OPINION

# Urgent need for warming experiments in tropical forests

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## Abstract

Although tropical forests account for only a fraction of the planet's terrestrial surface, they exchange more carbon dioxide with the atmosphere than any other biome on Earth, and thus play a disproportionate role in the global climate. In the next 20 years, the tropics will experience unprecedented warming, yet there is exceedingly high uncertainty about their potential responses to this imminent climatic change. Here, we prioritize research approaches given both funding and logistical constraints in order to resolve major uncertainties about how tropical forests function and also to improve predictive capacity of earth system models. We investigate overall model uncertainty of tropical latitudes and explore the scientific benefits and inevitable trade-offs inherent in large-scale manipulative field experiments. With a Coupled Model Intercomparison Project Phase 5 analysis, we found that model variability in projected net ecosystem production was nearly 3 times greater in the tropics than for any other latitude. Through a review of the most current literature, we concluded that manipulative warming experiments are vital to accurately predict future tropical forest carbon balance, and we further recommend the establishment of a network of comparable studies spanning gradients of precipitation, edaphic qualities, plant types, and/or land use change. We provide arguments for long-term, single-factor warming experiments that incorporate warming of the most biogeochemically active ecosystem components (i.e. leaves, roots, soil microbes). Hypothesis testing of underlying mechanisms should be a priority, along with improving model parameterization and constraints. No single tropical forest is representative of all tropical forests; therefore logistical feasibility should be the most important consideration for locating large-scale manipulative experiments. Above all, we advocate for multi-faceted research programs, and we offer arguments for what we consider the most powerful and urgent way forward in order to improve our understanding of tropical forest responses to climate change.

*Keywords:* carbon flux, CMIP5, ecosystem processes, global warming, net ecosystem production, temperature, temperature threshold, tipping point, tropics, warming manipulation

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## Introduction

Tropical forests represent one of the planet's most active biogeochemical engines. Although only 15% of the planet's terrestrial surface supports tropical forests, they account for over 2/3 of live terrestrial plant biomass (Pan *et al.*, 2013), nearly one-third of all soil carbon (C) (Jobbagy & Jackson, 2000; Tarnocai *et al.*, 2009), and exchange more carbon dioxide ($CO_2$) with the atmosphere than any other biome (Foley *et al.*, 2003; Beer *et al.*, 2010). In the coming decades, the tropics will experience unprecedented changes in temperature, rapid increases in atmospheric $CO_2$ concentrations, and significant alterations in the timing and amount of rainfall (Diffenbaugh & Scherer, 2011; IPCC, 2011; Anderson, 2012; Mora *et al.*, 2013). Given the large amounts of C tropical forests store and cycle, investigations of tropical forest response to these environmental drivers will be critical for our understanding of future global-scale climate and biogeochemical cycling. However, the vulnerability of tropical forests to climate-related change is a topic of much debate (Lloyd & Farquhar, 2008; Lewis *et al.*, 2009; Clark *et al.*, 2013; Cox *et al.*, 2013; Good *et al.*, 2013; Randerson, 2013), and our limited ability to characterize their responses to altered climate and increasing $CO_2$ represents our largest hurdle in accurately predicting the earth's future climate (Bonan & Levis, 2010; Huntingford *et al.*, 2013; Piao *et al.*, 2013).

Our poor understanding of tropical forest responses stems not only from a striking paucity of data, but also from the diversity of these systems. Tropical forests

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span a wide range of mean annual temperatures, seasonality, precipitation, edaphic conditions, and species diversity (Richards, 1952; Townsend *et al.*, 2008). In fact, of the 116 Holdridge life zones (a global bioclimatic classification scheme), the tropics maintain more than the sum of all other geographic regions combined (Holdridge, 1967). Furthermore, the vast majority of tropical field studies have occurred within only two USDA soil orders and on sites with mean annual precipitation (MAP) >1500 mm, while the tropical forest biome spans 10 soil orders and 500–8000+ mm MAP (Holdridge, 1967; Powers *et al.*, 2011; Marin-Spiotta & Sharma, 2013). Thus, the concept of a 'representative' tropical forest is a myth, and a substantial number of existing forest types in the tropics are chronically undersampled.

Given the disproportionate role tropical forests play in the global climate, combined with the high uncertainty surrounding their responses to change, funding agencies are increasingly interested in how these ecosystems will respond to future climatic conditions (e.g. DOE US, 2012). Thus, it is imperative that the scientific community identify key research priorities to resolve major uncertainties about the functioning of tropical forests and to improve predictive capacity of earth system models. With these goals in mind, we ask (1) can we quantify the uncertainty in C balance response to climate change in the tropics? (2) why should we implement large-scale manipulation experiments in tropical forests? (3) how many environmental factors should be manipulated? (4) which environmental factor(s) to manipulate?, and (5) at what spatial and temporal scales should these manipulations occur? We investigate overall model uncertainty of tropical latitudes with a Coupled Model Intercomparison Project Phase 5 (CMIP5) analysis and review current literature to discuss the scientific benefits and inevitable tradeoffs inherent in large-scale manipulative field experiments. We discuss how to prioritize research approaches given both funding and logistical constraints to optimize the knowledge gained from the limited resources available for such research. Our goal is not to argue *against* any particular research approach, but rather to offer arguments for what we consider the most powerful and urgent way forward to improve our understanding of tropical forest response to climate change. Above all, we advocate for multifaceted research programs involving a combination of observational, experimental, and modeling approaches.

## Can we quantify the uncertainty in C balance response to climate change in the tropics?

Recent global inventories highlight the vast amounts of C stored and cycled in tropical forests (Pan *et al.*, 2011, 2013). Due in part to these large amounts of C, the lack of data on how tropical plants and soil respond to environmental perturbations is one of the greatest sources of uncertainty in modeling future C cycling and climate, globally (Bonan & Levis, 2010; Ziehn *et al.*, 2011; Booth *et al.*, 2012; Huntingford *et al.*, 2013; Piao *et al.*, 2013). To quantify this tropical uncertainty, we compared estimates of the rate of net ecosystem $CO_2$ uptake or release [net ecosystem production (NEP)] over time (2000–2099) from seven global coupled C climate models represented in the CMIP5 archive (Taylor *et al.*, 2012) under a scenario of relatively high rates of greenhouse gas emissions [representative concentration pathway (RCP) 8.5, (Riahi *et al.*, 2007), Table 1, Fig. 1]. We found that model disagreement and variability were indeed highest in the tropics, where the range in NEP variability was nearly three times greater than for any other region (Fig. 1a). Using a standard conversion factor of 2.124 Pg C $ppm^{-1}$ (Ballantyne *et al.*, 2012), this intermodel variability in tropical NEP suggests changes in atmospheric $CO_2$ concentrations by the end of the 21st century that range from an increase of ~0.6 ppm to a decrease of ~1.4 ppm. We also found substantial variability in annual change in tropical NEP over time

**Table 1** CMIP5 models and modeling groups

| Modeling Center or group | Institute ID | Model name |
| --- | --- | --- |
| Beijing Climate Center, China Meteorological Administration | BCC | BCC-CSM1-1 |
| College of Global Change and Earth System Science, Beijing Normal University | GCESS | BNU-ESM |
| Canadian Center for Climate Modeling and Analysis | CCCMA | CanESM2 |
| Community Earth System Model Contributors | NSF-DOE-NCAR | CESM1-BGC |
| Institut Pierre-Simon Laplace | IPSL | IPSL-CM5A-MR |
| Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies | MIROC | MIROC-ESM |
| Norwegian Climate Center | NCC | NorESM1-M |
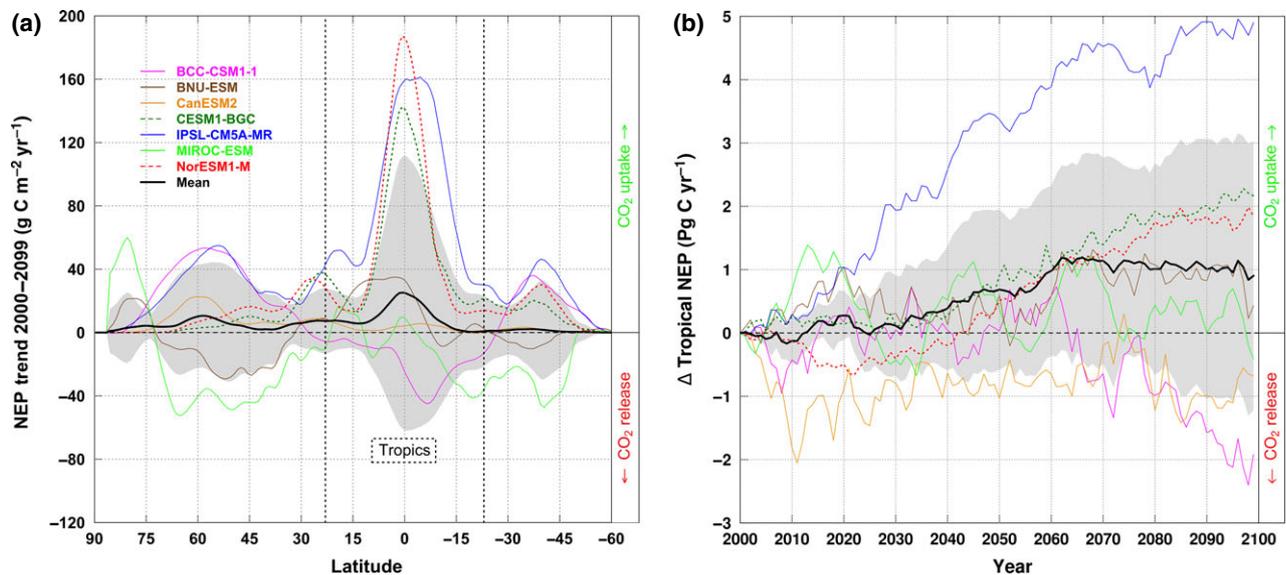
**Fig. 1** Net ecosystem productivity (NEP) from seven climate models of the CMIP5 (Coupled Model Intercomparison Project Phase 5) ensemble under the RCP 8.5 representative concentration pathway. (a) The global latitudinal trend in NEP over the time period 2000–2099. Latitudinal trends were calculated as the 5°-latitude sliding mean of the linear trend in NEP over the projection period. Spatial data were normalized by first resampling to a common 1° global grid using the bilinear method of interpolation. (b) The annual change in tropical (23°N–23°S) NEP over the time period 2000–2099. Annual data were smoothed using a 10-year sliding mean. In both plots, the heavy black line represents the ensemble mean while the gray shading represents a one standard deviation ($1\sigma$) range in climate model variability. Dashed lines in both plots represent models that include coupled carbon–nitrogen (C-N) biogeochemistry; solid lines represent models with no explicit nutrient cycling component.

across the CMIP5 models (Fig. 1b). The ensemble mean of modeled annual NEP was predicted to increase by ~37% across the tropics by the year 2100 (solid black line, Fig. 1b); yet, there was great disagreement among models, with a nearly three standard deviation range which significantly overlapped zero. These results not only show variability in the magnitude of $CO_2$ exchanged, but also disagreement in the direction of change; some models projected an increase and others a decrease in tropical C sink strength. The model discrepancy in Fig. 1b represents an enormous amount of C (~7 Pg C yr$^{-1}$), nearly equivalent to current annual anthropogenic C emissions (~9 Pg C yr$^{-1}$; Boden et al., 2010). This overall uncertainty underscores the dramatic need for an enhanced understanding of the mechanisms controlling tropical forest responses to change to improve the ability of earth system models to accurately predict future atmospheric $CO_2$ concentrations and climate.

## Why should we implement large-scale manipulation experiments in the tropics?

A holistic scientific approach combining observational studies (e.g. long-term plots, tree rings, eddy covariance, and environmental gradients) and manipulative experiments is critical for assessing questions like 'how

will ecosystems respond to global change?' (e.g. Luo et al., 2011; Zuidema et al., 2013). In the tropics, however, field-based manipulative experiments remain underutilized (DOE US, 2012; Wood et al., 2012; Zhou et al., 2013; Zuidema et al., 2013), and we argue for their explicit inclusion in current tropical forest research planning. Rich insight has been gained from climate and atmospheric $CO_2$ manipulation experiments in nontropical ecosystems (e.g. Rustad et al., 2001; Norby & Zak, 2011), as well as from the few such manipulations in the tropics (e.g. Nepstad et al., 2002). In situ experimental manipulations allow for greatly improved model representations of highly complex systems and offer a rare opportunity to test whether models accurately capture patterns observed in the field. For example, experimentation could elucidate mechanisms explaining seemingly contradictory patterns in observational studies such as both increased photosynthesis (Saleska et al., 2007) and increased mortality (Phillips et al., 2010) of Amazonian rain forest trees during the 2005 drought. While manipulative experiments have numerous caveats (e.g. Aronson & McNulty, 2009; Leuzinger et al., 2011), they nevertheless enable researchers to isolate the effects of individual treatments to test mechanistic hypotheses and can reveal important insights about system responses to extreme, infrequent, or abrupt climatic events (Jentsch et al., 2007).

Recent reviews have advocated for the implementation of large-scale, multiple-factor, long-term experiments to investigate responses of terrestrial ecosystems to climate change (Rustad, 2008; Lukac *et al.*, 2010; Zhou *et al.*, 2013; Zuidema *et al.*, 2013). In every ecosystem on Earth, multiple environmental factors are interacting with each other simultaneously, creating complex direct and indirect effects on C, water, and nutrient pools and fluxes. For example, because nutrient availability can exert strong control over tropical forest processes (Cleveland & Townsend, 2006; Reed *et al.*, 2011; Wright *et al.*, 2011), temperature changes to nutrient mineralization rates could result in large, indirect changes in C cycling of tropical forests. Similarly, warming and water are inextricably linked via indirect temperature effects on soil evaporation and plant transpiration. Given the potential for strong feedbacks between tree canopy, root, and soil function with respect to net C exchange, the ideal experimental design would involve manipulating the entire ecosystem (Wood *et al.*, 2012). In addition, ecosystem-level changes in C balance occur over timescales longer than the average 3-year funding cycle (Rustad, 2008). However, implementation of manipulative experiments is both challenging and expensive, a fact particularly true in tropical forested ecosystems. We agree that, with unlimited resources, multiple-factor, full factorial, long-term experiments spanning multiple spatial scales and investigating both aboveground and belowground components are clearly the gold standard. Yet, current realities mandate that decisions be made about allocation of time, energy, and funding, and here, we offer specific recommendations in the face of limited resources and logistical challenges.

## How many environmental factors should be manipulated?

Many trade-offs are involved in the decision of whether to experimentally manipulate multiple environmental variables simultaneously or only a single factor (e.g. $CO_2$ and temperature vs. $CO_2$ alone). Multiple-factor experiments allow for the detection of interactive effects of two or more environmental drivers and have been successfully implemented in higher latitude ecosystems with low-stature plants (reviewed in Rustad, 2008). A meta-analysis of ecosystem warming manipulation experiments found that the magnitude of treatment effect size decreased with increasing experimental complexity (Leuzinger *et al.*, 2011), meaning that experiments with only single variable manipulations were more likely to overestimate ecosystem responses compared with experiments that manipulated multiple variables. Nevertheless, establishing multiple-factor experiments in highly diverse, tall-stat-ure tropical forests (e.g. tree canopies > 40 m and hundreds of tree species per hectare) is hindered by both financial and logistical constraints. The high cost of implementing multiple treatments would very likely come at the expense of the replication needed to detect interactive effects. Indeed, some larger scale $CO_2 \times$ warming experiments have found no interactions among plant growth responses to treatments (Norby & Luo, 2004). An additional trade-off exists between the number of treatments and the number of potential tropical research sites. The number of experimental plots needed for a full-factorial design increases exponentially with the number of experimental factors, making each experiment logistically challenging and expensive to maintain. As a result, the establishment of a network of multiple-factor experiments would be improbable. In contrast, single-factor experiments would be more likely to enable sufficient within-site replication to detect experimental effects and to allow for the inclusion of a network of tropical forest sites. The diversity within and among tropical forests would make such a network invaluable.

Given the uncertainty surrounding climate predictions for any given region, we cannot hope to duplicate future conditions with any certainty in an experimental system. We can, however, use single-factor experiments to test hypotheses and gain mechanistic understanding in conjunction with models that can explore interactive effects of multiple factors (Luo *et al.*, 2011). Additionally, natural climatic variation could enable the exploration of interactions; for example, a network of field warming experiments across environmental gradients could reveal interactions between soil moisture and warming. Because logistical and financial realities mandate decisions between treatment number, plot number/size, and site number, we suggest a mechanistic approach that focuses on fewer treatments but with sufficient replication at multiple tropical forest sites.

## Which environmental factor(s) should be manipulated?

Here, we discuss the three abiotic variables associated with climatic change that are most likely to affect C cycling of plants and soil in tropical forests: elevated atmospheric $[CO_2]$, altered precipitation, and elevated temperature. Disturbance and land-use change may affect the global C cycle as much or more than climate change in the coming decades, especially in tropical systems (Bonan & Levis, 2010; Brando *et al.*, 2014; Espírito-Santo *et al.*, 2014; Shiels & Gonzalez, 2014). While these are important complementary discussions, they are outside the scope of this commentary.

*Elevated atmospheric $CO_2$*

Elevated $CO_2$ concentrations can affect forest C cycling via changes to productivity, C allocation, water use, and nutrient cycling. Long-term plot-based evidence of aboveground biomass accrual in tropical forests has been attributed to elevated $CO_2$ 'fertilization' effects (Lewis *et al.*, 2009); however, some studies suggest that this would be difficult to distinguish from the effects of increasing nutrient availability or recovery after disturbance (Chambers *et al.*, 2004; Korner, 2009; Lewis *et al.*, 2009; Wright, 2010, 2013). Further, remotely sensed data have provided evidence of a steady decline in net primary production (NPP) of Amazonian tropical forests despite steadily increasing atmospheric $CO_2$, likely due to drought effects (Zhao & Running, 2010). Some long-term tropical forest field measurements, as well as global monitoring efforts, suggest that the negative effects of warming on aboveground productivity and C sink behavior could exceed any positive effects of increasing $CO_2$ concentrations (Clark *et al.*, 2013; Piao *et al.*, 2013; Wang *et al.*, 2013), although other model simulations suggest tropical forests may be somewhat resilient to climate-induced change (Cox *et al.*, 2013; Huntingford *et al.*, 2013). Thus, while elevated $CO_2$ experiments could clearly affect processes such as NPP, climatic changes such as drought and increasing temperature may counteract the stimulatory effects of increasing $CO_2$ concentrations.

$CO_2$ fertilization effects on tropical plants may also be constrained by nutrient limitation (Luo *et al.*, 2004; Reich & Hobbie, 2013). In the lowland tropics, soil nutrient availability can constrain plant growth, soil C storage, and tree species community composition (Cusack *et al.*, 2010; Townsend *et al.*, 2011; Wright *et al.*, 2011; Condit *et al.*, 2013). Indeed, results from outside the tropics suggest plant responses to experimentally elevated $CO_2$ without concurrent increases in nutrient availability may be ephemeral or relatively small (Luo *et al.*, 2004), and this may be particularly likely in tropical forests where light and nutrient availability tend to regulate plant growth more strongly than $CO_2$ (Graham *et al.*, 2003; Wright, 2013). Interestingly, in the NEP simulations we present here, the only two models that included coupled C–N biogeochemistry (dashed lines, Fig. 1) both show a larger positive effect of $CO_2$ fertilization than almost all of the other models. Due to assumptions of N-rich tropical forest soils, the models do not expect N availability to constrain $CO_2$ fertilization in tropical latitudes as strongly as it does in temperate latitudes (Fig. 1a). However, the modeled tropical NEP projections of an increased tropical C sink are likely unrealistic because *none* of these models consider coupled carbon–nitrogen–phosphorus (C-N-P)

biogeochemistry. As P has been well established as an important limiting factor in the tropics (Cleveland & Townsend, 2006; Elser *et al.*, 2007; Wood *et al.*, 2009; Peñuelas *et al.*, 2013), it is likely that P limitation, if included in model simulations, would significantly constrain $CO_2$ effects on tropical forest C balance (Hungate *et al.*, 2003; Bonan & Levis, 2010; Piao *et al.*, 2013).

*Altered precipitation*

Earth system models predict substantial spatial variation in both the sign and magnitude of tropical precipitation changes in the coming decades, such that mean precipitation is expected to increase in the wet tropics but decline in the subtropics and dry tropics, with an overall expected increase in wet-dry seasonality (Collins *et al.*, 2013; Fu *et al.*, 2013). Storm events are also expected to increase in frequency and intensity, particularly in the wet tropics, while it remains unclear whether droughts will increase in duration or intensity (Collins *et al.*, 2013; Kirtman *et al.*, 2013). Given the broad range of anticipated changes in precipitation regime, manipulative studies would need to evaluate the effects of both increased and reduced rainfall as well as distribution changes to encompass the full range of future scenarios.

Several *in situ* precipitation manipulation studies have been implemented in tropical forested ecosystems, including dry season irrigation experiments (e.g. Wieder & Wright, 1995), and drought or 'throughfall exclusion' experiments, which reduce soil moisture by diverting rainfall (e.g. Nepstad *et al.*, 2002). While observational studies have found strong links between seasonality of precipitation and tree growth (Schuur, 2003; Clark *et al.*, 2010), tropical dry season irrigation experiments have largely not affected tree growth (Wieder & Wright, 1995; Vasconcelos *et al.*, 2008). In contrast, larger scale (1-ha), longer term (>3 years) throughfall exclusion studies have resulted in increased mortality of large trees, while surviving trees appear to be resilient to repeated cycles of soil drying (Brando *et al.*, 2008; da Costa *et al.*, 2010). This experimentally induced tree mortality, however, is less severe and dramatic than mortality in response to natural tropical drought (Meir *et al.*, In Press). These manipulative experiments generally alter the soil water environment without affecting the micrometeorology of the forest canopy, while natural changes in precipitation regime result in concomitant changes in soil moisture, temperature, and vapor pressure deficit (Meir & Grace, 2005; Phillips *et al.*, 2010). Thus, a strong 'top-down' control of canopy microclimate on tropical trees could explain the long duration of throughfall exclusion needed to induce tree mortality

(>3 years), the discrepancy between natural vs. experimentally induced drought effects on mortality (Meir *et al.*, In Press), and the general lack of dry season irrigation effects on tree growth (Wieder & Wright, 1995). Adding a layer of complexity, dry season irrigation and throughfall exclusion experiments have had highly variable effects on soil attributes and processes, such as soil nutrient availability, soil microbe response, and greenhouse gas emissions (e.g. Vasconcelos *et al.*, 2004; Sotta *et al.*, 2007; Wood & Silver, 2012; Bouskill *et al.*, 2013; Hall *et al.*, 2013), making it difficult to draw definitive conclusions not only on the magnitude of effects, but also the direction.

Going forward, scientists should think critically about canopy microclimate vs. soil moisture controls on forest processes, as well as the strong range of mean annual and intra-annual variation in precipitation found among tropical forests. One way forward could be to implement a standardized network of water manipulation experiments across a natural precipitation gradient so that a wide range of canopy microclimates could be considered. However, given the high degree of uncertainty and the large spatial heterogeneity surrounding expected changes in precipitation regime, determining the most relevant precipitation scenario to implement may be challenging.

*Warming*

In contrast to variable predictions for precipitation in the tropics, temperature is expected to increase rapidly across all tropical land surfaces, resulting in temperature regimes that do not exist in the tropics today (Christensen *et al.*, 2007). Climate models project an imminent novel heat regime across the tropics within the next 20 years, with seasonal minimum temperatures hotter than current seasonal maximums (Diffenbaugh & Scherer, 2011; Mora *et al.*, 2013) and a greater frequency of extreme temperature events relative to higher latitude systems (Anderson, 2011, 2012). Tropical species may be more susceptible to warming than species of other biomes as a consequence of millions of years of evolution under relatively narrow temperature variation (Wright *et al.*, 2009; Krause *et al.*, 2013). Representation of plant or soil thermal acclimation, however, is missing from most global-scale models due to a lack of experimental data, particularly for tropical ecosystems (Smith & Dukes, 2012). Nevertheless, the world's tropical forests may already be functioning near thermal biological thresholds (Doughty & Goulden, 2008; but see Lloyd & Farquhar, 2008). Currently, 88% of tropical forested areas already experience mean annual temperatures (MAT) >20 °C (Wood *et al.*, 2012), and areas with MAT above 28 °C do not main-

tain closed canopy forest (Wright *et al.*, 2009). Increased temperature could therefore dramatically alter or even eliminate tropical forested ecosystems from their current locations.

Forest inventory data and C balance studies reveal that intact and regrowing (secondary) tropical forests combined represent a relatively small net sink of $CO_2$ when deforestation and land-use change are not taken into account (Pan *et al.*, 2011). However, tropical forests could become a net source of $CO_2$ to the atmosphere if warming reduces C storage in aboveground biomass and/or spurs increased $CO_2$ loss from soils due to enhanced respiration (Holland *et al.*, 2000; Wood *et al.*, 2012). For example, if increased temperature results in reduced photosynthesis (Doughty & Goulden, 2008), but increased heterotrophic soil respiration (Townsend *et al.*, 1997; Holland *et al.*, 2000), forests that are currently acting as net sinks of $CO_2$ could become net sources of $CO_2$ to the atmosphere, further exacerbating climatic warming in a positive feedback loop. A clear signal has already been detected whereby global $CO_2$ concentrations are tightly linked to year-to-year variability of tropical temperature via its effects on tropical forest C flux (Wang *et al.*, 2013, 2014). These data imply that temperature-induced fluctuations in tropical ecosystem function are already creating feedbacks to affect global atmospheric $CO_2$ concentrations. While the mechanisms driving this trend are likely the result of increased fire (Langenfelds *et al.*, 2002; van der Werf *et al.*, 2006; Gurney *et al.*, 2012), other ecophysiological factors may also be relevant, including increased mortality, increased heterotrophic or autotrophic respiration, and/or decreased photosynthesis.

An experimental warming approach could provide unparalleled insight into currently debated mechanistic hypotheses about temperature effects on forest ecosystems. For example, climate-C modeling studies simulating massive dieback in Amazonian forests (e.g. Cox *et al.*, 2000) have been interpreted as primarily caused by either warming-induced drought (Betts *et al.*, 2004) or direct influences of elevated temperatures (Galbraith *et al.*, 2010), a dichotomy that could be addressed experimentally within the framework discussed here. The causes of tree mortality are of much interest in the current literature (McDowell *et al.*, 2008), as are emerging paradigms for modeling ecosystem function within a C sink (i.e. growth) rather than C source (i.e. photosynthesis) frame of reference (Fatichi *et al.*, 2014). Temperature manipulation could help tease apart several of these contending theories. For example, high temperatures could induce C starvation via reducing photosynthesis (Doughty & Goulden, 2008) and/or increasing autotrophic respiration, while mortality due directly to hydraulic failure may be more likely in plants relying

on anisohydric regulation (McDowell *et al.*, 2008). Warming experiments could also address the debate in the literature about the extent of water limitation in tropical forests, where early studies showed strong water limitation (reviewed in Hasler & Avissar, 2007; Saleska *et al.*, 2009), but later whole-system flux studies showed little evidence of water limitation in either water flux (da Rocha *et al.*, 2009) or C flux (Restrepo-Coupe *et al.*, 2013).

Natural temperature or elevational gradients in the tropics offer great opportunities for observational studies of temperature effects on plant and ecosystem functioning (Malhi *et al.*, 2010), yet predicted temperature regimes do not currently exist in the lowland tropics today. The warm ends of such gradients will see further warming over the coming decades, and this additional warming of lowland tropical forests is of greatest interest for our understanding of tropical C cycling in the face of climate change. Thus, the only way to achieve the projected temperature regime is to manipulatively warm the warmest forests.

### At what spatial and temporal scales should these manipulations occur?

Tropical forests support incredibly high levels of diversity (often 100s of species per hectare, Losos & Leigh, 2004). Given the significant expense involved in establishing a forest-scale warming manipulation, it is unlikely that such an experiment would be sufficiently large to investigate questions related to tree species diversity and demography, with the possible exception of microbial communities, arthropods, or tree seedlings. No *in situ* ecosystem-level warming experiment has ever been accomplished in *any* mature forest (Norby & Luo, 2004), and no active field warming experiment has been successfully implemented anywhere in the tropics (Luo *et al.*, 2011). While it is theoretically possible to scale a warming experiment to whole trees (e.g. Kimball *et al.*, 2012), the time and expense needed to develop and implement such an experiment is well beyond the scope of a standard research grant. As such, priority should be to start with field warming experiments investigating the temperature responses of the most biogeochemically active components of the system: canopy leaves, roots, and soil microbes, and at the scale needed to monitor changes in C, water, and nutrient fluxes (e.g. Fig. 2). While a detailed intercomparison of warming methodologies is beyond the scope of this commentary (see Aronson & McNulty, 2009), we advocate for multiple methodologies to warm component parts of ecosystems (e.g. infrared lamps, resistance cables, and soil rods; Fig. 2), as each method has pros and cons with respect to research goals, installation and
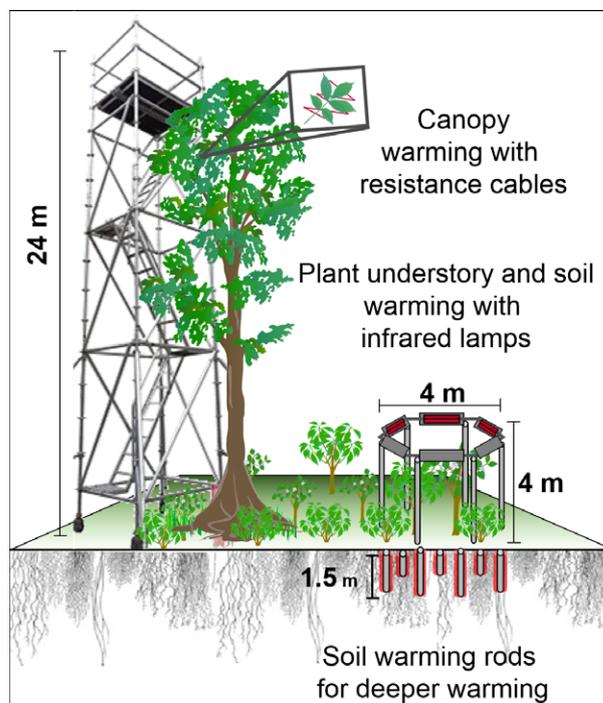


**Fig. 2** Diagram (to scale) of an example scenario whereby various ecosystem components are warmed using different methods. Methods include branch- and leaf-level warming using resistance heater cables affixed to branches, which requires canopy access with tree climbing, towers, or cranes (e.g. Slot *et al.*, 2014); plant understory and shallow soil warming using an array of infrared warming lamps (e.g. Kimball *et al.*, 2008); and soil warming rods to warm deeper soil profiles (e.g. Hanson *et al.*, 2011). Red regions indicate warmed infrastructure.

maintenance cost, spatial scale, and experimental artifacts. Additionally, we recommend adopting a functional trait approach (e.g. Reich, 2014) with respect to plants and microbial communities to help address the complexities stemming from high species diversity (Fisher *et al.*, 2010; Diamond *et al.*, 2012). If effects of warming can be linked to functional traits, predictive insights may reach beyond the scale of the experiment.

Effect size tends to diminish with longer term climate change experiments (e.g. >3 years, Leuzinger *et al.*, 2011). As such, predictions made from extrapolating experimental responses of plants or soil microbes from shorter timeframes could be misleading in both magnitude and direction of response (Leuzinger *et al.*, 2011; Luo *et al.*, 2011). Plants, for example, can instantaneously respond to increased temperature within minutes, acclimate biochemically over days or years, respond to biogeochemical feedbacks over timescales from years to decades, and adapt on the order of centuries to millennia (Smith & Dukes, 2012). Similarly, many higher latitude warming experiments have observed a dampening over time of initial increases in

soil respiration, due to biochemical acclimation of organisms, substrate limitation, adaptation of soil microbes, and/or declines in root biomass (Oechel *et al.*, 2000; Luo *et al.*, 2001; Melillo *et al.*, 2011; Jarvi & Burton, 2013). Although improving our understanding of thermal acclimation has recently been cited as one of the most critical research needs for improving current model representations of tropical forests (Booth *et al.*, 2012; DOE US, 2012), algorithms simulating plant gas exchange are still largely derived from leaf-level responses to short-term change (minutes), and current model simulations of C cycling rarely represent acclimation of soil microbes (Smith & Dukes, 2012). Finally, potential tree mortality events due to experimental manipulations may take several years to occur, as shown in tropical forest rainfall exclusion experiments (e.g. Nepstad *et al.*, 2007), yet these events could be critical in considering future tropical forest structure, function, and C cycling. Thus, experimental timescales long enough to capture these changes are required. We therefore encourage the creation of longer term experiments (5+ years) to accurately capture ecosystem-scale trends, acclimation, and/or biogeochemical feedbacks in response to warming, and to inform robust predictive numerical models of tropical C cycling responses to climate change.

With respect to the temporal resolution of warming treatments, we recommend 24-h diurnal warming to examine thermal thresholds of photosynthesis (Doughty & Goulden, 2008) and hysteresis of soil respiration (Vargas & Allen, 2008). Alternatively, nighttime-only warming of plants is relevant to better understand the effects on plant respiratory acclimation (Slot *et al.*, 2014). Tropical tree growth has been negatively correlated with nighttime temperatures (Clark *et al.*, 2003, 2013), which have increased faster than daytime temperatures globally, resulting in overall decreased amplitude of diurnal temperature ranges (Xia *et al.*, 2014). While most warming experiments cannot realistically duplicate the slow rate of climate change within the lifetime of even a long-term experiment, employing a step-change in temperature may be used to test important mechanistic hypotheses and also yield critical model parameterization information as long as experimental temperature and moisture responses of soil, leaf surfaces, and air are well characterized in space and time.

## Conclusions

Priority should be placed on investigating the effects of the environmental factors most likely to have large, long-term effects on growth, productivity, and C sink behavior of tropical forests. Other groups have suggested $CO_2$ enrichment experiments should be of paramount importance in the tropics (e.g. Cernusak *et al.*, 2013; Zuidema *et al.*, 2013), and we do not disagree with the value of these types of experiments. However, we argue that, if forced to select among treatments, we would gain more tropical-specific insight and a better return on investment from climate manipulations (e.g. temperature and precipitation). Furthermore, the tropical forest biome currently experiences a large natural range of precipitation, yet there is no existing analog for projected temperature change (Wright *et al.*, 2009). Given the narrow temperature confines under which tropical organisms have evolved, they may have limited ability to acclimate or adapt to warming temperature regimes (Janzen, 1967; Deutsch *et al.*, 2008; Wright *et al.*, 2009). We therefore propose that ecosystem warming experiments are vital to accurate predictions of future tropical forest C balance, and we further recommend the establishment of a network of warming studies using comparable methodologies across a range of tropical forest sites spanning gradients of precipitation, plant functional types, land-use change, and/or soil fertilities.

Overall, we argue for longer term (>5 year), single-factor warming experiments that incorporate both aboveground and belowground assessment (Fig. 2). Mechanism-based hypothesis testing should be a primary goal, along with improving earth system model parameterization and constraint. As no single tropical forest represents all tropical forests, logistical feasibility should be central for locating large-scale manipulative experiments. Sites that allow for access, security, infrastructure (e.g. electricity), straightforward permitting, and open collaboration will provide more opportunity for significant scientific achievement than those that are especially remote or involve particularly troublesome logistics.

In temperate and boreal zones, dozens of field experiments have revealed critical information about ecosystem-level responses to warming, elevated $CO_2$, and altered precipitation (Rustad, 2008). Tropical forests, on the other hand, are among the most understudied biomes in the world, likely because of both logistical barriers (e.g. remote, undeveloped locations) and environmental challenges (e.g. climate, diversity, complex ecosystem structure). Nevertheless, the combination of large C fluxes and high uncertainty (e.g. Fig. 1) underscores recent suggestions in the literature that the tropics are indeed a 'high priority region' for future climate change research (Luo *et al.*, 2011; DOE US, 2012; Reed *et al.*, 2012; Wood *et al.*, 2012; Zhou *et al.*, 2013; Zuidema *et al.*, 2013). As a scientific community, we possess the technology, expertise, and motivation necessary to address these complex questions, and we offer this viewpoint to guide discussions of how best to meet the globally relevant goal of improving our understanding of tropical forest responses to global change.

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## Author contributions

M.A.C, S.C.R. and T.E.W. conceived the ideas for the manuscript. M.A.C. led the writing effort, while S.C.R. and T.E.W. provided edits and comments to the manuscript at all stages. W.K.S. performed the modeling analysis and provided edits to the final stages of the manuscript.

## Competing interests

The authors declare no competing financial interests. Reprints and permissions information is available online at http://www.nature.com/reprints. Correspondence and requests for materials should be addressed to M.A.C.

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