A classic model for ecological stability revised, 40 years later

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A famous mathematical formula which shook the world of ecology 40 years ago has been revisited and refined by two University of Chicago researchers in the current issue of *Nature*.

In 1972, physicist Robert May rankled ecologists by publishing a simple model describing the relationship between diversity and stability in a theoretical ecosystem. Though ecologists had long believed that richer, more diverse environments were inherently more resistant to disruption, May's formula argued that more species in fact creates more instability.

But rich ecosystems exist in nature, such as those found in coral reefs or rain forests. For 40 years, ecologists have attempted to expand May's formula to explain how these highly diverse natural systems persist. For the new paper, University of Chicago researchers Stefano Allesina and Si Tang returned to the original equation, and with small mathematical tweaks, reconciled the disagreement between theory and reality.

Adjusting May's formula to incorporate predator-prey or consumer-resource relationships, where one species profits at the expense of another, allows the model to describe an ecosystem where stability is possible even with an infinite number of species.

"Predator-prey relationships are stabilizing. We can fit much larger ecosystems if there's a backbone of predator-prey interactions, and see a lot of species happily co-existing ever after," said Allesina, PhD, assistant professor of Ecology & Evolution at the University of Chicago.

"We kind of solved this one puzzle of how can we see very many species in an ecosystem. But then we open different puzzles."

May's original model, also published by *Nature*, sought to challenge the ecological belief that diverse ecosystems were more resistant to perturbations such as invasive species or abrupt climate change. With his physics training, May set out to create a model of the relationship between diversity and stability with the fewest possible factors, settling upon a model that used only the number of species and the strength of their interactions with each other.

The surprising result of May's model was that large or complex ecosystems were so unstable that their existence was statistically improbable. While that conclusion did not match what ecologists observe in natural systems such as rain forests, which may contain thousands of species in a single tree, the model challenged the simplistic assumption of more diversity leading to more stability.

"May made the beautiful point that nature must adopt some 'devious strategies' to cope with this fact, because if mathematically there is this impossibility of complexity, how come we then observe it in nature?," Allesina said. "It must be that nature uses some sneaky way to violate this rule."

May's article launched the "diversity-stability debate," as ecologists proposed many such "devious strategies" to explain the persistence of rich ecosystems in nature by adding complex qualifiers to his formula. Instead of following this trend, Allesina and Tang went back to the original model and made a small adjustment. They replaced the random species interactions of May's model with three general types of relationships observed between species in nature.

In the "eat-or-be-eaten" world of a predator-prey relationship, one species (the predator) benefits while another species (the prey) suffers a loss of fitness. A competitive relationship between two species can have a negative effect on both, while a relationship of mutualism produces a positive effect for the two species involved.

When each of these interactions is inputted separately into May's formula, the predicted stability for a given number of species changes from his original calculation using a random distribution of species-species interaction. In the predator-prey condition, the stability of the ecosystem is increased such that a large number of species can be supported. In the competition and mutualism systems, the ecosystem is highly unstable and vulnerable to perturbation.

"What we are showing is that of all the types of interactions you can have, only predator-prey can support an infinite number of species," Allesina said. "If you look in nature, there are very obvious consumer-resource relationships everywhere, and maybe this system assembles so easily because these relationships provide a lot of stability."

But just as the revised version of May's formula brings it in line with one natural observation, more counter-intuitive results are created. Many ecologists believe that strong interactions between species, such as when a predator relies upon only one prey species for food, make an ecosystem more vulnerable. However, the revised formula predicts that weak interactions, not strong interactions, are destabilizing to an ecosystem.

Another discrepancy occurs when the model is applied to a realistic food-web structure, rather than the theoretical, random structure used as a default. When a commonly observed natural structure— such as the "cascade" model where each predator eats prey smaller than themselves—is tested with the model, the resulting system is less stable than that produced by a random structure.

But like May's original formula, these disagreements between model and reality offer new opportunities to explore how nature subverts these predictions and produces diverse, stable ecosystems. Many of the "devious strategies" proposed as additions to the original model can now be tested with the revised formula as a reference point.

"I think this is a good step forward, especially because it resuscitates this result that has been so fundamental for theoretical ecology, but no one since has touched it," Allesina said. "Everybody cited it, and kind of disproved it metaphorically, but it's nice to go back to the original formulation and extend it."

More information: The paper, "Stability criteria for complex ecosystems," will be published online February 19th by *Nature* at doi:10.1038/nature10832

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