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

7 Tropical forests play a critical role in the global carbon (C) cycle. These ecosystems maintain the
8 highest rates of net primary production (NPP) on Earth (Hengl *et al.*, 2017), contain c. 30% of
9 terrestrial C stocks (Jobbagy & Jackson, 2000), and have some of the largest stores of fine-root
10 biomass globally (Jackson *et al.*, 1996), as well as higher fine-root production and turnover rates
11 compared with other biomes (Cusack *et al.*, 2021). Tropical forest responses to projected
12 warming, altered rainfall regimes, and elevated C dioxide (CO₂) concentrations (IPCC, 2021) are
13 likely to be different from other ecosystems because of the unique characteristics of these
14 ecosystems (Box 1), making targeted research and model development important for
15 understanding tropical forest–climate feedbacks. There is now a critical mass of long-term global
16 change field experiments and modelling efforts in tropical forests, yet thus far there has been
17 little synthesis, cross-site comparison, or multi-site standardized experiments among tropical
18 forests to help us understand how these biomes are changing. An organized INSPIRE session at
19 the 108th Annual Meeting of the Ecological Society of America set out to tackle just this.
20 Speakers covered large-scale tropical forest field experiments and modelling efforts, with an
21 emphasis on changes in ecosystem biogeochemistry under warming, drying, elevated
22 atmospheric CO₂, and changing nutrient status. In this meeting report we provide an overview of
23 the large-scale global change experiments presented and highlight the main objectives and
24 opportunities for tropical forest research that emerged.

26 **Overview of large-scale global change experiments in tropical forests**

27 The range and extent of large-scale tropical forest experiments and modeling efforts presented by
28 the speakers highlighted the recent accumulation of new data and papers. Across the presentations,
29 the importance of spatial and temporal variation in tropical forest responses to global change, and

30 variation in responses by different components of ecosystems (e.g. above- versus belowground),
31 was apparent.

32

33 Warming (Andrew Nottingham, Panama; Tana Wood, Puerto Rico) and drying (Lee Diatterich,
34 Panama) experiments included the Tropical Responses to Altered Climate Experiment (TRACE)
35 on canopy and soils in Puerto Rico, the Soil Warming Experiment in Lowland Tropical Rainforest
36 (SWELTR) in Panama, and the Panama Rainforest Changes with Experimental Drying
37 (PARCHED) experiment. Results illustrated that there are rapid and often large changes in C and
38 nutrient cycling in response to temperature and moisture shifts (Nottingham *et al.*, 2020; Reed *et*
39 *al.*, 2020; Diatterich *et al.*, 2022; Cusack *et al.*, 2023), including shifts in organism growth, activity,
40 and diversity. Emerging results presented by Nottingham indicated that alterations to
41 biogeochemical cycling rates are related to shifts in organism activity and biodiversity across
42 trophic levels. There was also substantial spatial and temporal variation in responses within and
43 among forest sites, with shifts in C cycling in particular varying over time within individual field
44 experiments (Cusack *et al.*, 2023), spatially among sites, and interacting with other disturbances
45 (e.g. hurricane and drought in Puerto Rico; (Reed *et al.*, 2020)). This group of talks emphasized
46 the importance of understanding tropical forest biogeochemical responses to both warming and
47 drying and highlighted the need to assess these effects in combination and across more sites.

48

49 Presentations on nutrient fertilization experiments in tropical forests (Kelly Andersen, Brazil;
50 Michelle Wong, Panama; Rebecca Ostertag, Hawai'i, USA) highlighted the complexity of plant,
51 soil, and microbial responses across time and space, and the importance of baseline site conditions
52 such as forest successional stage, litter chemistry, and soil nutrient status. These presentations
53 added to a meta-analysis of 14 large-scale fertilization experiments in lowland tropical forests,
54 which indicated that multi-nutrient (N and P) limitation to NPP is most common, and that earlier
55 successional forests are more nutrient limited than mature tropical forests (Wright, 2019).
56 Ostertag's talk on the Hawai'i Long Substrate Age Gradient (LSAG) showed data from multi-
57 nutrient (N, P) fertilization across stages of soil development, where NPP is limited by N on young
58 soils, and by P on older, more strongly weathered soils (Vitousek, 2004). Ostertag's talk focused
59 on nutrient effects on plant litter decomposition across plant species, showing that both litter
60 quality and site characteristics influenced decomposition rates, and effects were strongest in the P-

61 limited older soil. These results followed earlier results showing that fertilization with the limiting
62 nutrient had a larger effect on fine root production in the P-limited site compared with the N-
63 limited site (Ostertag, 2001). Wong showed that in Panama, N limitation to NPP was pronounced
64 in early successional tropical forests in Panama, using data from a multi-nutrient fertilization
65 across four stages of succession (Batterman *et al.*, 2013). Research presented by Andersen on
66 multi-nutrient fertilization in the Brazilian Amazon Fertilisation Experiment (AFEX)
67 demonstrated that P addition alone increased NPP on P-scarce soils by increasing leaf and fine
68 root production and turnover rates (Cunha *et al.*, 2022). Together, these presentations illustrated
69 that different nutrients or combinations of nutrients limit different ecosystems processes across
70 tropical forests, which will likely lead to complex sets of nutrient limitation to biological activity
71 under CO₂ fertilization. A requirement emerged for more synthetic efforts to identify plant and
72 ecosystem traits that will be important for overcoming or tolerating nutrient scarcity in the context
73 of global change.

74
75 Presentations on improving the representation of tropical forests in vegetation models (Matthew
76 Craig, Oak Ridge National Lab; Jennifer Holm, Lawrence Berkeley National Lab) highlighted the
77 importance of targeted data-model integration for better tropical forest representation of
78 biogeochemical feedbacks. For example, Holm discussed a mismatch between observed declines
79 in the tropical C sink (Rammig, 2020), compared with continual increase in tropical C sinks
80 predicted by climate-driven vegetation models (Arora *et al.*, 2020). Specifically, most of the global
81 models used for climate projections and in the coupled model intercomparison project (CMIP6)
82 predict a larger ongoing tropical C sink than plot data currently suggest, which may be due to
83 missing processes such as plant demography, nutrient competition, and disturbances. Holm argued
84 for applying global models at the site scale to look at model-observational agreement to better
85 understand larger scales that lack field data. With the emerging inclusion of finer scale plant
86 demography and competition into biogeochemical Earth System Models, such as using the
87 Functionally Assembled Terrestrial Ecosystem Simulator (FATES) model (Holm *et al.*, 2020), we
88 can now apply lessons learned at the site level back to the global scale. Craig highlighted ongoing
89 efforts to address cross-scale integration in dynamic vegetation demographic models (VDMs)
90 including: improving representation of nutrient cycling and C costs for nutrient acquisition in
91 tropical forests, and expanded representation of dynamic root responses to changing resources over

92 soil depths. Models at this scale can also be useful for predicting and understanding outcomes of
93 forest management and restoration strategies.

94

95 **Forefronts in tropical forest global change research**

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

97

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

110

111 **2. More Synthesis** of results from existing and past tropical forest global change experiments is
112 needed. The group noted that some of the ongoing nutrient and moisture manipulations in the
113 tropics have 20+ years of data (Wright, 2019; Almeida *et al.*, 2023), and newer temperature and
114 moisture manipulations, such as TRACE, SWELTR, PARCHED, and AFEX are approaching 5–
115 10 years of data collection. Therefore, efforts are needed to synthesize these data, assess what we
116 have learned, and to inform next steps for study. A model has been provided by the recent synthesis
117 of NPP responses to fertilization experiments in tropical forests (Wright *et al.*, 2019). As part of
118 this synthesis process, attention should be placed on the biogeographical context of each
119 experimental site (e.g. across-site variation in geology, rainfall patterns and plant communities).

120

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

124
125 a) More *cross-site comparisons* and coordinated studies for existing experiments. This effort could
126 include greater assessment of variation in response to global change among forests with different
127 levels of plant diversity, soil nutrient availability, climate, and symbiotic associations. For example
128 ectomycorrhizal fungi (EMF)-dominated dipterocarp forests of Asia compared with arbuscular
129 mycorrhizal fungi (AMF)-dominating forests in the Americas. The speakers noted that the African
130 tropics are poorly represented in large-scale global change experiments, despite the fact that
131 African rainforests appear to be the major net C sink among tropical regions (Rammig, 2020).
132 Attendees emphasized the need to improve standardization of measurements, methods, and
133 protocols among sites to improve comparability.

134
135 b) The participants identified a need to launch *small-scale, replicated, dispersed field experiments*
136 in multiple sites across tropical regions using standardized methods, creating a broad network of
137 replicated research, which could be linked to existing networks of forest plots (e.g. ForestGEO).
138 Ideas within this theme included: i) a dispersed network of small-scale rainfall exclusion
139 experiments, ii) distributed decomposition and root ingrowth experiments across natural P
140 gradients, and with attention to characterizing and spanning a diversity of microbial communities,
141 and iii) distributed branch, leaf, and/or soil column warming using heating cables.

142
143 c) There was also a call for the development of *multi-factorial experiments* in tropical forests,
144 which could be added onto existing experimental set-ups, such as multi-factor plots including
145 warming, drying, and/or fertilization. Unlike the smaller, dispersed experiments in b) above, these
146 would be larger-scale additions of factorial manipulation to existing field experiments, such as
147 adding a warming*drying*fertilization experiment to the nearby SWELTR, PARCHED and
148 fertilization experiments in Panama.

149
150 d) Greater representation of *disturbed and early successional tropical forests* within experimental
151 research is needed. Several participants identified the significance of secondary forests, not only

152 because of their large and growing footprint, but also because of their potential to act as
153 experiments for changing nutrient, temperature, moisture, and light dynamics. Since medium–long
154 term biogeochemical responses of tropical forests to global change are likely to be driven by shifts
155 in plant community composition and demography, rather than intraspecific plasticity or individual
156 adaptation (which is what is typically measured in manipulative experiments), secondary forests
157 offer a chance to study communities that have assembled under ongoing environmental
158 disturbance.

159

160 **4) Promoting iterative feedback between empirical and modeling approaches** will be key for
161 representing ecosystem processes in models and testing hypotheses (Holm *et al.*, 2023; Fig. 1).
162 Experimental design and data collection using model–field comparisons can ensure that empirical
163 data are the most useful for model integration. The need for modelers and empiricists to work
164 together throughout the lifetime of the research, rather than empiricists bringing in modelers at the
165 end, was stressed by several in the audience. With potentially infinite choices of experiments and
166 manipulations that could be used moving forward, Craig pointed out that using models at the
167 inception of new projects can guide which questions and hypotheses to prioritize. An example of
168 this approach is the new Free Air CO₂ Experiment (FACE) in the Amazon, which was preceded
169 by modeling work exploring the importance of representing P cycles in tropical forest vegetation
170 modeling studies (Fleischer *et al.*, 2019). Craig provided a reminder that models need equations:
171 mathematical representation of continuous, often nonlinear, relationships between ecosystem
172 responses and environmental drivers is most useful for model implementation. Model sensitivity
173 to different parameters shed light on where data are most needed to improve model equations or
174 constants and can help identify needs for the representation of additional processes in models.
175 Audience members also highlighted the need for ecosystem models to better represent plant–
176 microbe–soil interactions unique to tropical forests (e.g. (Dallstream *et al.*, 2023)) to better predict
177 responses to global change.

178

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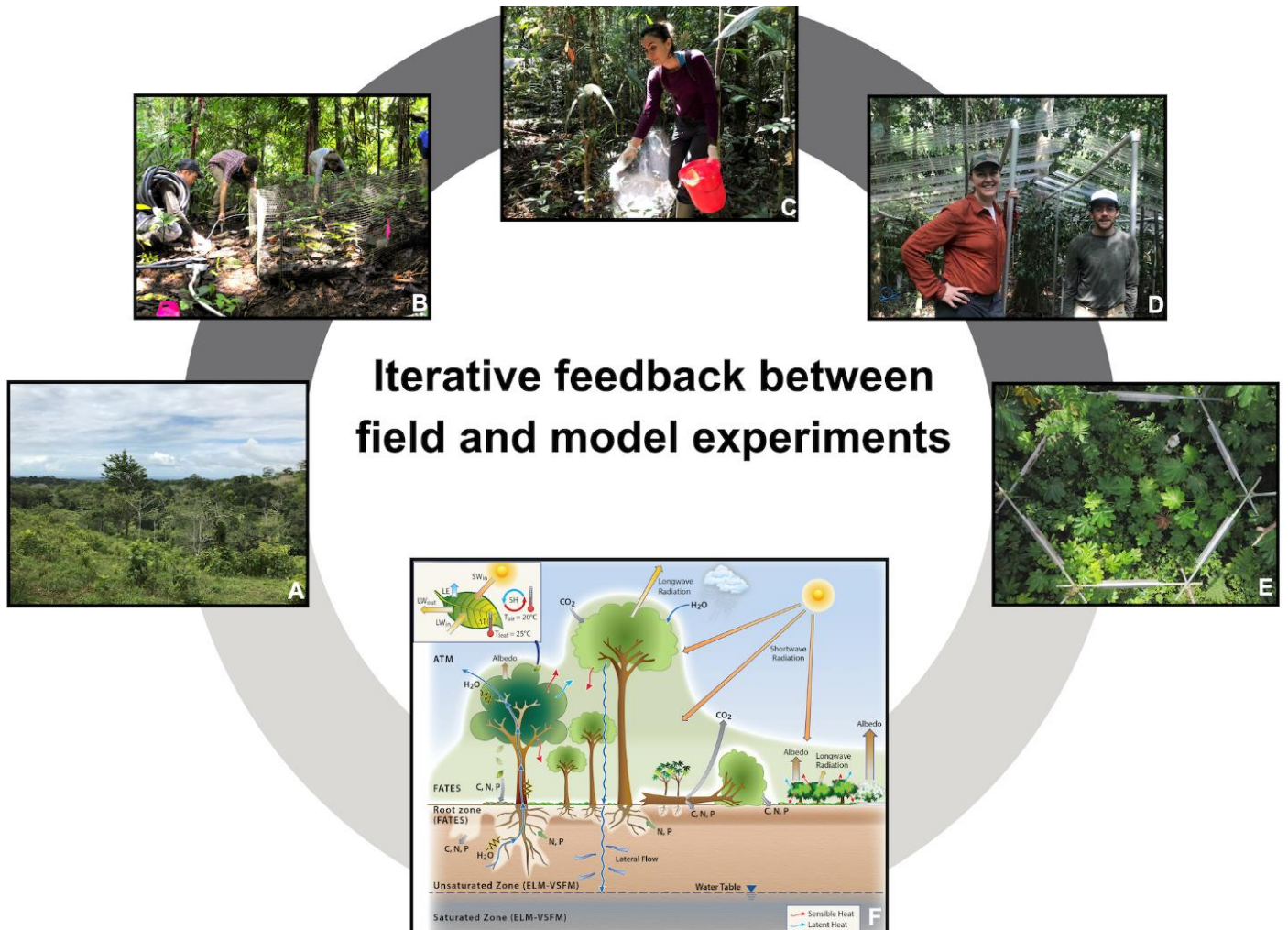
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324 **Key words:** drying, global change, nutrients, succession, warming.



326

327

328

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330

331 **Fig 1.** Promoting iterative feedback between empirical and modeling approaches to understanding
 332 tropical forests and their responses to change. Large-scale field experiments in the tropics as
 333 discussed at the ‘Tropical forests & global change: biogeochemical responses and opportunities
 334 for cross-sites comparisons’ INSPIRE session at the 108th Annual Meeting of the Ecological
 335 Society of America are shown. (a) Panama early successional forests, the site of a cross-
 336 successional fertilization experiment (image: Michelle Wong). (b) the Panama Soil Warming

337 Experiment in Lowland Tropical Rainforest (SWELTR), showing Andrew Nottingham and field
338 crew setting heating cables into soil (image: Geetha Iyer). (c) the Brazil Amazon Fertilisation
339 Experiment (AFEX), showing Laynara Lugli adding fertilizer (image: Kelly Andersen). (d) the
340 Panama Rainforest Changes with Experimental Drying (PARCHED) drying experiment, showing
341 Daniela Cusack and Lee Dietterich under a throughfall exclusion structure (image: Amanda L.
342 Cordeiro). e) the Puerto Rico Tropical Responses to Altered Climate Experiment (TRACE)
343 warming experiment, showing heating structures from above (image: Maxwell Farrington).
344 Iterative feedback between field projects (a-d) and dynamics vegetation models, such as the
345 Functionally Assembled Terrestrial Ecosystem Simulator (FATES) with C, N and P cycling
346 represented (e) is important to further understand tropical forest response to climate change.
347 (figure: NGEE-Tropics). Composite figure: D. Cinoglu.

348

349 **Box 1. Unique Ecosystem Attributes of Tropical Forests**

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

- 353 • In contrast to temperate and boreal ecosystems, tropical seasonality tends to be driven by
354 fluctuations in moisture rather than temperature..
- 355 • Soils in lowland tropical forests are most commonly scarce in rock-derived nutrients such
356 as phosphorus (P), rather than nitrogen (N) as is most common at higher latitudes (Du *et*
357 *al.*, 2020), giving rise to different nutrient constraints to ecological responses to climate
358 change and atmospheric "CO₂ fertilization" (Hungate *et al.*, 2003).
- 359 • Tropical forests have some of the highest alpha and beta tree species diversity on Earth
360 (Condit *et al.*, 2002), which contributes to a broad diversity of traits and strategies for
361 overcoming resource scarcity.

362 At the same time, there are exceptions to this broader context, such as monodominant
363 Dipterocarpaceae forests in SE Asia, and relative N scarcity in early successional and montane
364 tropical forests. Thus, tropical forests are often characterized by moisture seasonality, scarcity of
365 rock-derived nutrients, and high biodiversity, and these characteristics also vary among tropical
366 forests. Despite the global importance of tropical forests in the global C cycle and their distinctive

367 ecosystem characteristics, these ecosystems remain poorly characterized and underrepresented in
368 dynamic vegetation and Earth system models relative to other ecosystems (Bonan & Doney, 2018).