

Why not both? Rainforest diversity stems from two seemingly irreconcilable processes

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New research reveals how it's possible for so many tree species to survive in so few niches in tropical rainforests

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- Scientists have long been puzzled by the immense diversity of tropical rainforests, but a new study finds that both light and height are key to plant diversity.
- Diversity in the tropics isn't just about light-loving species versus shade-tolerant ones, but also about how tall plants are when they hit maturity.
- Research supports both niche theory and unified neutral theory, but with some twists.

It's crowded in the tropics. Take the plant world: 1,000 tree species can coexist in a small equatorial area of only a quarter kilometer squared, according to one forest ecologist, S. Joseph Wright. That's about as many tree species as in all the temperate forests of the northern hemisphere combined.



Though the habitat is known for being sunny, shade is an integral part of the rainforest, as seen from this Amazonian rainforest canopy. Photo courtesy Rhett Butler.

But the story of how rainforest plant biodiversity came to be – and rainforest biodiversity in general – suffers from critical gaps.

Almost all saplings must spend at least part of their lives in low-light conditions since the extensive rainforest canopy creates shady environments underneath. Forest ecologists know that tropical plants handle the limited light using a resourceful strategy: rather than devoting their energy to growing quickly to reach the light before the others, a great majority of plant species direct a very specific degree of energy into shade-tolerance. This dynamic, found in tropical forests across the world, makes plant diversity even harder to explain. Not only can hundreds of species pack amazingly into small physical spaces, but most also seem to inexplicably crowd into this one main niche space.

Scientists have debated what's potentially going on for decades. Last December, Daniel Falster from Macquarie University, Australia led a PNAS study that pinned down some answers, showing how plant diversity stems from niche competition – except when it doesn't.

"Competitive coexistence occurs when a group of species can all coexist without any of the species driving any of the others extinct, i.e. when each species has its own niche," the study author, Falster told Mongabay. "In our model plants compete for light. The fact that species can coexist means that no species is able to monopolize this resource for itself."

Falster produced a model that shows how competition for light enables the diverse yet stable landscapes we see in all tropical rainforests. The model landscape changes over time. Natural disruptions occasionally rip through it, leaving some patches bare.



Study author Daniel Falster in a patch immediately after a disturbance. Falster's model shows how these patches age into supporting high diversity. Photo courtesy Daniel Falster.

"Disturbance events are common to nearly all forests," Falster said. "These could be cyclones, fires, floods, disease outbreaks, or any other external agent causing a lot of trees to die. When a disturbance hits a small, local area we call this a 'patch.' A forest is made up of many such patches."

Evolution takes off on these bare spaces. Plants compete for light, and at first, the species that do best are those that grow quickly capturing as much sunlight as possible. In their race to the top, early-successional plants neglect putting much energy into leaf development, causing what scientists call low "leaf mass per unit leaf area" or LMA.

"Plants with low LMA have leaves which are cheap to build, the savings they make on leaf construction enable the whole plant to grow faster, when small," Falster said. "However, these cheaply built leaves are weak and therefore short-lived. As such, low LMA leaves need to be replaced often; the cost of this regular turnover makes it difficult to survive in low light where income is scarce."

But one plant's weakness is another's niche. As the forest matures and fast-growing, sun-hogging species block the light, plants that direct energy to building higher LMA start to have an advantage. They don't grow as quickly when they are seedlings, but their higher-quality leaves

equip them for survival in the low-light conditions common in rainforests.

Falster's model corroborated some findings from past studies. In the rainforest only three specific, widely different LMA values are viable. For any species with LMA values in between these three main types, the cost of trading growth for shade-tolerance doesn't pay off, and the species dies out. In other words, along the spectrum of possible amounts of shade-tolerance, there doesn't appear to be much room for diversity in fully developed forests.



Looking into a disrupted patch from the shade. Photo courtesy Daniel Falster.

This is the sticky point in niche theory. If competing species can only coexist because they all use different strategies to get enough light, then how come hundreds of species can huddle together around one place, in just a few niches? What's more, many succession models show that niche development makes room for only one highly shade-tolerant species. But in the real world, the overwhelming majority of rainforest species are those with the highest viable shade-tolerance.

Falster's study resolves the conundrum by revealing a whole new continuum of niches available only to shade-tolerant plants. This second variable is plants' height at maturation (HMAT). When low-HMAT plants reach maturity, they produce more seeds, but don't put much energy into further growth. In species with higher HMAT, mature plants might continue their upwards trajectory towards sunlight, but wait longer to reproduce.

Unlike with LMA, tropical forests do support a variety of niches in the "height at maturation" spectrum. The study calls this "evolutionary emergent near-neutrality." As long as the forest is old enough to host highly shade-tolerant plants, niches all along the HMAT continuum become available, enabling the species richness we see in the real-life tropics. Falster explains that high-LMA species have smaller populations, relaxing competition between each other, and allowing plants with different HMAT strategies to coexist.

Importantly, the "evolutionary emergent near-neutrality" found in Falster's study bridges gaps with the controversial "unified neutral theory" put forth in 2001 by Stephen Hubbell, an ecologist at the University of California, Los Angeles. Unified neutral theory assumes that plants coexist, not because they occupy different niches, but because no one trait gives one species an advantage over another.

Falster says his study "shows there is a role [for] both theories in understanding forest diversity."

Niche theory explains how shade-tolerant plants develop, while evolutionary emergent near-neutrality shows how plants with different HMAT strategies can coexist because they are almost equally fit to survive in the landscape.

"Our model is first and foremost a model of niche differentiation," he said. "At the same time, an outcome of niche differentiation is the fitness equivalence that neutral theory takes as its starting point."

Citations:

Falster, D. S., Brännström, Å., Westoby, M., & Dieckmann, U. (2017). Multitrait successional forest dynamics enable diverse competitive coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, 114(13), E2719–E2728. <https://doi.org/10.1073/pnas.1610206114>

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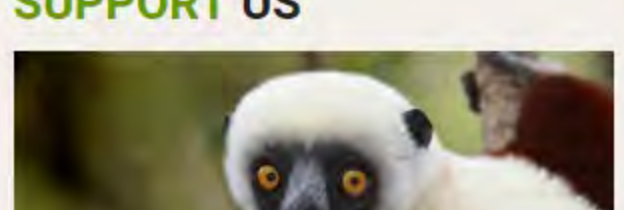
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