

# Multiple dimensions of resource limitation in tropical forests

Alan R. Townsend<sup>a,1</sup> and Gregory P. Asner<sup>b</sup>

<sup>a</sup>Department of Ecology and Evolutionary Biology, Environmental Studies Program and Institute of Arctic and Alpine Research, University of Colorado, Boulder, CO 80309; and <sup>b</sup>Department of Global Ecology, Carnegie Institution for Science, Stanford, CA 94305

The study of environmental resource constraints on plant life was born from humanity's quest for food security (1). Along with breakthroughs in plant breeding, identifying and then alleviating water and nutrient limitations to crop growth allowed a 20<sup>th</sup> century explosion in agricultural production (2). Yet, successes in both agriculture and industry have come at a price: massive transformations of biogeochemical cycles, which in turn alter climate and nutrient availability throughout the biosphere (3). How will Earth's ecosystems respond? In part, the answers depend on an improved understanding of resource limitation in natural communities. In a recent issue of *PNAS*, Condit et al. (4) report their progress in one of the most challenging systems on Earth: tropical forests.

Tropical forests do not give up these answers easily. In Condit et al.'s (4) Panamanian study region, hundreds of tree species can be found in a single hectare, as is the case across much of the tropics. Species rarity is the norm, creating vast and unexplored potential for varied biotic responses to resource availability (Fig. 1). Although the general importance of climate and soil fertility to sorting out tropical forest community structure is well recognized (5–7), unraveling specific connections between species distributions and environmental variables has remained notoriously difficult. Condit et al. (4) combine a rich, long-term dataset with a unique analytical approach to overcome challenges of species rarity, ultimately offering fresh insights into who lives where, and why.

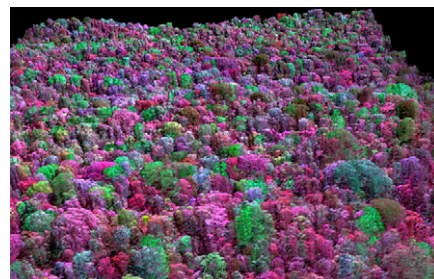
The study takes advantage of strong gradients in both rainfall and soil nutrient availability. As expected, drought wields a heavy hand over species distributions, but a nearly equal role for soil phosphorus was more of a surprise. In multiple cases, abundance patterns for trees previously assumed to be structured by seasonal drought were better predicted by soil phosphorus. Despite a longstanding belief that phosphorus

limitation is widespread across lowland tropical forests (8), the nature of such evidence typically focuses on growth response. Here, Condit et al. (4) show a different dimension of phosphorus limitation, one that is expressed over much longer timescales of plant community assembly.

The Panamanian results not only help clarify how these and other forests are structured, and thus how they may respond to environmental change, they evoke a seminal paper in ecosystem ecology. In 1986, Chapin et al. (1) illustrated the potential complexity of resource limitation in natural plant communities. The most limiting resource may not be the same for every species. One resource might constrain growth, another decomposition, and yet another reproduction. A shift in resource availability may affect responses one way today, and then reorder the entire community membership down the road. In other words, apply an agricultural lens tuned mainly for growth to a diverse natural ecosystem and here be dragons.

Perhaps nowhere are those dragons more daunting and varied than in tropical forests, where the biological diversity contributes to an equally impressive biogeochemical diversity (9). In the same region studied by Condit et al. (4), at least four different nutrients appear to regulate aspects of ecosystem function, all within the same patch of forest (10, 11). Right next door, a wetter swath of Costa Rican forests shares some patterns of nutrient limitation with those in central Panama, but others are notably different (12). Both of these study regions share broadly similar biota and soil types. However, in a slap to ecosystem theories forged largely in colder regions, soil nutrient concentrations are little help in predicting concentrations of those same nutrients in forest canopies, both here and across the tropics. Instead, most of the variance is taxonomic (Fig. 1) (13–14).

That link to evolutionary history is supported by Condit et al.'s (4) results, and



**Fig. 1.** Tropical forest canopies harbor great chemical variation organized by the life-history and physiological requirements of coexisting species. This 3D chemical map of a tropical forest canopy in central Panama was acquired and processed by the Carnegie Airborne Observatory (<http://cao.ciw.edu>). Diverse colors quantitatively demonstrate the existence of a kaleidoscope of growth and defense compounds in the foliage of trees and lianas, with brighter colors indicating greater investment in nutrients and light-capturing pigments, and darker colors showing preferential use of phenolics and other defense compounds.

highlights a major unmet challenge. Tropical forests exchange vast quantities of carbon, nitrogen, water, and energy with the atmosphere every year, making them a veritable engine of our climate system (15). Those material and energy exchanges are, in turn, regulated by canopy chemistry (16). Across a host of key processes that range from biogeochemical cycling to trophic interactions, one must know the chemistry of forest canopies to predict their function. Herein lies the challenge: if that chemistry cannot be estimated via more readily scalable metrics, such as soil type and climate, predictive models of tropical forest function become far more difficult.

Yet, those models are essential. Recent attempts to incorporate nutrient limitation into Earth system models of the coupled carbon and climate system (e.g., ref. 17) have revealed two things. First, representation of nutrient constraints is critical, and second, the tropics are the yet untold story. A recent analysis by Bonan and Levis (17) illustrates these points. By incorporating a simple

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<sup>1</sup>To whom correspondence should be addressed. E-mail: alan.townsend@colorado.edu.

routine for nitrogen limitation into the National Center for Atmospheric Research Community Land Model, the authors simulated more realistic estimates of biospheric constraints to CO<sub>2</sub> storage. However, the difference between models with and without nitrogen limitation was almost entirely because of tropical forests, in which nitrogen limitation is thought to be relatively rare (18).

The tropics dominate the response in Bonan and Levis (17) because of the sheer volume of CO<sub>2</sub> they cycle each year, but did the authors get a better answer for the wrong reasons? Nutrient limitation of tropical CO<sub>2</sub> exchange is likely to vary considerably in time and space, regulated by a suite of elements (19). If such limitation dynamics are strongly mediated by evolutionarily committed life history strategies that determine species abundance and canopy chemistry—as the Condit et al. (4) and other results (13, 14) suggest—then large-scale predictions of nutrient limitation and their consequences represent a grand challenge indeed.

How to move forward? Increasingly, data from the tropics suggest that accurate scaling relationships demand careful integration of the exceptional resource heterogeneity in tropical forests at the local scale (9, 13). That heterogeneity is not just spatial (e.g., differences among tree species), it's vertical. Competition for light combined with diverse and highly productive forests leads to notable variation in tropical forest form and function between the top of the canopy and the ground (6). In practice, all this variation—vertical and horizontal—means one cannot simply measure typical ecosystem metrics, such as foliar chemistry, in a few trees at a few positions in the forest and hope to produce accurate scaling relationships. Instead, some of the most remote and logistically challenging ecosystems on Earth also demand some of the highest data density.

It's a daunting reality, but one that can be addressed by combining a few exceptional long-term field efforts—such as the data used by Condit et al. (4)—with emerging new

technologies in airborne remote sensing (Fig. 1). Airborne platforms that include both hyperspectral imaging and laser-scanning systems (20) are capable of measuring the structure, light environment, and canopy

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chemistry of tropical forests with extraordinary fidelity at the local scale, and yet can extend such measurements across hundreds of kilometers (20). By targeting such measurements across key axes of variation (climate, landform, soil type, community shifts, and so forth), one can use the remotely sensed data in a classic “transect” sense, but have confidence that such transects are inte-

grating local-scale variation. In turn, linking such measurements with long-term datasets, such as those in Panama and elsewhere, lends a critical temporal perspective to a wealth of new spatial information.

In the end, it's all about having sufficient data to tease apart the intricate workings of an extraordinary biome. Condit et al.'s (4) innovative analytical approach depended upon a large and detailed dataset, highlighting the fact that resource limitation in tropical forests is a complex problem with multiple spatial and temporal dimensions. Happily, the authors also show that progress in understanding such complexity can be achieved.

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- 1 Chapin FS III, Vitousek PM, Van Cleve K (1986) The nature of nutrient limitation in plant communities. *Am Nat* 127:48–58.
- 2 Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S (2002) Agricultural sustainability and intensive production practices. *Nature* 418(6898):671–677.
- 3 Finzi AC, et al. (2010) Alteration of coupled biogeochemical cycles in response to global change in the terrestrial biosphere. *Front Ecol Environ* 9(1):61–67.
- 4 Condit R, Engelbrecht BMJ, Pino D, Pérez R, Turner BL (2013) Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proc Natl Acad Sci USA* 110:5064–5068.
- 5 ter Steege H, et al. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443(7110):444–447.
- 6 Wright SJ (2002) Plant diversity in tropical forests: A review of mechanisms of species coexistence. *Oecologia* 130:1–14.
- 7 Quesada C, et al. (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* 9:2203–2246.
- 8 Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65:285–298.
- 9 Townsend AR, Asner GP, Cleveland CC (2008) The biogeochemical heterogeneity of tropical forests. *Trends Ecol Evol* 23(8):424–431.
- 10 Kaspari M, et al. (2008) Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecol Lett* 11(1):35–43.
- 11 Wright SJ, et al. (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology* 92(8):1616–1625.
- 12 Cleveland CC, Townsend AR (2006) Nitrogen and phosphorus additions cause substantial losses of soil carbon from a lowland tropical rainforest. *Proc Natl Acad Sci USA* 103(27):10316–10321.
- 13 Fyllas N, et al. (2009) Basin-wide variations in foliar properties of Amazonian forest: Phylogeny, soils and climate. *Biogeosciences* 6:2677–2708.
- 14 Asner GP, Martin RE (2011) Canopy phylogenetic, chemical and spectral assembly in a lowland Amazonian forest. *New Phytol* 189(4):999–1012.
- 15 Lewis SL, Malhi Y, Phillips OL (2004) Fingerprinting the impacts of global change on tropical forests. *Philos Trans R Soc Lond B Biol Sci* 359(1443):437–462.
- 16 McGroddy ME, Daufresne T, Hedin LO (2004) Scaling of C:N:P stoichiometry in forests worldwide: Implications of terrestrial Redfield-type ratios. *Ecology* 85:2390–2401.
- 17 Bonan GB, Levis S (2010) Quantifying carbon-nitrogen feedbacks in the Community Land Model (CLM4). *Geophys Res Lett* 37:L07401.
- 18 Hedin LO, Brookshire ENJ, Menge DNL, Barron AR (2009) The nitrogen paradox in tropical forest ecosystems. *Annu Rev Ecol Syst* 40:613–635.
- 19 Townsend AR, Cleveland CC, Houlton BZ, Alden CB, White JWC (2011) Multi-element regulation of the tropical forest carbon cycle. *Front Ecol Environ* 9(1):9–17.
- 20 Asner GP, et al. (2012) Carnegie Airborne Observatory-2: Increasing science data dimensionality via high-fidelity multi-sensor fusion. *Remote Sens Environ* 124:454–465.