicago. "But if you have three or more competitors and you use this rock-paper-scissor model, you can prove that many of these species can co-exist forever."

Co-author Jonathan Levine, professor of ecology, evolution & marine biology at UCSB, and Allesina began their research collaboration when Allesina was a postdoctoral researcher at UCSB's National Center for Ecological Analysis and Synthesis. In this study, they combined the advanced mathematics of game theory, graph theory, and dynamical systems to simulate the outcome when different numbers of species compete for various amounts of "limiting factors" with variable success.

"What we put together shows that when you allow species to compete for multiple resources, and allow different resources to determine which species win, you end up with a complex tournament that allows numerous species to coexist because of the multiple rock-paper-scissors games embedded within," Levine said.

Allesina cited as an example a group of tree species competing for multiple resources such as nitrogen, phosphorus, light, and water. When more limiting factors are added to the model, the amount of biodiversity quickly increases as a "tournament" of rock-paper-scissors matches develops between species, eliminating some weak players but maintaining a stable balance between multiple survivors.

The rock-paper-scissors rules are an example of an "intransitive" competition, where the participants cannot be simply ordered from best to worst. When placed in pairs, winners and losers emerge: Rock beats scissors, paper beats rock, and scissors beat paper. But when all three strategies compete, an impasse is reached where no one element is the undisputed winner.

In nature, this kind of rock-paper-scissors relationship has been observed for three-species groups of bacteria and lizards. But scientists had not yet studied how more complex intransitive relationships with more than three players -- think rock-paper-scissors-dynamite, and beyond -- could model the more complex ecosystems.

"No one had pushed it to the limit and said, instead of three species, what happens if you have 4,000? Nobody knew how," Allesina said. "What we were able to do is build the mathematical framework in which you can find out what will happen with any number of species."

In some models, where each species' advantage in one limiting factor is coupled to a disadvantage on another, a mere two limiting factors is capable of producing maximal biodiversity -- which stabilizes at half the number of species originally put into the model, no matter how large.

"It basically says there's no saturation," Allesina said. "If you have this tradeoff and have two factors, you can have infinite species. With simple rules, you can create remarkable diversity."

The model also produced a strange result: when the limiting factors are uniformly distributed, the total number of species that survive is always an odd number. Adjusting the model's parameters to more closely model the uneven distribution of resources in nature removed this intriguing quirk.

Allesina and Levine tested the realism of their model by successfully reverse-engineering a network of species relationships from field data on populations of tropical forest trees and marine invertebrates. Next, they will test whether the model can successfully predict the population dynamics of an ecosystem. Recently, Allesina was awarded a \$450,000 grant by the James S. McDonnell Foundation to conduct experiments on bacterial populations that test the rock-paper-scissors dynamics in real time.

In the meantime, the rock-paper-scissors model proposes new ideas about the stability of ecosystems -- or the dramatic consequences when only one species in the system is removed.

"The fact that many species co-exist could depend on the rare species, which are more likely to go extinct by themselves. If they are closing the loop, then they really have a key role, because they are the only ones keeping the system from collapsing," Allesina said.

Levine added: "If you're playing rock-paper-scissors and you lose rock, you're going to end up with only scissors in the system. In a more complex system, there's an immediate cascade that extends to a very large number of species."

The paper, "Competitive network theory of species diversity," was published online by the Proceedings of the National Academy of Sciences on March 14, 2011. The research was supported by the James S. McDonnell Foundation and the National Science Foundation.

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† Top photo: A schematic of a "rock-paper-scissors tournament" where species (represented by colored circles) are dominant (represented by arrow direction) over some, but not all, of their competitors.

Credit: Stefano Allesina, University of Chicago

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