Smithsonian Tropical Research Institute
Instituto Smithsonian de Investigaciones Tropicales

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Contact Helene Muller-Landau, hmuller@umn.edu

Diverse tropical forests defy metabolic ecology models
The complex patterns of tropical forest structure demand more complex explanations

Summary:
Better models of tropical forest dynamics are urgently needed to improve global change predictions. In hopes of modeling growth, mortality and size distributions of tropical trees, Helene Muller-Landau, University of Minnesota and colleagues from the Smithsonian's Center for Tropical Forest Science (CTFS) tested predictions based on the theory of metabolic ecology with data collected from tropical forests worldwide. The results— no good fit and improved alternative models-- are published in two articles in Blackwell's Ecology Letters.

As global change accelerates, quantifying the role of forests in the carbon cycle becomes ever more urgent. Modelers seek simple predictors of forest biomass and carbon flux. Over the last decade, the theory of metabolic ecology generated testable explanations, derived from physical and biochemical principles, for a wide range of ecological patterns. However, in two Ecology Letters articles, Helene Muller-Landau and colleagues show that tree growth, mortality and abundance in fourteen tropical forests deviate substantially from metabolic ecology predictions, especially for large trees. Instead, observed variation within and among forests supports alternative models presented by the CTFS team.

Are tropical forest structure and dynamics too complex for universal explanations?
"When you walk through different tropical forests, or graph data from different forests, there are certain features that, at first glance, look similar everywhere – the presence of some very large trees, or the general shape of the tree size distribution curve," explains first author, Helene Muller-Landau from the University of Minnesota. "So you start to think that there might be some general explanations. But the closer you look, the more differences you find – differences that can't be captured or even decently approximated by any single picture or formula."

Tropical forests give modelers a run for their money. Trees range from spindly understory shrubs to enormous buttress-rooted rainforest giants festooned with vines and peppered with orchids, ferns and bromeliads. Tropical trees depend on animals for pollination and seed dispersal and are constantly assaulted by insects, fungi, maelstrom and machete. Furthermore, soils, rainfall, the frequencies of hurricanes and fires, and assemblages of animals and plants in tropical forests all vary widely from one forest to another.

Prospecting in a gold mine of data
Twenty-five years ago a pair of dueling tropical forest ecologists (Robin Foster, now at the Chicago Field Museum and Steve Hubbell at the University of Georgia and the Smithsonian Tropical Research Institute, STRI) decided that the way to understanding was to measure and map every single tree in an area of lowland tropical forest on Panama's Barro Colorado Island. Tree abundance, distribution, growth and mortality data from repeated five-year censuses of this site proved so useful to ecologists and foresters alike that seventeen other tropical forests around the world adopted the same methodology. Now the

Smithsonian Institution
Smithsonian Tropical Research Institute
Apartado 2072
Balboa, Ancón
República de Panamá
Tel. 507.212.8216
FAX 507.212.8148
Email: kingb@tivoli.si.edu

consortium of universities and research organizations managing forest plots in South America, Africa, India and Asia: the Center for Tropical Forest Science (CTFS), is headquartered in Panama at STRI. And the race is on to find the basic principles governing tropical forest community composition and structure based on data from three million trees.

Metabolic ecology

At a U.S. National Science Foundation supported workshop, CTFS participants examined data from across the forest plot system and discussed possible multi-site comparisons. “A couple of the key papers on metabolic ecology had just come out and were generating a lot of excitement – as well as considerable skepticism. And we thought, hey, we have an unprecedented opportunity to test these predictions, and to see whether these patterns are really similar across all these forests,” remembers Muller-Landau. “If the proposed general rules truly applied, they would be tremendously useful - for example, they would help us predict how much above ground carbon is stored in tropical forests. There are some general similarities among sites in the tree size distributions, so it seemed plausible that there might be a general underlying explanation.”

“Specifically, metabolic energy proposes a rule that total tree abundances scale as the -2 power of diameter, and we were hopeful that it would apply. But we tested that prediction on data from 14 sites around the world --over 2 million trees--and it just did not hold up anywhere,” continues Muller-Landau.

The CTFS team subsequently tested other metabolic ecology-based predictions relating tree size to growth and mortality against data from 10 CTFS forests, and found that those were not supported either.

“The predictions of metabolic ecology were wrong in fundamental ways, and no one had noticed before because few datasets spanned the range from saplings to large trees. Most impressive was the consistency in the big discrepancies between observation and prediction, even in very different forests,” articulates coauthor Richard Condit, STRI Staff Scientist, “For instance, diameter distribution always deviated by having far fewer large trees than the -2 slope predicts.”

Shedding light on the process

The CTFS team did not stop at merely demonstrating that metabolic ecology failed to explain tropical forest structure – they examined what alternative models might do better. Organisms live within the limits of their environment. Maybe by modifying the metabolic ecology model to include light as a limiting resource that varies with tree size, the predictions could be improved. The necessary light data were available from only one site, and, in that case, observed growth and mortality patterns were consistent with predictions. Similarly, tree size distributions corresponded more closely to a model based on demographic equilibrium theory that incorporated differences in growth and mortality among sites.

What next?

The results of these two studies clearly demonstrate that there are both qualitative similarities and significant quantitative differences in forest structure among tropical sites. This complexity defies simple characterization – its explanation requires consideration of the diversity of environmental conditions and species traits in tropical forests, and complex feedbacks and interactions among species and resources. Muller-Landau and Condit are currently working on mechanistic models that attempt to better capture

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Smithsonian Tropical Research Institute
Apartado 2072
Balboa, Ancón
República de Panamá
Tel. 507.212.8216
FAX 507.212.8148
Email: kingb@tivoli.si.edu

these complexities, and thereby attain a better understanding of what factors drive tropical forest structure and dynamics. Achieving such an understanding is particularly critical today, as tropical forests are threatened by global anthropogenic change, with still unknown implications for the integrity of their tremendous carbon stores.

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The Smithsonian Tropical Research Institute (STRI), a unit of the Smithsonian Institution, headquartered in Panama City, Panama, furthers our understanding of tropical nature and its importance to human welfare, trains students to conduct research in the tropics and promotes conservation by increasing public awareness of the beauty and importance of tropical ecosystems.

Refs.

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Photo captions:

Ziegler1317.jpg Tropical forest tree growth, distribution and mortality may be difficult to model. Photo: Christian Ziegler, STRI Archives.
Ziegler1469.jpg Liza Comita measures tree seedling stem diameter. Photo: Christian Ziegler, STRI Archives.
Salomon Aguilar.jpg Salomon Aguilar measures tree diameter. Photo: Christian Ziegler, STRI Archives.
Ctfsplot.jpg Spatial distribution for three of the roughly 300 tree species present in the 50 hectare forest dynamics plots on Barro Colorado Island in Panama.

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Apartado 2072
Balboa, Ancón
República de Panamá
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