Meeting report

Tropical forests and global change: biogeochemical responses and opportunities for cross-site comparisons, an organized INSPIRE session at the 108th Annual Meeting, Ecological Society of America, Portland, Oregon, USA, August 2023

Tropical forests play a critical role in the global carbon (C) cycle. These ecosystems maintain the highest rates of net primary production (NPP) on Earth (Hengl *et al.*, 2017), contain *c.* 30% of terrestrial C stocks (Jobbagy & Jackson, 2000), and have some of the largest stores of fine-root biomass globally (Jackson *et al.*, 1996), as well as higher fine-root production and turnover rates compared with other biomes (Cusack *et al.*, 2021). Tropical forest responses to projected warming, altered rainfall regimes, and elevated C dioxide (CO_2) concentrations (IPCC, 2021) are likely to be different from other ecosystems because of their unique characteristics (Box 1), making targeted research and model development important for understanding tropical forest–climate feedbacks. There is now a critical mass of long-term global change field experiments and modeling efforts in tropical forests, yet thus far there has been little synthesis, cross-site comparison, or multi-site standardized experimentation among tropical forests to help us understand how these biomes are changing. An organized INSPIRE session at the 108th Annual Meeting of the Ecological Society of America set out to tackle just this. Speakers covered large-scale tropical forest field experiments and modeling efforts, with an emphasis on changes in ecosystem biogeochemistry under warming, drying, elevated atmospheric CO_2, and changing nutrient status. In this meeting report, we provide an overview of the large-scale global change experiments presented and highlight the main objectives and opportunities for tropical forest research that emerged, including cross-site comparisons and integration with ecosystem-scale models (Fig. 1).

Overview of large-scale global change experiments in tropical forests

The range and extent of large-scale tropical forest experiments and modeling efforts presented by the speakers highlighted the recent accumulation of new data and papers. Across the presentations, the importance of spatial and temporal variation in tropical forest responses to global change and variation in responses by different components of ecosystems (e.g. above- vs belowground), was apparent.

Talks on warming experiments included the Tropical Responses to Altered Climate Experiment (TRACE) on canopy and soils in Puerto Rico, and the Soil Warming Experiment in Lowland Tropical Rainforest (SWELTR) in Panama. The Panama Rainforest Changes with Experimental Drying (PARCHED) experiment (Tana Wood, Puerto Rico; Andrew Nottingham, Panama; Lee Dietterich, Panama, respectively, Fig. 1) provided an example of a drying experiment. Results illustrated that there are rapid and often large changes in tropical forest C and nutrient cycling in response to temperature and moisture shifts (Nottingham *et al.*, 2020; Reed *et al.*, 2020; Dietterich *et al.*, 2022; Cusack *et al.*, 2023), including shifts in organism growth, activity, and diversity. Emerging results presented by Nottingham indicated that alterations to biogeochemical cycling rates are related to shifts in organism activity and biodiversity across trophic levels. There was substantial spatial and temporal variation in responses within and among forest sites, with shifts in C cycling, in particular, varying over time and space among individual forests included in PARCHED (Cusack *et al.*, 2023), and interacting effects with other disturbances (e.g. hurricane and drought) in TRACE (Reed *et al.*, 2020). This group of talks emphasized the importance of understanding tropical forest biogeochemical responses to both

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Box 1 Unique ecosystem attributes of tropical forests.

Tropical forests have some unique ecosystem attributes, such that these ecosystems merit focused study and modeling efforts to understand their responses and feedbacks to global change. For example:

- In contrast to temperate and boreal ecosystems, tropical seasonality tends to be driven by fluctuations in moisture rather than temperature.
- Soils in lowland tropical forests are most commonly scarce in rock-derived nutrients such as phosphorus (P), rather than nitrogen (N) as is most common at higher latitudes (Du *et al.*, 2020). This gives rise to different nutrient constraints over ecological responses to climate change and atmospheric 'CO_2 fertilization' (Hungate *et al.*, 2003).
- Tropical forests have some of the highest alpha and beta tree species diversity on Earth (Condit *et al.*, 2002), which contributes to a broad diversity of traits and strategies for overcoming resource scarcity.

At the same time, there are exceptions to this broader context, such as monodominant Dipterocarpaceae forests in SE Asia, and relative N scarcity in early successional and montane tropical forests. Still, tropical forests are most often characterized by moisture seasonality, scarcity of rock-derived nutrients, and high biodiversity. The extent of these characteristics varies among tropical forests. Despite the global importance of tropical forests in the global C cycle and their distinctive ecosystem characteristics, these ecosystems remain poorly characterized and underrepresented in dynamic vegetation and Earth System Models relative to other ecosystems (Bonan & Doney, 2018).
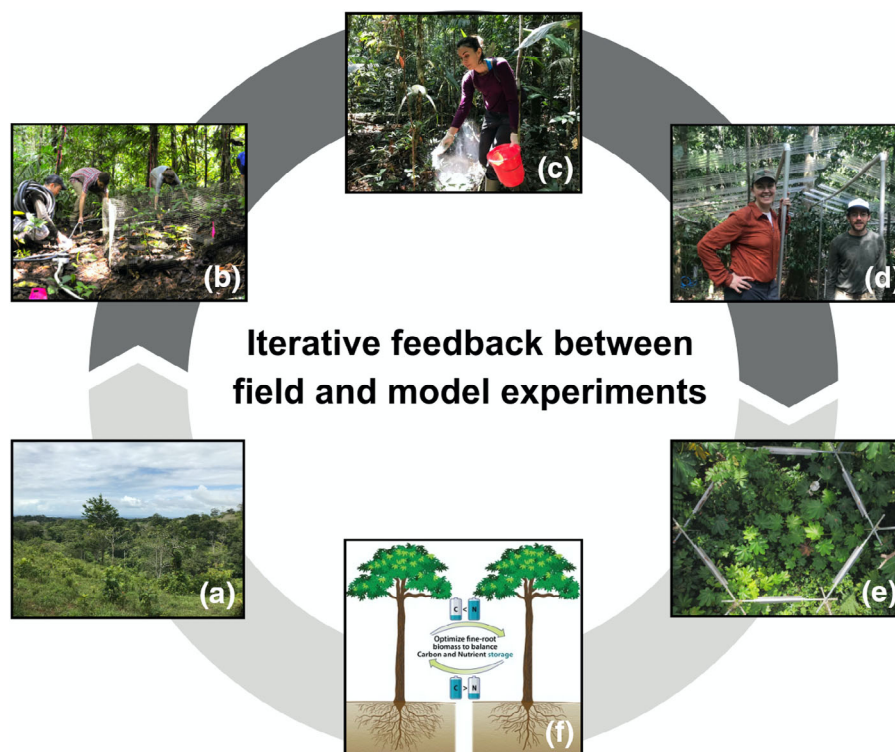
Fig. 1 Iterative feedbacks between empirical and modeling approaches are promoted to understand tropical forests and their responses to change. Large-scale field experiments in the tropics as discussed at the 'Tropical forests & global change: biogeochemical responses and opportunities for cross-sites comparisons' INSPIRE session at the 108th Annual Meeting of the Ecological Society of America are shown. (a) Panama early successional forests, the site of a cross-successional fertilization experiment (image: Michelle Wong). (b) the Panama Soil Warming Experiment in Lowland Tropical Rainforest (SWELTR), showing Andrew Nottingham and field crew setting heating cables into soil (image: Geetha Iyer). (c) The Brazil Amazon Fertilisation Experiment (AFEX), showing Laynara Lugli adding fertilizer (image: Kelly Andersen). (d) the Panama Rainforest Changes with Experimental Drying (PARCHED) drying experiment, showing Daniela Cusack and Lee Dietterich under a throughfall exclusion structure (image: Amanda L. Cordeiro). (e) the Puerto Rico Tropical Responses to Altered Climate Experiment (TRACE) warming experiment, showing heating structures from above (image: Maxwell Farrington). Iterative feedback between field projects (a–e) and dynamics vegetation models, such as the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) with C, N and P cycling represented (f), are important to further understand how tropical forests respond to climate change (image: DOE Next Generation Ecosystem Experiments – Tropics). Composite figure: D. Cinoglu.

warming and drying and highlighted the need to assess these effects in combination, across more sites, and over decadal timescales.

Presentations on nutrient fertilization experiments in tropical forests (Kelly Andersen, Brazil; Michelle Wong, Panama; Rebecca Ostertag, Hawai'i, USA) also highlighted the complexity of plant, soil, and microbial responses across time and space, and the importance of baseline site conditions such as forest successional stage, litter chemistry, and soil nutrient status. These presentations added to a recent meta-analysis of 36 large-scale fertilization experiments in lowland tropical forests, which indicated that multi-nutrient (N and P) limitation to NPP is most common and that earlier successional forests are more nutrient-limited than mature tropical forests (Wright, 2019). Ostertag's talk on the Hawai'i Long Substrate Age Gradient (LSAG) showed data from multi-nutrient (N, P) fertilization across stages of soil development, where NPP is limited by N on young soils, and by P on older, more strongly weathered soils (Vitousek, 2004). Ostertag's talk focused on nutrient effects on plant litter decomposition across plant species, showing that both litter quality and site characteristics influenced decomposition rates, and effects were strongest in the P-scarce older soil.

These results followed earlier results showing that fertilization with the limiting nutrient had a larger effect on fine root production in the P-scarce site compared with the N-scarce site (Ostertag, 2001). Wong discussed results from a multi-nutrient fertilization across a forest successional gradient in Panama (Fig. 1), where biological N fixation is active in N-scarce, early successional sites, and declines in older, more P-scare forests, suggesting N limitation to NPP in early successional tropical forests (Batterman *et al.*, 2013). Research presented by Andersen on multi-nutrient fertilization in the Brazilian Amazon Fertilisation Experiment (AFEX, Fig. 1) demonstrated that P addition alone increased NPP on P-scarce soils by increasing leaf and fine root production and turnover rates (Cunha *et al.*, 2022). Together, these presentations illustrated that different nutrients or combinations of nutrients limit different ecosystem processes across tropical forests, which will likely lead to the emergence of complex sets of nutrient limitations to biological activity under elevated atmospheric CO_2 (i.e., CO_2 fertilization). A need emerged from these talks for more synthetic efforts to identify plant and ecosystem traits that will be important for overcoming or tolerating nutrient scarcity in the context of global change.

Presentations on improving the representation of tropical forests in vegetation models (Matthew Craig, Oak Ridge National Lab; Jennifer Holm, Lawrence Berkeley National Lab) highlighted the importance of targeted data model integration for better tropical forest representation of biogeochemical feedbacks. For example, Holm discussed a mismatch between observed declines in the tropical C sink (Rammig, 2020), compared with the continual increase in tropical C sinks predicted by climate-driven vegetation models (Arora *et al.*, 2020). Specifically, most of the global models used for climate projections and in the coupled model inter-comparison project (CMIP6) predict a growing tropical C sink, contrary to what plot-scale empirical data currently suggest, which may be due to missing processes such as plant demography, nutrient competition, and disturbances. Holm argued for applying global models at the site scale to look at model-observation agreement to better predict at larger scales. With the emerging inclusion of finer-scale plant demography and competition into biogeochemical Earth System Models (ESMs), such as inclusion of the Functionally Assembled Terrestrial Ecosystem Simulator (FATES, Fig. 1) model (Holm *et al.*, 2020), we can now apply lessons learned at the site level back to the global scale. Craig highlighted ongoing efforts to address cross-scale integration in dynamic vegetation demographic models (VDMs) including: improving representation of nutrient cycling and C costs for nutrient acquisition in tropical forests, and expanded representation of dynamic root responses to changing resources over soil depths. Models at the ecosystem scale can also be useful for predicting and understanding outcomes of forest management and restoration strategies.

Forefronts in tropical forest global change research

Going forward, the discussion among speakers and audience highlighted four main goals.

(**1**) *Increasing inclusivity and diversity of participants* in tropical forest research should be a forefront of all efforts, with an emphasis on building collaboration in-country at tropical research sites (Haelewaters *et al.*, 2021). Increased representation should equitably include scientists within tropical countries, and expand research into understudied regions of the tropics, such as African forests. A common theme of this INSPIRE session and the broader ESA 2023 meeting was 'For All Ecologists', highlighting the need to consciously: (a) design research to maximize the participation of local communities, (b) provide incentives and agency for projects led by local peoples, (c) recognize the value of local knowledge, ideas, and understanding of ecosystems, (d) bolster local financial and educational infrastructure, and (e) form lasting, mutually beneficial partnerships with local communities and organizations. A concrete step in this direction could be taken with an open letter to US funding agencies lobbying to be allowed to allocate grant funds directly to local organizations as partners.

(**2**) *More synthesis* of results from existing and past tropical forest global change experiments is needed. The group noted that some of the ongoing nutrient and moisture manipulations in the tropics have 20+ yr of data (Wright, 2019; Almeida *et al.*, 2023), and newer temperature and moisture manipulations, such as TRACE, SWELTR, PARCHED, and AFEX are approaching 5–10 yr of data collection. Therefore, efforts are needed to synthesize these data, assess what we have learned, and to inform next steps for the study. An example has been provided by the recent synthesis of NPP responses to fertilization experiments in tropical forests (Wright, 2019). As part of ongoing synthesis efforts, attention should be placed on the biogeographical context of each experimental site (e.g. among-site variation in geology, rainfall patterns, and plant communities).

(**3**) *Planning the next broad-scale, coordinated experiments across tropical forests* is needed to address key questions. New experiments should focus on data gaps and broader geographical representation within the tropics. Several important research needs emerged from the discussion:

(a) More *cross-site comparisons* and coordinated studies using existing experiments. This effort could include greater assessment of variation in response to global change among forests with different levels of plant diversity, soil nutrient availability, climate, and symbiotic associations (Fig. 1). For example, ectomycorrhizal fungi (EMF)-dominated dipterocarp forests of Asia should be compared more directly with parallel measurements in arbuscular mycorrhizal fungi (AMF)-dominating forests in the Americas. The speakers noted that the African tropics are poorly represented in large-scale global change experiments, despite the fact that African rainforests appear to be the major net C sink among tropical regions (Rammig, 2020). Attendees emphasized the need to improve standardization of measurements, methods, and protocols among sites to improve comparability.

(b) The participants identified a need to launch *small-scale, replicated, dispersed field experiments* in multiple sites across tropical regions using standardized methods, creating a broad network of replicated research, which could be linked to existing networks of forest plots (e.g. ForestGEO). Ideas within this theme included (1) a dispersed network of small-scale rainfall exclusion experiments, (2) distributed decomposition and root ingrowth experiments across natural P gradients, and with attention to characterizing and spanning a diversity of microbial communities, and (3) distributed branch, leaf, and/or soil column warming using heating cables.

(c) There was also a call for the development of *multi-factorial experiments* in tropical forests, which could be added onto existing experimental setups, such as multi-factor plots including warming, drying, and/or fertilization. Unlike the smaller, dispersed experiments in (b) above, these would be larger-scale additions of factorial manipulation to existing field experiments, such as adding a warming*drying*fertilization experiment to the nearby SWELTR, PARCHED and fertilization experiments in Panama.

(d) Greater representation of *disturbed and early successional tropical forests* within experimental research is needed. Several participants identified the significance of secondary forests, not only because of their large and growing footprint, but also because of their potential to act as experiments for changing nutrient, temperature, moisture, and light dynamics. Since medium to long term biogeochemical responses of tropical forests to global change are likely to be driven by shifts in plant community composition and

demography, rather than intraspecific plasticity or individual adaptation (which is what is typically measured in manipulative experiments), secondary forests offer a chance to study communities that have assembled under ongoing environmental disturbance. (**4**) Promoting iterative feedback between empirical and modeling approaches will be key for representing ecosystem processes in models, testing hypotheses, and predicting change at large scales (Holm *et al.*, 2023). Experimental design and data collection using model–field comparisons can ensure that empirical data are the most useful for model integration. The need for modelers and empiricists to work together throughout the lifetime of the research (Fig. 1), rather than empiricists bringing in modelers at the end, was stressed by several in the audience. With potentially infinite choices of experiments and manipulations that could be used moving forward, Craig pointed out that using models at the inception of new projects can guide which questions and hypotheses to prioritize. An example of this approach is the new Free Air CO_2 Experiment (FACE) in the Amazon, which was preceded by modeling work exploring the importance of representing P cycles in tropical forest vegetation modeling studies (Fleischer *et al.*, 2019). Craig provided a reminder that models need equations: mathematical representation of continuous, often nonlinear, relationships between ecosystem processes and environmental drivers is most useful for model implementation. Model sensitivity to different parameters shed light on where data are most needed to improve model equations or constants and can help identify needs for the representation of additional processes in models. Audience members also highlighted the need for ecosystem models to better represent plant–microbe–soil interactions unique to tropical forests (e.g. Dallstream *et al.*, 2023) to better predict responses to global change.

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References

Almeida RPS, Silva RR, da Costa ACL, Ferreira LV, Meir P, Ellison AM. 2023. Induced drought strongly affects richness and composition of ground-dwelling ants in the eastern Amazon. *Oecologia* **201**: 299–309.

Arora VK, Katavouta A, Williams RG, Jones CD, Brovkin V, Friedlingstein P, Schwinger J, Bopp L, Boucher O, Cadule P *et al.* **2020.** Carbon-concentration and carbon-climate feedbacks in CMIP6 models and their comparison to CMIP5 models. *Biogeosciences* **17**: 4173–4222.

Batterman SA, Wurzburger N, Hedin LO. 2013. Nitrogen and phosphorus interact to control tropical symbiotic N_2 fixation: a test in *Inga punctata*. *Journal of Ecology* **101**: 1400–1408.

Bonan G, Doney S. 2018. Climate, ecosystems, and planetary futures: the challenge to predict life in Earth system models. *Science* **359**. doi: 10.1126/science.aam83.

Condit R, Pitman N, Leigh EG, Chave J, Terborgh J, Foster RB, Nunez P, Aguilar S, Valencia R, Villa G *et al.* **2002.** Beta-diversity in tropical forest trees. *Science* **295**: 666–669.

Cunha V, Fernanda H, Andersen KM, Lugli LF, Santana FD, Aleixo IF, Moraes AM, Garcia S, Di Ponzio R, Mendoza EO *et al.* **2022.** Direct evidence for phosphorus limitation on Amazon forest productivity. *Nature* **608**: 558.

Cusack DF, Addo-Danso SD, Agee EA, Andersen KM, Arnaud M, Batterman SA, Brearley FQ, Ciochina MI, Cordeiro AL, Dallstream C *et al.* **2021.** Tradeoffs and synergies in tropical forest root traits and dynamics for nutrient and water acquisition: field and modeling advances. *Frontiers in Forests and Global Change* **4**: 704469.

Cusack DF, Dietterich L, Sulman BN. 2023. Soil respiration responses to throughfall exclusion are decoupled from changes in soil moisture for four tropical forests, suggesting processes for ecosystem models. *Global Biogeochemical Cycles* **37**: e2022GB007473.

Dallstream C, Weemstra M, Soper FM. 2023. A framework for fine-root trait syndromes: syndrome coexistence may support phosphorus partitioning in tropical forests. *Oikos* **2023**: e08908.

Dietterich LH, Bouskill NJ, Brown M, Castro B, Chacon SS, Colburn L, Cordeiro AL, García EH, Gordon AA, Gordon E *et al.* **2022.** Effects of experimental and seasonal drying on soil microbial biomass and nutrient cycling in four lowland tropical forests. *Biogeochemistry* **161**: 227–250.

Du E, Terrer C, Pellegrini AFA, Ahlstrom A, van Lissa CJ, Zhao X, Xia N, Wu X, Jackson RB. 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. *Nature Geoscience* **13**: 221.

Fleischer K, Rammig A, De Kauwe MG, Walker AP, Domingues TF, Fuchslueger L, Garcia S, Goll DS, Grandis A, Jiang MK *et al.* **2019.** Amazon forest response to CO_2 fertilization dependent on plant phosphorus acquisition. *Nature Geoscience* **12**: 736–741.

Haelewaters D, Hofmann TA, Romero-Olivares AL. 2021. Ten simple rules for Global North researchers to stop perpetuating helicopter research in the Global South. *PLoS Computational Biology* **17**: e1009277.

Hengl T, de Jesus J, Heuvelink G, Gonzalez M, Kilibarda M, Blagotic A, Shangguan W, Wright M, Geng X, Bauer-Marschallinger B. 2017. SoilGrids250m: global gridded soil information based on machine learning. *PLoS ONE* **12**: e0169748.

Holm JA, Knox RG, Zhu Q, Fisher RA, Koven CD, Lima AJN, Riley WJ, Longo M, Negron-Juarez RI, de Araujo AC *et al.* **2020.** The Central Amazon Biomass sink under current and future atmospheric CO_2: predictions from big-leaf and demographic vegetation models. *Journal of Geophysical Research-Biogeosciences* **125**: e2019JG005500.

Holm JA, Medvigy DM, Smith B, Dukes JS, Beier C, Mishurov M, Xu X, Lichstein JW, Allen CD, Larsen KS *et al.* **2023.** Exploring the impacts of unprecedented climate extremes on forestecosystems: hypotheses to guide modeling and experimental studies. *Biogeosciences* **20**: 2117–2142.

Hungate BA, Dukes JS, Shaw MR, Luo YQ, Field CB. 2003. Nitrogen and climate change. *Science* **302**: 1512–1513.

IPCC. 2021. Climate change 2021: the physical science basis. In: Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI *et al.*, eds. *Contribution of working group I to the sixth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* **108**: 389–411.

Jobbagy EG, Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* **10**: 423–436.

Nottingham AT, Meir P, Velasquez E, Turner BL. 2020. Soil carbon loss by experimental warming in a tropical forest. *Nature* **584**: 234.

Ostertag R. 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. *Ecology* **82**: 485–499.

Rammig A. 2020. Tropical carbon sinks are out of sync. *Nature* **579**: 38–39.

Reed SC, Reibold R, Cavaleri MA, Alonso-Rodriguez AM, Berberich ME, Wood TE. 2020. Tropical Ecosystems in the 21st Century: soil biogeochemical responses of a tropical forest to warming and hurricane disturbance. In: Service UF, ed. *Advances in ecological research, vol. 62*. London, UK: Academic Press, 2–468.

Vitousek PM. 2004. *Nutrient cycling and limitation: Hawai'i as a model system.* Princeton, NJ, USA: Princeton University Press.

Wright SJ. 2019. Plant responses to nutrient addition experiments conducted in tropical forests. *Ecological Monographs* **89**: 18.

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