The hidden structure of tropical forests

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Humans seem to constantly seek patterns, and their explanations, in nature, even when doing so has no obvious intrinsic value. Many years ago, I walked around in a tropical forest, overwhelmed by the complexity around me. I wondered to what extent there was order, some underlying explanation as to why each plant was where it was, and to what extent the placement of plants was random. Have you ever wondered too – on a trip to a wildlife sanctuary perhaps – what affects the placement of trees and shrubs and herbs of different sizes and shapes? Ecologists who study plant communities have pondered this question for decades. Before you read on, you might want to take a moment to intuit the answer to this seemingly-innocuous question.

Perhaps you guessed that it has something to do with the conditions the plants require for their survival: after all, that's trivially true of all living organisms (take a fish out of water or submerge a land plant into water and they die). But conditions don't change so drastically *within* a few tens of meters of forest… or do they? To answer that question, we first need to know what the conditions are. Fortunately, this has largely been worked out.

Plants need resources: water, light, carbon dioxide, and about a dozen nutrients they largely extract from the soil. They also have optimal preferred ranges for environmental conditions such as the temperature of the air and humidity. Finally, there are things that may be detrimental to plant growth and survival including toxic elements such as aluminium, natural enemies, fire, heavy winds, and so on, that they need to avoid. Being sessile, most plant species tolerate a wide range of these conditions that, considered together, is called the "niche" of a species. Most grasses, for example, require a lot of sunlight (Figure 1). You won't find many grasses in rainforests in the Western Ghats or north-eastern India, because the densely-packed trees don't allow much sunlight to reach the forest floor. Rainforest trees, on the other hand, can handle shade but need a lot of water. They wouldn't survive very long in a savanna where there is far less water and a lot more sunlight. Thus, grasses and rainforest trees have different niches. Savannas may be thought of as "home sites" for grasses – a place where they do better than other plant species – and rainforests as home sites for rainforest trees. If the niches of a set of species aren't identical in every way, it means the species potentially have home sites where they "win" (do better than all other species). However, if the niches of the species are identical

Figure 1: Open forest with ground flora

in every way, it means all species do not simultaneously have home sites where they win. In such a case, the species that is even slightly more efficient than others in utilizing resources or escaping shared enemies or tolerating adverse conditions will eventually displace the other species entirely in a process known as competitive exclusion.

Now, it had previously speculated that competitive exclusion might exist, but when it was first shown mathematically around the late 1920s, plant ecologists began to wonder what allowed hundreds of plant species to coexist in tropical forests. As you may know, tropical forests are species-rich, having, for instance, dozens or hundreds of different tree species in a single hectare.

Over many decades of research, plant ecologists have found that within tropical forests, there is a lot of site-to-site variation in the conditions of relevance to plants. For instance, there may be sites that are wetter – such as the bottom of a valley, where rainwater tends to flow and accumulate – and ones that are drier – such as on the top of a hill. Similarly, there are sites that differ in soil nutrient levels. Then there are open, sunlit sites and closed, shaded ones. As you might imagine, the latter kind of site variation can be ephemeral (a large tree might die and fall down, leaving behind a sunlit gap that remains open only until one or more younger trees grow up and fill that gap). So, there may be one species that wins in sites with drier soils and direct sunlight, while the wins in sites with wetter soils and shade. So long as such site variations exist in a larger general area, multiple species can coexist – each winning in their respective home sites. Thus, came about "niche theory", which postulated that it must be that plant species in a forest have different niches – it *must* be so, because they coexist, don't they?[1]

Because almost all land plants require more or less the same, small set of resources we listed above, variation in resources itself can only explain the coexistence of a few dozen species at most, not hundreds. However, plants have a number of other ways in which to differ from each other in their niches. For instance, species could differ in abilities to avoid natural enemies.

[1] It's a different matter that it is rarely known *how long* the plant species in any given forest have been coexisting.

Just as one plant species may be most efficient in utilizing soil phosphorous, another may be most efficient in avoiding a particular species of insect herbivore or disease-causing fungus.

Niche theory provides a potential explanation as to why each plant is where it is – it is because there is variation in niche conditions, subtle or drastic, perhaps invisible to us – like high soil aluminium that one species tolerate better than all others, or visible – like a steep slope that only one species does best on. So, plant species can "specialize" to different conditions: resources like low water or high light or high soil phosphorous, habitat conditions like substrate type, natural enemies like a particular species of butterfly larvae… well, the list could go on. We certainly seem to have a number of potential ways in which species can differ from each other in their specializations so they are able to coexist as niche theory predicts. But the difficult part is figuring out which of these potential ways is actually important at any given place. For example, soil moisture differences may be irrelevant to the species present at the site, perhaps because there simply isn't enough variation in soil moisture to support both wet- and dry- site specialists. Or perhaps there *is* enough variation, but for some reason, all species present prefer the drier condition. It's hard to overstate how challenging figuring out what the species preferences are and the role those preferences play in preventing competitive exclusion! It involves measuring various niche conditions across space and across time and trying to figure out their relative influence on the survival and growth of individuals of each species. Finally, in order to be consistent with niche theory, we must also show that the niche requirement of every species is distinct. Not surprisingly, we aren't close to proving that any given forest is partitioned between species in a way that allows them to coexist. Nevertheless, niche theory remains the most popular theoretical explanation of observed patterns in forests.

Ecologists have toyed with another potential explanation as to why each plant is where it is: randomness or chance, by which it is meant that if we replayed the reel of time, another plant belonging to another species could just as easily have been in the exact same place. There is no determinism. By contrast, a niche-structured forest has a large degree of determinism. Yes, there is still the element of chance – a specialist may never reach its home site, allowing the non-specialist to win that site by "default." A lightning strike may kill a specialist, opening up a site for a non-specialist to grow in. And yet, on average, you will tend to see the same broad order reappear, time and again, as the reel of time is replayed. It's a bit like the difference between tides and waves. Tides, which are caused by the gravitational pull of the moon and sun, are predictable, but individual waves, which are caused by the wind, are not. A niche-structured forest is like a seashore whose tidal fluctuations are large relative to waves, so there is a large degree of predictability of what the shoreline will look like at any given time. A neutral forest is like a seashore whose waves are very large relative to tidal fluctuations, so it is very hard to predict what the shoreline will look like at any given time. So, to what extent is a forest niche structured and to what extent is it random? This is a major open question in plant ecology today.

About two decades ago, some ecologists asked what a plant community might look like if the slider was moved completely to the randomness (the "wave") end. In other words, what if the niches of all species were identical? Think about this for a moment.

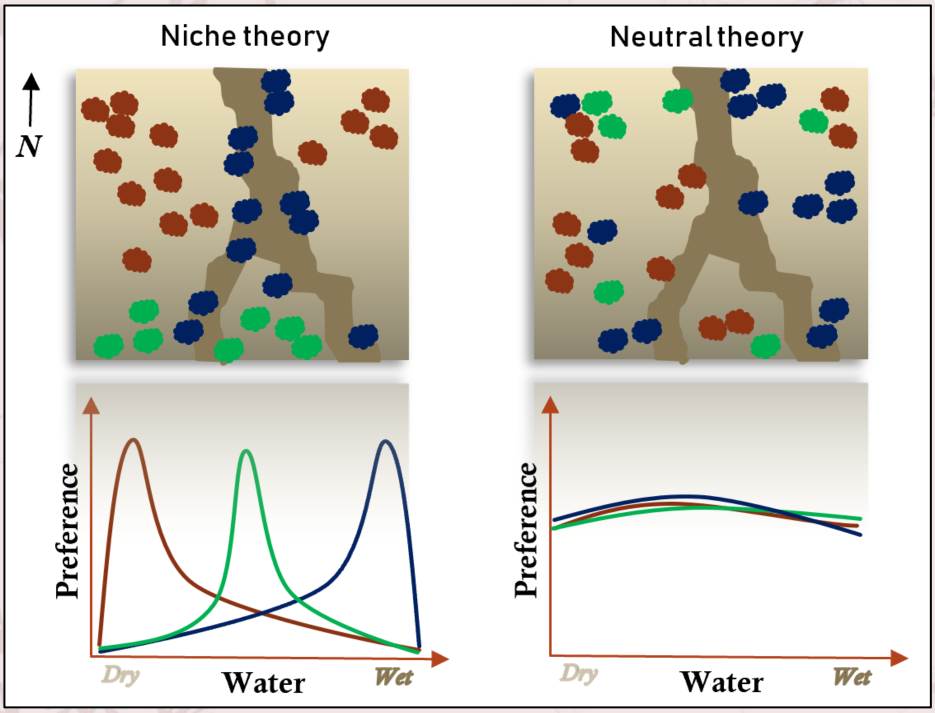

Figure 2. Illustration of three plant species in a niche-structured forest versus a neutral forest. Soil moisture varies across in this patch of forest, with the driest sites up north (shown in light brown), wetter sites at down south, and wettest sites alongside a stream that flows through the forest (shown in dark brown). In a niche-structured forest, the species in brown prefers driest sites, the one in blue wettest sites, and the one in green sites of intermediate wetness. Thus, each of the three species has a set of home sites where it grows and survives better than other species. In a neutral forest, the three species do not have a preference for any soil moisture condition. Thus, any species is equally likely to be found anywhere in the forest. In both cases, species tend to form clusters because seeds from parent trees tend to fall close to them.

If you've been paying attention, you would answer it would lead to competitive exclusion of all other species by the one species that was slightly more efficient at utilizing resources, or escaping enemies, etc. But these ecologists made one more assumption – that the efficiencies of all species are equal as well. The answer, they showed, was that the populations would fluctuate randomly, every species would be equally likely to be at any given site, and species would locally go extinct if their populations became too small by chance. However, the process of local extinction would be so low for most reasonably-sized plant communities that it would be offset by the periodic influx of new species from elsewhere, thereby maintaining the same number of species, even though their identities would keep changing. This is known as neutral theory (Figure 2). Now, everyone – including the proponents of neutral theory – realizes that both "identical niches" and "identical efficiencies" are unrealistic simplifications of the real world. In a real rainforest, for instance, you often find species, called "pioneers" that grow rather fast provided there's ample sunlight. They are called pioneers because they rapidly colonize open areas. However, pioneers do poorly in the absence of sunlight. Others species, called "shade tolerants," tolerate shade (as their name implies), but grow relatively slowly even in open areas. Thus, the niches of pioneers and shade tolerants is distinct, as are their efficiencies in utilizing sunlight. Similarly, some species seem to do fine even when there's a severe drought, while others dry out and die. So, we know that some amount of species-to-species variation exists both in niches and in efficiencies in practically all forests. But the surprising outcome of the mathematics of neutral theory was that many aspects of these real-world forests were accurately predicted even with such grossly simplifying assumptions. Have you heard of the phrase "assume a spherical cow?" It's a humorous metaphor alluding to the gross simplifications theoretical physicists make about real-world phenomena in order to make their calculations easier – simplifications that sometimes make the results of the calculations difficult to apply to the real world. Neutralists, it would seem, had pulled off a "spherical cow" simplification on a tropical forest – successfully. Neutralists had challenged the preeminence of niche theory in a way that shook its foundations.

So, what do most ecologists and other thinkers agree upon about the hidden structure of forests today? Everyone agrees that some important niche differences do exist, but also that there is a large element of randomness that determines the structure of a forest. Most would agree that topography, soil and sunlight play a very important role in structuring forests. For example, if there is a valley between two steep hills, you will quite likely see different species on the hilltops and in the valley. Similarly, you will also quite likely see different species in open, sunlit gaps compared to closed, shaded locations. Most ecologists would agree most plant species form clusters in forests because most seeds don't travel very far from parent plants. These clusters form despite the fact that seedlings, having germinated together from seeds dropped by the parent plant, compete strongly with each other, resulting in death of large fraction of a cohort. They would agree that seeds dropped near a plant attract species-specific insect herbivores and disease-causing fungi from nearby parent plants, which is why parent plants try to send their seeds as far away from themselves as possible (they do so by encasing their seeds in an edible package – fruit – that animals carry along with them as they eat or digest the package, or by hitchhiking on animals, the wind, water, and so on).

My own reading of the literature suggests that most tropical forests are unlikely to be either completely niche structured or completely neutral. Niche differences frequently exist, but not in a structured way such that niches as neatly partitioned between all species. Instead, plant niches are somewhat haphazard because every species has a unique evolutionary history independent of the other species present in the forest. As a result, two plant species might have identical niches (by chance), while two others could have distinct niches (also by chance). In other words, every plant species is, for the most part, doing its own thing, independently of other species in the forest. As you might guess, coexistence is not guaranteed, and instead, the composition of the forest keeps continually changing at long timescales.

These are fascinating insights, but they are hard won – having taken decades of back-breaking work by hundreds of ecologists and field workers in forests around the world. Think about these the next time you drive by a forest!

Further reading

1. J Polechova´ and D Storch. Ecological Niche. In Sven Erik Jørgensen and Brian D. Fath (Editor-in-Chief), Evolutionary Ecology. Vol. [2] of Encyclopedia of Ecology, 5 vols. pp. [1088-1097] Oxford: Elsevier (https://www.academia.edu/26363906/Ecological_niche)

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