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Meeting Report

Tropical forests & 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 the unique characteristics of these ecosystems (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 modelling efforts in tropical forests, yet thus far there has been little synthesis, cross-site comparison, or multi-site standardized experiments 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 modelling 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.

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- versus belowground), was apparent.

Warming (Andrew Nottingham, Panama; Tana Wood, Puerto Rico) and drying (Lee Dietterich, Panama) experiments included the Tropical Responses to Altered Climate Experiment (TRACE) on canopy and soils in Puerto Rico, the Soil Warming Experiment in Lowland Tropical Rainforest (SWELTR) in Panama, and the Panama Rainforest Changes with Experimental Drying (PARCHED) experiment. Results illustrated that there are rapid and often large changes in 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 also substantial spatial and temporal variation in responses within and among forest sites, with shifts in C cycling in particular varying over time within individual field experiments (Cusack *et al.,* 2023), spatially among sites, and interacting with other disturbances (e.g. hurricane and drought in Puerto Rico; (Reed *et al.*, 2020)). This group of talks emphasized the importance of understanding tropical forest biogeochemical responses to both warming and drying and highlighted the need to assess these effects in combination and across more sites.

Presentations on nutrient fertilization experiments in tropical forests (Kelly Andersen, Brazil; Michelle Wong, Panama; Rebecca Ostertag, Hawai‘i, USA) 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 meta-analysis of 14 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-limited 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-limited site compared with the N-limited site (Ostertag, 2001). Wong showed that in Panama, N limitation to NPP was pronounced in early successional tropical forests in Panama, using data from a multi-nutrient fertilization across four stages of succession (Batterman *et al.*, 2013). Research presented by Andersen on multi-nutrient fertilization in the Brazilian Amazon Fertilisation Experiment (AFEX) 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 ecosystems processes across tropical forests, which will likely lead to complex sets of nutrient limitation to biological activity under CO_2 fertilization. A requirement emerged 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 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 intercomparison project (CMIP6) predict a larger ongoing tropical C sink than plot 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-observational agreement to better understand larger scales that lack field data. With the emerging inclusion of finer scale plant demography and competition into biogeochemical Earth System Models, such as using the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) 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 this 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 expanded research into under-studied 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+ years 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 years of data collection. Therefore, efforts are needed to synthesize these data, assess what we have learned, and to inform next steps for study. A model has been provided by the recent synthesis of NPP responses to fertilization experiments in tropical forests (Wright *et al.,* 2019). As part of this synthesis process, attention should be placed on the biogeographical context of each experimental site (e.g. across-site variation in geology, rainfall patterns and plant communities).

3. Planning the next broad-scale, coordinated experiments across tropical forests to address key questions, should focus on data gaps and broader geographical representation within the tropics. Several important gaps emerged from the discussion, including:

a) More ***cross-site comparisons*** and coordinated studies for 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. For example ectomycorrhizal fungi (EMF)-dominated dipterocarp forests of Asia compared with 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: i) a dispersed network of small-scale rainfall exclusion experiments, ii) distributed decomposition and root ingrowth experiments across natural P gradients, and with attention to characterizing and spanning a diversity of microbial communities, and iii) 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 set-ups, 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–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 and testing hypotheses (Holm *et al.*, 2023; Fig. 1). 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, 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 responses 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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Key words: drying, global change, nutrients, succession, warming.

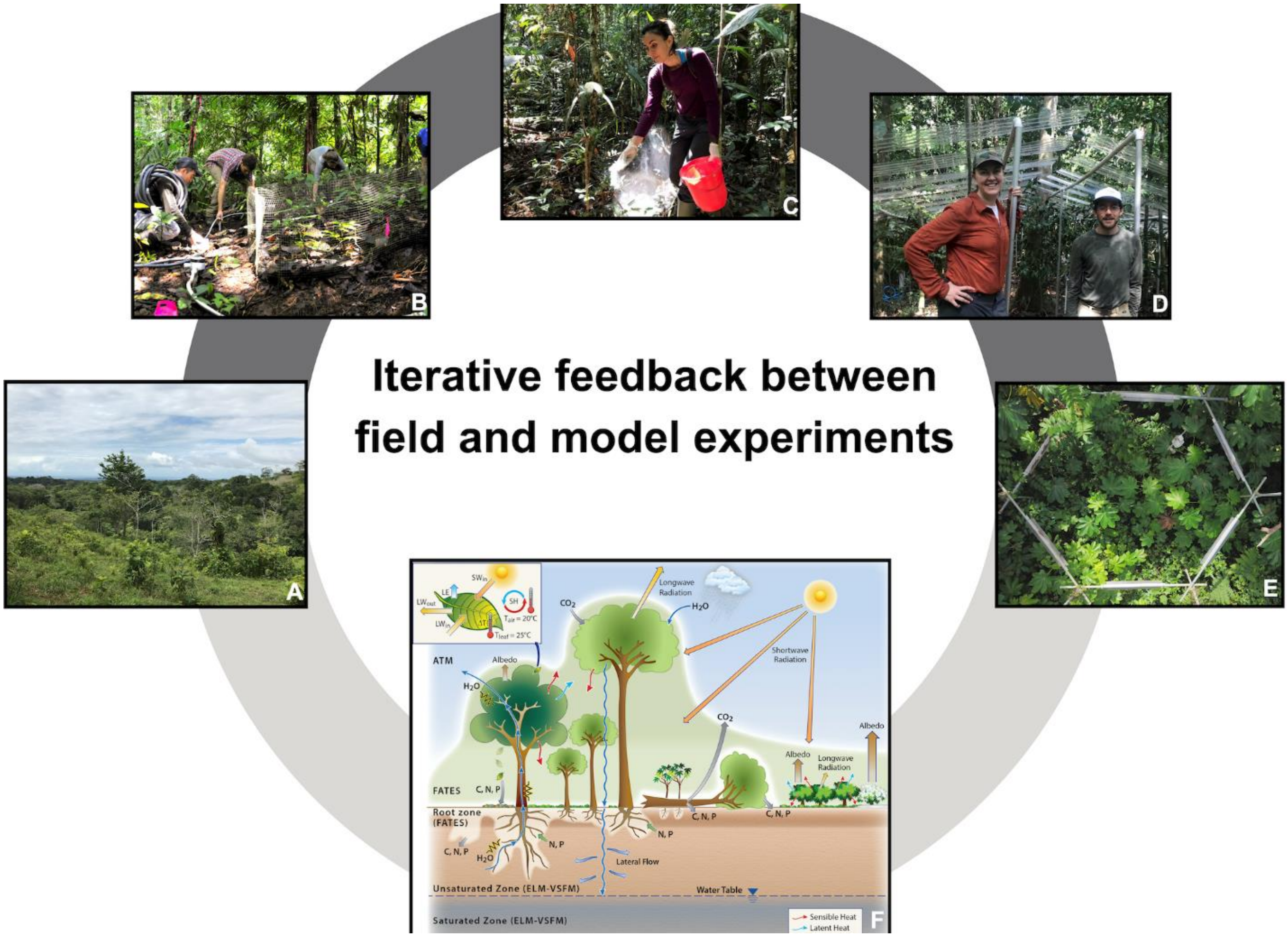

Fig 1. Promoting iterative feedback between empirical and modeling approaches to understanding tropical forests and their responses to change. Large-scale field experiments in the tropics as discussed at the ‘Tropical forests & global change: biogeochemical responses and opportunities for cross-sites 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-d) and dynamics vegetation models, such as the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) with C, N and P cycling represented (e) is important to further understand tropical forest response to climate change. (figure: NGEE-Tropics). Composite figure: D. Cinoglu.

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), giving rise to different nutrient constraints to 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. Thus, tropical forests are often characterized by moisture seasonality, scarcity of rock-derived nutrients, and high biodiversity, and these characteristics also vary 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).