

 COMMENTARY

Functional megadiversity

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Western Amazonian and Andean forests have Earth's highest biodiversity and are globally important for ecosystem services and climate regulation. Straddling the planet's longest ecological gradients, they have captured the imagination of scientists since von Humboldt (1). However, ecological studies and theory have incorporated that spectacular biological variation in only the most rudimentary ways, or not at all. It is widely understood that there are many traits that are important to plant performance, consequential not only for things like carbon gain and loss, but also timing of life histories, evolutionary patterns, and interactions with symbionts. In PNAS, Asner et al. (2) focus on one of the best known suites of traits, those comprising the biochemical functions of canopy leaves, on a breathtaking number of species drawn from nearly all major angiosperm clades. The study crosses ecological gradients spanning lowland Amazonian soil fertilities from poor white sands to rich clays, and an altitudinal gradient stretching 3.5 km from the hot lowlands to the frost and ice near the limit of tree growth in the Andes. The authors' findings show that there is immense variability in functional traits found in the canopies of tropical forests: indeed, as much variability in the forests of western South America as was previously known for all tropical forests on the planet.

Understanding how tropical tree communities are put together—what determines their diversities and the relative abundances of their members—is a longstanding and contentious issue in ecology. Given the importance of tropical forests in terms of carbon and hydrological cycles, climate regulation, and a vast array of ecosystem services, the question becomes much more acute as we proceed through the Anthropocene. Human-caused changes to tropical forests can alter not only their biodiversity, but also the basic provisioning, regulating, supporting, and cultural services they provide to humanity.

However, for most of the history of their study, tropical forest community members were treated as monolithic; a tree was a tree, even though they are organisms with radically different evolutionary histories, being drawn from every major clade of flowering plants. A rain forest tree may be much more closely

related to a temperate zone herb than to the other trees growing near it. Ecologists were forced to ever more esoteric theories of coexistence, diversity, and ecosystem function, relying on communities being assembled randomly from source pools of different sizes, or with functional traits being reduced to average values of demographic performance.

That is, until now. Big Science and the -omics revolution is changing the study of tropical forests. Measurements that once required heroic effort to make for a few species can now be done for entire assemblages. The revolution is giving a detailed understanding of evolutionary relationships among organisms and the ways that they make their living. Trees have gone from being anonymous stems in a vast woods characterized only by size, growth, and the rate at which stems appear or disappear, to organisms where we characterize their traits and try to understand how they relate to environmental gradients and the myriad organisms with which they interact. Big Science is vastly increasing the data available, and promises to change and give mechanism to the patterns we see in tropical forests.

Big Science Meets Megadiversity

There is no bigger science in terms of understanding how tropical forests scale from individuals to landscapes than that by Asner et al. (2). Their study looks at the functional traits of forest canopies in the western Amazon and Andes, examining foliage traits and biochemistry of 2,420 canopy tree species at 19 sites in Earth's highest diversity tropical forests. The traits measured are similarly extraordinary in scope, ranging from elemental analyses to the major components and classes of photosynthetic and antiherbivore compounds.

Why study forest canopies? Leaves are where the rubber meets the road for trees; they are where light is captured, water is traded for carbon dioxide, and photosynthesis is carried out. Leaves couple the processes of nutrients coming from soils and carbohydrate exports to other areas of the plant for biosynthesis. Moreover, the supplies of the resources required and their rates of synthesis—and hence the rate at which leaves can be replaced and plants can grow—vary with soils and other environmental conditions, and the leaves have

to be defended against herbivores and pathogens. This creates a complex set of trade-offs between investment in a leaf, its lifetime return, and risk of loss that is encapsulated in what is broadly called the “leaf economic spectrum” (3). The leaf economic spectrum is not only important in understanding the ways that leaves relate to the environment, but is also incorporated into models that couple ecosystem processes to climate and atmospheric changes (4). Furthermore, trees in the forest canopy are not only diverse, but also disproportionately important compared with smaller stems. Economic inequality is familiar to us, but the forest also has its 1%. The largest canopy trees are only 1–2% of individuals, but make up 30–50% of forest biomass, with all canopy trees, generally those greater in diameter than the width of an iPad, totaling ~90% of forest biomass (5). Light capture, carbon cycling, and forest-atmosphere exchange are also all highly skewed toward trees exposed to the sun.

Asner et al. (2) found that canopy functional traits varied across elevation and soils gradients in predictable ways. Moving from lowland communities to the Andean highlands, leaves got thicker, held more soluble carbon, and had changes in isotopic fractionation of C consistent with CO₂ limitation compared with the gradient mean. As leaves were getting thicker they had lower concentrations of most nutrients and structural compounds. Although the patterns are clear, causal interpretation is difficult. Some of this is evidence of the trend in pachyphyllly at high elevations thought to maximize CO₂ uptake relative to water loss (6), and other interpretations vary depending on whether the quantity is expressed on a per area or per mass basis. The region of greatest cloud inundation in the Andes, running from cloud base at 1,700 m to 3,000 m, is unsampled in the current effort, but in many cases the data show enticing evidence of a change point that may correspond to a functional ecotone in these elevations.

Even more striking than the trends in leaf traits is the scale of variability, and that the variability is housed among taxa rather than

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within taxa. Asner et al. (2) found enormous variability in leaf traits in tropical forests, approaching that known for global and terrestrial vegetation (7). Individual biochemical traits spanned over two orders-of-magnitude in some cases. This result is surprising, although tempered when one considers that the tropical forests have members from every major clade of the Angiosperm phylogeny, plus gymnosperms in the Podocarpaceae, and that the gradient covered is as long as one can get terrestrially, ranging over 3.5 km in elevation from Amazonian lowlands to the upper limit of forests in the Andes. The among-community variability in the lowlands for most traits encompasses all of the variability found along the entire gradient, demonstrating that lowland forests harbor exceptional and varied functional diversity, and in some senses are as different from each other as they are from forests 3 km higher in elevation. There are many lowland sites and few in the mountains, begging the question whether Andean forests are similarly variable among different substrates, or just poorly explored.

Biodiversity Matters

However, the major result of Asner et al.'s (2) work is that the high phylogenetic diversity of western Amazonian forests (and by extension very likely all tropical forests) is interconnected with high functional diversity. Most of the functional variation in communities was a result of among-species differences, with within-species variability being small. The variation was also taxonomically (and hence phylogenetically) conserved, with variability among lineages accruing at all taxonomic levels. More than that, differences in species composition, not individual species plasticity, explains community and ecosystem-level changes in canopy traits across the major gradients, and that the enormous variability in leaf chemical traits is not simply a characteristic of sites. Biodiversity isn't just a curiosity in tropical forests, it is functionally important, and central to understanding ecosystem services.

The study (2) also casts light on what may be a major flaw in how we predict climate change effects on ecosystem properties of high-diversity systems. Trends in ecosystem function across environmental gradients are used to predict responses to climate change in a time for space substitution. However, what has been shown in taxonomically restricted studies (8), and what Asner et al. (2) dramatically demonstrate, is that species-level responses remain stable across gradients or show trends different from the ecosystems they comprise. Taxonomic turnover drives changes in ecosystem function. We live in

a world of gradients, and even vast areas of what we study as "lowland rain forest" are realizations of ever-changing environmental gradients in time and species responses to them. Explanations for diversity and function that ignore this are bound to be wrong. At any time some members of a community will be in the "center" of their respective environmental distributions. However, many will be away from their environmental optima, creating a portfolio of species at different distances from their optima. Does this portfolio effect buffer ecosystem response to climate change, as species with more appropriate optima will simply increase in abundance as climate shifts? Or will there be large lags in ecosystem responses as species must migrate and reestablish for ecosystem properties to change? Given the climate change predicted for tropical forests by 2100, particularly Andean forests (9), we'll find out within the century.

Establishing that biodiversity is tied to function raises interesting questions about the very nature of rain forests, and affords tests of longstanding questions about how changes in biodiversity affect the nature of functional diversity, not just the variability. Plant diversity increases threefold from the latitudinal limit of rain forest to the equator in Amazonia, even though animal diversity within the forest is nearly stable (10). How does canopy functional diversity change along this gradient? More than that, how is the trait space filled? Is there a basic suite of functional traits that comprise what we recognize as rain forest that is present even at low diversity, with increasing diversity "filling in" that volume in largely redundant ways? Or does increasing diversity explore an increasingly large volume of trait space, such that biological diversity begets functional diversity, even within forests in the same geographic area?

Although Asner et al. (2) show a clear set of patterns and map out the range of variation in canopy function, the causes are less clear. A plant ecophysicist might relate the community shifts to photosynthetic traits, or the

exigencies of metabolic pathways required for manufacturing antiherbivore compounds. However, tree life histories are long and complex, and small changes in trade-offs between growth and survival—and much less studied, the production of flowers and fruits—can also lead to success and failure of species along environmental gradients. Tropical forests harbor complex interactions, positive and negative, among trees and species at higher trophic levels. How many of these trends are enforced by the species interactions that make up the functioning forest remain to be seen, and reconciling the myriad theories of species coexistence and community assembly from a functional perspective is a new and important frontier of research.

Why has this not been done before? Much of the work in Amazonian and Andean forests through the end of the 20th century was limited by even putting names on the more common species. In better-studied Amazonia there are hypothesized to be 16,000 species of trees, of which we have names for at most 10,000 species, and only 5,000 of them have been found in inventories of networks of >1,000 ha of plots (11). This limitation, along with the costs of field work and laboratory analysis, and difficulties in sequencing large number of taxa, directed questions of functional traits and evolutionary relationships to smaller groups of relatively well-known species in easily accessible areas. It is only now that field ecology in the remote corners of the tropics is being coupled to scientists working on the frozen forests of specimens in the laboratory.

However, maybe the most important part of Asner et al.'s study (2) isn't what it found, but what it shows us we can do: understand the longstanding patterns in tropical forests based on mechanisms, and shift from finding ways to simply deal with the immense diversity of tropical forests, embracing a functional understanding of the causes and effects of high biodiversity—functional megadiversity—as the next big challenge.

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