

OPINION

Urgent need for warming experiments in tropical forests

MOLLY A. CAVALERI¹, SASHA C. REED², W. KOLBY SMITH³ and TANA E. WOOD^{4,5}¹*School of Forest Resources & Environmental Science, Michigan Technological University, 1400 Townsend Dr., Houghton, MI 49931, USA,* ²*U.S. Geological Survey, Southwest Biological Science Center, 2290 S. West Resource Blvd, Moab, UT 84532, USA,*³*Department of Ecosystem and Conservation Sciences, University of Montana, 32 Campus Dr., Missoula, MT 59812, USA,*⁴*USDA Forest Service, International Institute of Tropical Forestry, Jardín Botánico Sur, 1201 Calle Ceiba, Río Piedras 00926-1115, Puerto Rico,* ⁵*Fundación Puertorriqueña de Conservación, P.O. Box 362495, San Juan 00936-2495, Puerto Rico***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

Received 2 September 2014; revised version received 28 November 2014 and accepted 23 December 2014

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 (CO₂) 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 CO₂ concentrations, and significant alterations in the timing and amount of rain-

fall (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 CO₂ 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

Correspondence: Molly Cavaleri, tel. +970 215 4817, fax +906 487 2915, e-mail: macavale@mtu.edu

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 trade-offs inherent in large-scale manipulative field experiments. We discuss how to prioritize research approaches given both funding and logistical con-

straints 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 CO₂ 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 CO₂ 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 |

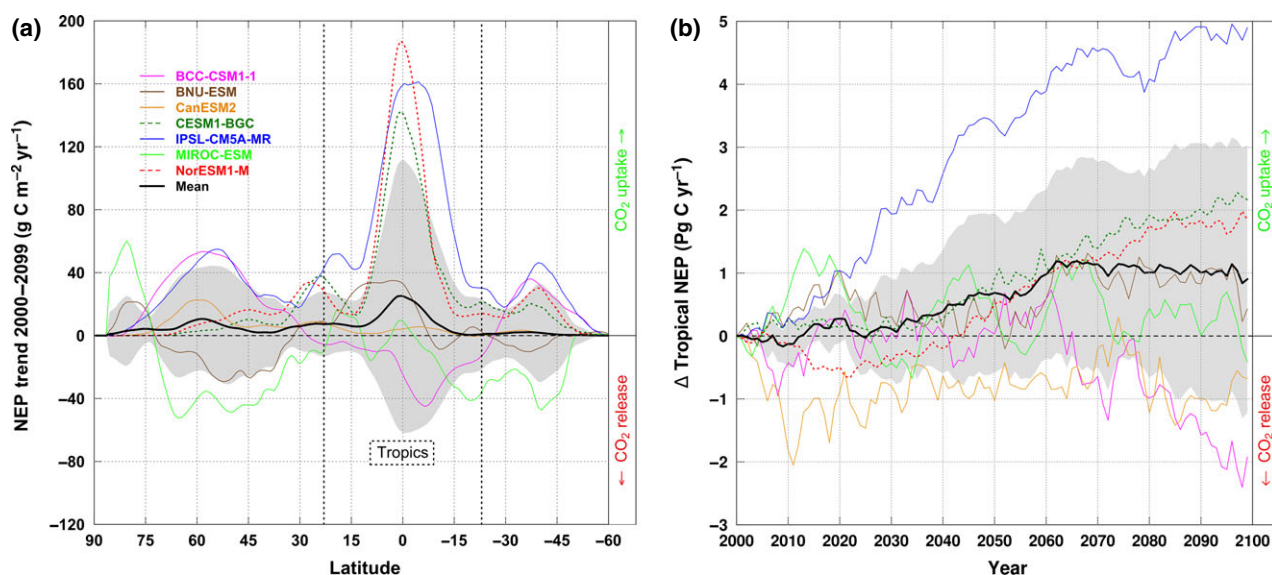


Fig. 1 Net ecosystem productivity (NEP) from seven climate models of the CMIP5 (Coupled Model Intercomparison Project Phase 5) ensemble under the RCP 8.5 representative concentration pathway. (a) The global latitudinal trend in NEP over the time period 2000–2099. Latitudinal trends were calculated as 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 (1σ) 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 ($\sim 7 \text{ Pg C yr}^{-1}$), nearly equivalent to current annual anthropogenic C emissions ($\sim 9 \text{ Pg C yr}^{-1}$; 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. CO₂ and temperature vs. CO₂ 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 CO₂ × 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 [CO₂], 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 CO₂

Elevated CO₂ 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 CO₂ ‘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 CO₂, 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 CO₂ 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 CO₂ experiments could clearly affect processes such as NPP, climatic changes such as drought and increasing temperature may counteract the stimulatory effects of increasing CO₂ concentrations.

CO₂ 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 CO₂ 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 CO₂ (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 CO₂ 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 CO₂ 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 CO₂ 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 (Schoor, 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 (Difftbaugh & 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 CO₂ when deforestation and land-use change are not taken into account (Pan *et al.*, 2011). However, tropical forests could become a net source of CO₂ to the atmosphere if warming reduces C storage in aboveground biomass and/or spurs increased CO₂ 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 CO₂ could become net sources of CO₂ to the atmosphere, further exacerbating climatic warming in a positive feedback loop. A clear signal has already been detected whereby global CO₂ 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 CO₂ 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

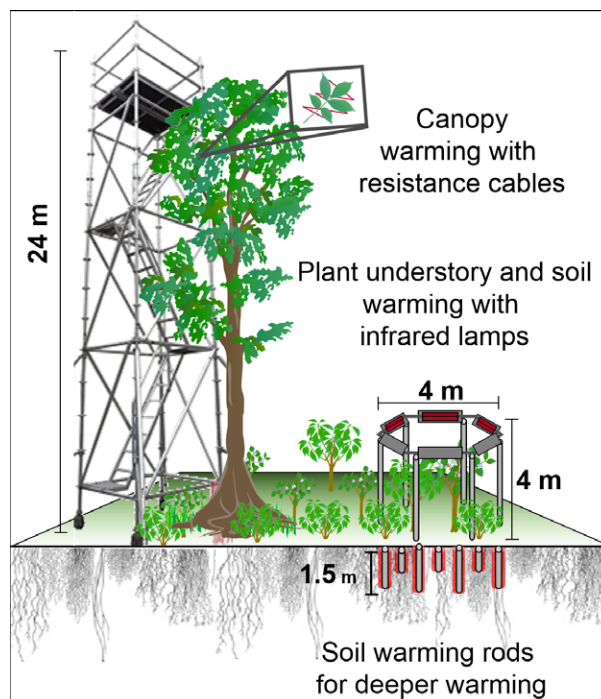


Fig. 2 Diagram (to scale) of an example scenario whereby various ecosystem components are warmed using different methods. Methods include branch- and leaf-level warming using resistance heater cables affixed to branches, which requires canopy access with tree climbing, towers, or cranes (e.g. Slot *et 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 CO₂ enrichment experiments should be of para-

mount 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 CO₂, 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.

Acknowledgements

We gratefully acknowledge A.E. Lugo, A.J. Burton, and M. Slot for friendly reviews of this manuscript, and the helpful suggestions of two anonymous reviewers. This synthesis was supported by the U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research, Terrestrial Ecosystem Sciences Program, under Award Number DE-SC-0011806 and the U.S. Geological Survey John Wesley Powell Center for Analysis and Synthesis. We thank the climate modeling groups (Table 1) for making available their model output, and we also acknowledge the World Climate Research Programme's Working Group on Coupled Modelling for the development of CMIP. The U.S. Department of Energy's Program for Climate Model Diagnosis and Intercomparison provides coordinating support for CMIP and led development of software infrastructure in partnership with the Global Organization for Earth System Science Portals. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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.

References

- Anderson BT (2011) Near-term increase in frequency of seasonal temperature extremes prior to the 2 degrees C global warming target. *Climatic Change*, **108**, 581–589.
- Anderson BT (2012) Intensification of seasonal extremes given a 2 degrees C global warming target. *Climatic Change*, **112**, 325–337.
- Aronson EL, McNulty SG (2009) Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, **149**, 1791–1799.
- Ballantyne AP, Alden CB, Miller JB, Tans PP, White JWC (2012) Increase in observed net carbon dioxide uptake by land and oceans during the past 50 years. *Nature*, **488**, 70–73.
- Beer C, Reichstein M, Tomelleri E *et al.* (2010) Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science*, **329**, 834–838.
- Betts RA, Cox PM, Collins M, Harris PP, Huntingford C, Jones CD (2004) The role of ecosystem-atmosphere interactions in simulated Amazonian precipitation decrease and forest dieback under global climate warming. *Theoretical and Applied Climatology*, **78**, 157–175.
- Boden TA, Marland G, Andres RJ (2010) *Global, Regional, and National Fossil-Fuel CO₂ Emissions*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, TN, USA.
- Bonan GB, Levis S (2010) Quantifying carbon-nitrogen feedbacks in the Community Land Model (CLM4). *Geophysical Research Letters*, **37**, L07401.
- Booth BBB, Jones CD, Collins M *et al.* (2012) High sensitivity of future global warming to land carbon cycle processes. *Environmental Research Letters*, **7**, 024002.
- Bouskill NJ, Lim HC, Borglin S, Salve R, Wood TE, Silver WL, Brodie EL (2013) Pre-exposure to short-term drought increases the resistance of subtropical forest soil bacterial communities to extended drought. *International Society of Microbial Ecology*, **3**, 384–394.
- Brando PM, Nepstad DC, Davidson EA, Trumbore SE, Ray D, Camargo P (2008) Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 1839–1848.
- Brando PM, Balch JK, Nepstad DC *et al.* (2014) Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 6347–6352.
- Cernusak LA, Winter K, Dalling JW *et al.* (2013) Tropical forest responses to increasing atmospheric CO₂: current knowledge and opportunities for future research. *Functional Plant Biology*, **40**, 531–551.
- Chambers JQ, Higuchi N, Teixeira LM, dos Santos J, Laurance SG, Trumbore SE (2004) Response of tree biomass and wood litter to disturbance in a Central Amazon forest. *Oecologia*, **141**, 596–611.
- Christensen JH, Hewitson B, Busuioic A *et al.* (2007) Regional climate projections. In: *Climate Change 2007: The Physical Science Basis, Summary for Policymakers. Contribution of Working Group 1 to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL), pp. 849–940. Cambridge University Press, New York.
- Clark DA, Piper SC, Keeling CD, Clark DB (2003) Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 5852–5857.
- Clark DB, Clark DA, Oberbauer SF (2010) Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO₂. *Global Change Biology*, **16**, 747–759.
- Clark DA, Clark DB, Oberbauer SF (2013) Field-quantified responses of tropical rain-forest aboveground productivity to increasing CO₂ and climatic stress, 1997–2009. *Journal of Geophysical Research-Biogeosciences*, **118**, 1–12.
- Cleveland CC, Townsend AR (2006) Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 10316–10321.
- Collins M, Knutti R, Arblaster J *et al.* (2013) Long-term climate change: projections, commitments and irreversibility. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM), pp. 1029–1136. Cambridge University Press, Cambridge, UK and New York, NY.
- Condit R, Engelbrecht BMJ, Pino D, Perez R, Turner BL (2013) Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 5064–5068.
- da Costa ACL, Galbraith D, Almeida S *et al.* (2010) Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytologist*, **187**, 579–591.
- Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184–187.
- Cox PM, Pearson D, Booth BB, Friedlingstein P, Huntingford C, Jones CD, Luke CM (2013) Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature*, **494**, 341–344.
- Cusack DF, Torn MS, McDowell WH, Silver WL (2010) The response of heterotrophic activity and carbon cycling to nitrogen additions and warming in two tropical soils. *Global Change Biology*, **16**, 2555–2572.
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 6668–6672.
- Diamond SE, Nichols LM, McCoy N *et al.* (2012) A physiological trait-based approach to predicting the responses of species to experimental climate warming. *Ecology*, **93**, 2305–2312.
- Diffenbaugh NS, Scherer M (2011) Observational and model evidence of global emergence of permanent, unprecedented heat in the 20th and 21st centuries. *Climatic Change*, **107**, 615–624.
- DOE US (2012) Research Priorities for Tropical Ecosystems Under Climate Change Workshop Report. DOE/SC-0153 U.S. Department of Energy Office of Science, science.energy.gov/ber/news-and-resources/

- Doughty CE, Goulden ML (2008) Are tropical forests near a high temperature threshold? *Journal of Geophysical Research-Biogeosciences*, **113**, G00B07.
- Elsler JJ, Bracken MES, Cleland EE *et al.* (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, **10**, 1135–1142.
- Espirito-Santo FDB, Gloor M, Keller M *et al.* (2014) Size and frequency of natural forest disturbances and the Amazon forest carbon balance. *Nature Communications*, **5**, 3434.
- Fatih S, Leuzinger S, Korner C (2014) Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. *New Phytologist*, **201**, 1086–1095.
- Fisher R, McDowell N, Purves D *et al.* (2010) Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations. *New Phytologist*, **187**, 666–681.
- Foley JA, Costa MH, Delire C, Ramankutty N, Snyder P (2003) Green surprise? How terrestrial ecosystems could affect earth, Åos climate. *Frontiers in Ecology and the Environment*, **1**, 38–44.
- Fu R, Yin L, Li WH *et al.* (2013) Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 18110–18115.
- Galbraith D, Levy PE, Sitch S, Huntingford C, Cox P, Williams M, Meir P (2010) Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change. *New Phytologist*, **187**, 647–665.
- Good P, Jones C, Lowe J, Betts R, Gedney N (2013) Comparing tropical forest projections from two generations of Hadley Centre Earth System Models, HadGEM2-ES and HadCM3LC. *Journal of Climate*, **26**, 495–511.
- Graham EA, Mulkey SS, Kitajima K, Phillips NG, Wright SJ (2003) Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 572–576.
- Gurney KR, Castillo K, Li B, Zhang X (2012) A positive carbon feedback to ENSO and volcanic aerosols in the tropical terrestrial biosphere. *Global Biogeochemical Cycles*, **26**, GB1029.
- Hall SJ, McDowell WH, Silver WL (2013) When wet gets wetter: decoupling of moisture, redox biogeochemistry, and greenhouse gas fluxes in a humid tropical forest soil. *Ecosystems*, **16**, 576–589.
- Hanson PJ, Childs KW, Wullschlegel SD, Riggs JS, Thomas WK, Todd DE, Warren JM (2011) A method for experimental heating of intact soil profiles for application to climate change experiments. *Global Change Biology*, **17**, 1083–1096.
- Hasler N, Avissar R (2007) What controls evapotranspiration in the amazon basin? *Journal of Hydrometeorology*, **8**, 380–395.
- Holdridge LR (1967) *Life Zone Ecology*. Tropical Science Center, San Jose, Costa Rica.
- Holland EA, Neff JC, Townsend AR, McKeown B (2000) Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: implications for models. *Global Biogeochemical Cycles*, **14**, 1137–1151.
- Hungate BA, Dukes JS, Shaw MR, Luo Y, Field CB (2003) Nitrogen and climate change. *Science*, **302**, 1512–1513.
- Huntingford C, Zelazowski P, Galbraith D *et al.* (2013) Simulated resilience of tropical rainforests to CO₂-induced climate change. *Nature Geoscience*, **6**, 268–273.
- IPCC (2011) Special report on managing the risks of extreme events and disasters to advance climate change adaptation (SREX). Summary for Policymakers. Intergovernmental Panel on Climate Change Secretariat. Geneva, Switzerland.
- Janzen DH (1967) Why mountain passes are higher in the tropics. *American Naturalist*, **101**, 233–249.
- Jarvi MP, Burton AJ (2013) Acclimation and soil moisture constrain sugar maple root respiration in experimentally warmed soil. *Tree Physiology*, **33**, 949–959.
- Jentsch A, Kreyling J, Beierkuhnlein C (2007) A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment*, **5**, 365–374.
- Jobbagy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications*, **10**, 423–436.
- Kimball BA, Conley MM, Wang S, Lin X, Luo C, Morgan J, Smith D (2008) Infrared heater arrays for warming ecosystem field plots. *Global Change Biology*, **14**, 309–320.
- Kimball BA, Conley MM, Lewin KF (2012) Performance and energy costs associated with scaling infrared heater arrays for warming field plots from 1 to 100 m. *Theoretical and Applied Climatology*, **108**, 247–265.
- Kirtman B, Power SB, Adedoyin JA *et al.* (2013) Near-term climate change: projections and predictability. In: *Climate Change 2013: The Physical Science Basis*. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM), pp. 953–1028. Cambridge University Press, Cambridge, UK and New York, NY.
- Korner C (2009) Responses of humid tropical trees to rising CO₂. *Annual Review of Ecology Evolution and Systematics*, **40**, 61–79.
- Krause GH, Cheesman AW, Winter K, Krause B, Virgo A (2013) Thermal tolerance, net CO₂ exchange and growth of a tropical tree species, *Ficus insipida*, cultivated at elevated daytime and nighttime temperatures. *Journal of Plant Physiology*, **170**, 822–827.
- Langenfelds RL, Francey RJ, Pak BC, Steele LP, Lloyd J, Trudinger CM, Allison CE (2002) Interannual growth rate variations of atmospheric CO₂ and its delta C-13, H-2, CH₄, and CO between 1992 and 1999 linked to biomass burning. *Global Biogeochemical Cycles*, **16**, 230.
- Leuzinger S, Luo YQ, Beier C, Dieleman W, Vicca S, Korner C (2011) Do global change experiments overestimate impacts on terrestrial ecosystems? *Trends in Ecology & Evolution*, **26**, 236–241.
- Lewis SL, Lloyd J, Sitch S, Mitchard ETA, Laurance WF (2009) Changing ecology of tropical forests: evidence and drivers. *Annual Review of Ecology Evolution and Systematics*, **40**, 529–549.
- Lloyd J, Farquhar GD (2008) Effects of rising temperatures and [CO₂] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 1811–1817.
- Losos EC, Leigh EG (2004) *Tropical Forest Diversity and Dynamism*. University of Chicago Press, Chicago, IL.
- Lukac M, Calfapietra C, Lagomarsino A, Loreto F (2010) Global climate change and tree nutrition: effects of elevated CO₂ and temperature. *Tree Physiology*, **30**, 1209–1220.
- Luo YQ, Wan SQ, Hui DF, Wallace LL (2001) Acclimatization of soil respiration to warming in a tall grass prairie. *Nature*, **413**, 622–625.
- Luo Y, Su BO, Currie WS *et al.* (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience*, **54**, 731–739.
- Luo Y, Melillo J, Niu S *et al.* (2011) Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Global Change Biology*, **17**, 843–854.
- Malhi Y, Silman M, Salinas N, Bush M, Meir P, Saatchi S (2010) Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. *Global Change Biology*, **16**, 3171–3175.
- Marin-Spiotta E, Sharma S (2013) Carbon storage in successional and plantation forest soils: a tropical analysis. *Global Ecology and Biogeography*, **22**, 105–117.
- McDowell N, Pockman WT, Allen CD *et al.* (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, **178**, 719–739.
- Meir P, Grace J (2005) The response to drought by tropical rain forest ecosystems. In: *Tropical Forests and Global Climate Change* (ed. Malhi Y), pp 75–84. OUP, Oxford.
- Meir P, Wood TE, Galbraith DR, Brando PM, da Costa ACL, Rowland L, Ferreira LV (In Press) Threshold responses to drought by trees and soil in tropical forests – Insights from field experiments. *Bioscience*.
- Melillo JM, Butler S, Johnson J *et al.* (2011) Soil warming, carbon-nitrogen interactions, and forest carbon budgets. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 9508–9512.
- Mora C, Frazier AG, Longman RJ *et al.* (2013) The projected timing of climate departure from recent variability. *Nature*, **502**, 183–187.
- Nepstad DC, Moutinho P, Dias MB *et al.* (2002) The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. *Journal of Geophysical Research-Atmospheres*, **107**, D20, 8085.
- Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G (2007) Mortality of large trees and lianas following experimental drought in an amazon forest. *Ecology*, **88**, 2259–2269.
- Norby RJ, Luo YQ (2004) Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world. *New Phytologist*, **162**, 281–293.
- Norby RJ, Zak DR (2011) Ecological lessons from free-air CO₂ enrichment (FACE) experiments. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 181–203.
- Oechel WC, Vourlitis GL, Hastings SJ, Zulueta RC, Hinzman L, Kane D (2000) Acclimation of ecosystem CO₂ exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, **406**, 978–981.
- Pan Y, Birdsey RA, Fang JY *et al.* (2011) A large and persistent carbon sink in the world's forests. *Science*, **333**, 988–993.
- Pan Y, Birdsey RA, Phillips OL, Jackson RB (2013) The structure, distribution, and biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics*, **44**, 593–622.
- Peñuelas J, Poulter B, Sardans J *et al.* (2013) Human-induced nitrogen-phosphorus imbalances alter natural and managed ecosystems across the globe. *Nature Communications*, **4**, 230.

- Phillips OL, van der Heijden G, Lewis SL *et al.* (2010) Drought-mortality relationships for tropical forests. *New Phytologist*, **187**, 631–646.
- Piao SL, Sitch S, Ciais P *et al.* (2013) Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO₂ trends. *Global Change Biology*, **19**, 2117–2132.
- Powers JS, Corre MD, Twine TE, Veldkamp E (2011) Geographic bias of field observations of soil carbon stocks with tropical land-use changes precludes spatial extrapolation. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 6318–6322.
- Randerson JT (2013) Climate science: global warming and tropical carbon. *Nature*, **494**, 319–320.
- Reed SC, Townsend AR, Taylor PG, Cleveland CC (2011) Phosphorus cycling in tropical forests growing on highly weathered soils. In: *Phosphorus in Action. Soil Biology* (eds Bünemann E, Oberson A, Frossard E), pp. 339–369. Springer-Verlag, Berlin-Heidelberg.
- Reed SC, Wood TE, Cavaleri MA (2012) Tropical forests in a warming world. *New Phytologist*, **193**, 27–29.
- Reich PB (2014) The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *Journal of Ecology*, **102**, 275–301.
- Reich PB, Hobbie SE (2013) Decade-long soil nitrogen constraint on the CO₂ fertilization of plant biomass. *Nature Climate Change*, **3**, 278–282.
- Restrepo-Coupe N, da Rocha HR, Hutryra LR *et al.* (2013) What drives the seasonality of photosynthesis across the Amazon basin? A cross-site analysis of eddy flux tower measurements from the Brasil flux network. *Agricultural and Forest Meteorology*, **182**, 128–144.
- Riahi K, Grubler A, Nakicenovic N (2007) Scenarios of long-term socio-economic and environmental development under climate stabilization. *Technological Forecasting and Social Change*, **74**, 887–935.
- Richards PW (1952) *The Tropical Rain Forest: An Ecological Study*. Cambridge University Press, Cambridge.
- da Rocha HR, Manzi AO, Cabral OM *et al.* (2009) Patterns of water and heat flux across a biome gradient from tropical forest to savanna in Brazil. *Journal of Geophysical Research-Biogeosciences*, **114**, G00B12.
- Rustad LE (2008) The response of terrestrial ecosystems to global climate change: towards an integrated approach. *Science of the Total Environment*, **404**, 222–235.
- Rustad LR, Campbell JC, Marion GM *et al.* (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543–562.
- Saleska SR, Didan K, Huete AR, da Rocha HR (2007) Amazon forests green-up during 2005 drought. *Science*, **318**, 612.
- Saleska SR, da Rocha HR, Kruijt B, Nobre A (2009) Ecosystem carbon fluxes and Amazon forest metabolism. In: *Amazonia and Global Change* (eds Keller M, Bustamante M, Gash J, Silva Dias P), pp. 389–407. Geophysical Monograph Series, American Geophysical Union, Washington, DC. doi: 10.1029/2008GM000739
- Schuur EAG (2003) Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation. *Ecology*, **84**, 1165–1170.
- Shiels AB, Gonzalez G (2014) Understanding the key mechanisms of tropical forest responses to canopy loss and biomass deposition from experimental hurricane effects. *Forest Ecology and Management*, **332**, 1–10.
- Slot M, Rey-Sánchez C, Gerber S, Lichstein JW, Winter K, Kaoru K (2014) Thermal acclimation of leaf respiration of tropical trees and lianas: response to experimental canopy warming, and consequences for tropical forest carbon balance. *Global Change Biology*, **20**, 2915–2926.
- Smith NG, Dukes JS (2012) Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and CO₂. *Global Change Biology*, **19**, 45–63.
- Sotta ED, Veldkamp E, Schwendenmann L *et al.* (2007) Effects of an induced drought on soil carbon dioxide (CO₂) efflux and soil CO₂ production in an Eastern Amazonian rainforest, Brazil. *Global Change Biology*, **13**, 2218–2229.
- Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G, Zimov S (2009) Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, **23**, GB2023.
- Taylor KE, Stouffer RJ, Meehl GA (2012) An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society*, **93**, 485–498.
- Townsend AR, Vitousek PM, Desmarais DJ, Tharpe A (1997) Soil carbon pool structure and temperature sensitivity inferred using CO₂ and (13)CO₂ incubation fluxes from five Hawaiian soils. *Biogeochemistry*, **38**, 1–17.
- Townsend AR, Asner GP, Cleveland CC (2008) The biogeochemical heterogeneity of tropical forests. *Trends in Ecology & Evolution*, **23**, 424–431.
- Townsend AR, Cleveland CC, Houlton BZ, Alden CB, White JWC (2011) Multi-element regulation of the tropical forest carbon cycle. *Frontiers in Ecology and the Environment*, **9**, 9–17.
- Vargas R, Allen MF (2008) Diel patterns of soil respiration in a tropical forest after Hurricane Wilma. *Journal of Geophysical Research-Biogeosciences*, **113**, G03021.
- Vasconcelos SS, Zarin DJ, Capanu M *et al.* (2004) Moisture and substrate availability constrain soil trace gas fluxes in an eastern Amazonian regrowth forest. *Global Biogeochemical Cycles*, **18**, GB2009.
- Vasconcelos SS, Zarin DJ, Araujo MM, Rangel-Vasconcelos LGT, de Carvalho CJR, Staudhammer CL, Oliveira FD (2008) Effects of seasonality, litter removal and dry-season irrigation on litterfall quantity and quality in eastern Amazonian forest regrowth, Brazil. *Journal of Tropical Ecology*, **24**, 27–38.
- Wang WL, Ciais P, Nemani RR *et al.* (2013) Variations in atmospheric CO₂ growth rates coupled with tropical temperature. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 13061–13066.
- Wang XH, Piao SL, Ciais P *et al.* (2014) A two-fold increase of carbon cycle sensitivity to tropical temperature variations. *Nature*, **506**, 212–215.
- van der Werf GR, Randerson JT, Giglio L, Collatz GJ, Kasibhatla PS, Arellano AF (2006) Interannual variability in global biomass burning emissions from 1997 to 2004. *Atmospheric Chemistry and Physics*, **6**, 3423–3441.
- Wieder RK, Wright SJ (1995) Tropical forest litter dynamics and dry season irrigation on barro-colorado island, panama. *Ecology*, **76**, 1971–1979.
- Wood TE, Silver WL (2012) Strong spatial variability in trace gas dynamics following experimental drought in a humid tropical forest. *Global Biogeochemical Cycles*, **26**, GB3005.
- Wood TE, Lawrence D, Clark DA, Chazdon RL (2009) Rain forest nutrient cycling and productivity in response to large-scale litter manipulation. *Ecology*, **90**, 109–121.
- Wood TE, Cavaleri MA, Reed SC (2012) Tropical forest carbon balance in a warmer world: a critical review spanning microbial- to ecosystem-scale processes. *Biological Reviews*, **87**, 912–927.
- Wright JS (2010) The future of tropical forests. *Annals of the New York Academy of Sciences*, **1195**, 1–27.
- Wright SJ (2013) The carbon sink in intact tropical forests. *Global Change Biology*, **19**, 337–339.
- Wright SJ, Muller-Landau HC, Schipper J (2009) The future of tropical species on a warmer planet. *Conservation Biology*, **23**, 1418–1426.
- Wright SJ, Yavitt JB, Wurzbarger N *et al.* (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology*, **92**, 1616–1625.
- Xia JY, Chen JQ, Piao SL, Ciais P, Luo YQ, Wan SQ (2014) Terrestrial carbon cycle affected by non-uniform climate warming. *Nature Geoscience*, **7**, 173–180.
- Zhao MS, Running SW (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science*, **329**, 940–943.
- Zhou XH, Fu YL, Zhou LY, Li B, Luo YQ (2013) An imperative need for global change research in tropical forests. *Tree Physiology*, **33**, 903–912.
- Ziehn T, Kattge J, Knorr W, Scholze M (2011) Improving the predictability of global CO₂ assimilation rates under climate change. *Geophysical Research Letters*, **38**, L10404.
- Zuidema PA, Baker PJ, Groenendijk P, Schippers P, van der Sleen P, Vlam M, Sterck F (2013) Tropical forests and global change: filling knowledge gaps. *Trends in Plant Science*, **18**, 413–419.