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Introduction



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New insights into the variability of the tropical land carbon cycle from the El Niño of 2015/2016

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1. Introduction

A pivotal question in global change science is what role the biosphere plays in ameliorating the rate of climate change and what risks exist that there may be possible tipping points in the Earth System where the biosphere switches from being a brake to an accelerator of climate change [1]. Of the potential major global tipping points, the fate of the tropical forests is among the most important and iconic, with some studies suggesting that climate change could lead to extensive dieback of tropical forests (and the Amazon forest in particular), resulting in further carbon release, major loss of biodiversity, drying of regional climates and thereby further forest dieback and intensification of global warming [2]. However, these scenarios have been the subject of much debate, with questions about whether existing biosphere models sufficiently capture the consequences for key ecological processes, which are dependent on complex system attributes such as species' functional diversity and demography, and on factors such as forest fire that are poorly described [3].

One issue of particular concern is the interannual variability of the tropical land carbon cycle, in particular during El Niño events. During such events, a pool of warm surface water migrates across from the Western Pacific to the Central and Eastern Pacific, disrupting global atmospheric circulation patterns associated with the Walker circulation and causing warming of the tropics in particular. The El Niño Southern Oscillation (ENSO) is the largest mode of interannual variability both in the climate system [4] and in the global carbon cycle [5]. It has long been noted that El Niño events correlate with a surge in the rate of rise of atmospheric carbon dioxide concentrations (e.g. [6]). Global studies of the spatial pattern of carbon dioxide concentration tend to trace the source of almost all of this extra carbon dioxide to the terrestrial tropics and demonstrate strong correlation with the mean temperature of tropical land regions [7–9], but the exact mechanism that causes this switch is still poorly understood. Do the tropics emit more carbon during El Niño events because of reduced photosynthesis, enhanced plant, necromass or soil respiration, increased incidence and intensity of fire, or some combination of these factors? And do particular regions of the tropics play a dominant role in this variability? Perhaps most importantly, a better understanding of the mechanisms may give us insight into a critical question: is this flickering of the tropical carbon cycle an early warning of a potentially dangerous tipping point or merely an interesting biogeochemical curiosity of the Earth System?

The 2015/16 El Niño was the strongest such event since at least 1997/98 and possibly since much earlier. Moreover, because each new El Niño event occurs in the context of a trend of anthropogenic global warming, in many regions of the tropics it resulted in the hottest mean temperatures yet observed [10]. These hotter and drier conditions are closer to those anticipated under future model-generated climate scenarios. As expected, the rate of rise of atmospheric CO₂ surged during this event, increasing by a record 3.4 ppm in 2016, and resulting in the mean global atmospheric CO₂ concentration staying above the

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symbolically significant value of 400 ppm for the entire year [6]. One-quarter of this record rise was caused by the biosphere's response to the El Niño (the rest was from direct anthropogenic emissions) and in particular response of the tropical biosphere [7,11].

The original concept of a potential tropical forest tipping point was raised through biosphere modelling studies (e.g. [2,12]), but the topic has engaged a much wider range of approaches in the burgeoning, many-stranded disciplines of the Earth System Sciences. These disciplines include (i) spaceborne and airborne remote sensing of vegetation cover and properties, fire patterns and impacts, atmospheric conditions and trace gas concentrations; (ii) in situ monitoring of ecosystem demography and dynamics at timescales ranging from annual or multi-annual, through forest inventories reaching back a decade or more; (iii) intensive studies of vegetation and soil ecophysiological processes connected to carbon and water cycling; (iv) inversion techniques applied to the spatial pattern of CO2 and other trace gas concentrations, obtained either from global networks of in situ observations or more recently from satellite observations; (v) ecosystem models of vegetation and soil processes, many of these nested in Earth System models.

All these methodologies have made major conceptual and analytical advances over the past decade and already interact with each other. El Niño events provide an opportunity to test and challenge our integrated understanding across these disciplines. The global observed enhanced rise of CO₂ during an El Niño is an unambiguous benchmark observation that these various approaches can dissect and disentangle to arrive at a consistent mechanistic understanding.

In 1997/98, both field and satellite observation networks for the tropics had been nascent. There were no extensive forest observation networks with high temporal resolution (e.g. [13]) and a few detailed field studies of ecophysiological processes. Satellite observations were limited [14]: for example, there were no RADAR-platform satellites focused on tropical rainfall, no high-frequency coverage of land cover change, no routine monitoring of moisture, canopy fluorescence, biomass and structure, no monitoring of atmospheric column concentrations of carbon monoxide, formaldehyde and other fire-associated pollutants, and global biosphere models, and atmospheric inversion studies were at a relatively primitive stage with no operational global model incorporating carbon cycle feedbacks from the biosphere.

The 2015/16 El Niño, in contrast, received much more attention and provided a natural showcase for these multiple strands of Earth System monitoring, with the advent of novel and multiple satellite-based systems, networks of forest monitoring plots, detailed ecophysiological studies and flux tower networks. However, given that such events are hard to predict, international efforts were not coordinated and coherent across the broad reach of field observation, atmospheric observation, remote sensing and biosphere modelling.

This paper introduces a thematic issue that attempts to combine and integrate these various approaches to arrive at a multidisciplinary synthesis of our understanding of the carbon dynamics associated with the El Niño. Research is presented focusing on the range of techniques available across the Earth System Science community to obtain a more coherent picture of the scale, geography, impact and understanding derived from the 2015/16 El Niño.

A multidisciplinary synthesis of the 2015/6 El Niño provides a number of opportunities for the advancement of our scientific understanding of the functioning of the tropical biosphere. These include opportunities to:

- (1) test our integrated understanding of the Earth System: how well do different scientific disciplines converge in explaining the causes, patterns and mechanisms of the biosphere carbon emissions during the El Niño?
- (2) identify and quantify the relative importance of the key processes (e.g. photosynthesis, respiration, mortality) involved in driving the variability in the tropical carbon sink;
- (3) briefly explore vegetation responses to mean temperatures not previously experienced for many centuries or millennia;
- (4) explore what possible clues this El Niño event gives into long-term pathways of how the tropical biosphere is responding to a warming and more variable climate;
- (5) identify areas that are particularly impacted or sensitive, and that may be more at risk to current and future climate change and climate extremes;
- (6) examine whether human-modified forests (e.g. logged, secondary, fragmented or previously burnt), an increasingly prevalent feature of the tropics, differ from intact forests in their sensitivity to extreme climate events.

2. The climate context

To understand the effects and biosphere feedbacks of the El Niño, we first need to understand its meteorological footprint. This is not as straightforward as it might seem: a range of global meteorological products exist and are widely employed, each using varying combinations of ground weather station and atmospheric radiosonde observations, satellite data products and meteorological models. The tropical forest and savanna regions can be particularly challenging, as in situ observations are frequently sparse and have poor continuity. Burton et al. [15] map and explore the consistencies and discrepancies of these various products in terms of temperature and rainfall, to provide recommendations on which products seem more robust. Jimenez et al. [10] provide a more expansive analysis of temperature and drought anomalies associated with the 2015/16 event and compare its patterns with those of previous strong El Niño events.

The two studies find overall temperature anomalies of +1°C during the El Niño event, with areas up to 3°C above average in NE Amazonia in late 2015. Temperature anomalies for Africa were smaller and more divergent between products (0.5-1°C). Annual rainfall anomalies of around 200 mm below the long-term mean were consistently recorded across Eastern Amazonia and insular southeast Asia, but not in central Africa. Despite some overall consistency, there is large variance between alternative climate re-analysis products across the spatial and temporal domains of the 2015/16 El Niño event. This illustrates the pressing need for improvements in the generation of historical climate datasets, both for attribution of other observed biospheric signals and for driving land surface models, which have often proven highly sensitive to their meteorological inputs [16,17].

3. Remote sensing

The 2015/16 El Niño was the first major global climate fluctuation when a wide range of satellite observations were available that simultaneously observed land, ocean and atmospheric properties associated with the carbon cycle. Palmer [14] provides an overview of these new technologies, which include satellite-retrieved data to characterize photosynthesis (solar-induced fluorescence, SIF), fire (active fire data, burned area), vegetation cover and leaf phenology (vegetation indices), hydrology (water storage inferred from gravitational anomalies) and column atmospheric concentrations of carbon dioxide and other informative trace gases such as carbon monoxide and formaldehyde (both indicators of fire emissions). Many of these new methods (in particular SIF) still have methodological and interpretation challenges, and the El Niño provided an excellent opportunity to test these approaches. The full potential of these multiple simultaneous datasets has yet to be exploited, but several of the studies in this theme issue use some of these data, including SIF [7,18,19], gravitational anomalies [7] and atmospheric trace gases (e.g. [7,20]).

Luo et al. [18] explore six models of changes in gross primary productivity (GPP) with satellite-derived inputs, together with four remote-sensed datasets of SIF. During the El Niño, the models suggest a consistent reduction in GPP in the tropical forests of eastern Amazonia and central Africa, with large negative anomalies also observed in the savannah regions of southern Africa and eastern Australia. The four SIF datasets show both substantial inter-product variance as well as less of a decline in 2016, but overall their results agree with the GPP models, suggesting a strong decline in photosynthesis in Amazonia and in southern Africa and Australia. In total, this analysis suggests an overall negative anomaly in pan-tropical photosynthesis of around 1 Pg C over the duration of the El Niño. Koren et al. [19] present a more detailed study of SIF variation in Amazonia. They find a similar result of strongest declines in photosynthesis in eastern Amazonia, particularly focused in the dry season of late 2015. The decline appears strongly predictable from atmospheric water vapour deficit (more so than from soil moisture), suggesting that atmospheric conditions are particularly important in driving plants to experience water stress.

Additionally, Anderson *et al.* [21] present a long-term analysis of droughts from 1981 to 2016 for Brazilian Amazonia, quantifying the recent El Niño impact on vegetation using the enhanced vegetation index (EVI). By focusing on the concept of vulnerability that takes into consideration both exposure and sensitivity of forests to drought, they show that repeated exposure to recent droughts is increasing the sensitivity of Amazonian vegetation, as demonstrated by year-to-year increased intensity of negative EVI anomalies. This suggests that Amazonia is becoming more vulnerable to extreme drought events.

4. Atmospheric models

A key tool employed in global carbon cycle studies is the integration of atmospheric CO_2 observations with meteorological models with the goal of identifying the spatial pattern of CO_2 emissions and absorption (inversion models). While potentially very powerful, these approaches are challenged by the sparse observations of CO_2 concentrations in tropical latitudes, coupled with the vigorous mixing of the tropical atmosphere that rapidly dilutes spatial variation in CO_2 concentrations.

Gloor et al. [7] conduct a detailed inversion analysis for the 2015/16 El Niño, bringing in valuable additional datasets such as CO₂ observations from South America, water content information derived from gravitational anomalies from the Gravity Recovery and Climate Experiment (GRACE) mission, CO column measurements from the Measurements Of Pollution In The Troposphere (MOPITT) sensor as an indicator of fire-associated carbon emission and SIF as a metric of photosynthetic activity. They find a positive anomaly 1.9-2.1 Pg C of carbon emissions from land regions during the event, a magnitude consistent with previous strong El Niños. The combination of these biospheric emissions with steadily increasing fossil fuel-associated emissions led to record atmospheric CO2 rises in 2015 and 2016 (as documented by Betts et al. [6]). The sensitivity of the tropical biosphere carbon cycle to ENSO is large, but they find no evidence that it is increasing over time (in contrast to the remote sensing analysis for Brazilian Amazonia presented by Anderson et al. [21]). The carbon anomaly appears predominantly caused by water stress in central and eastern Amazonia (releasing 0.5 Pg C), tropical Africa (0.5 Pg C) and, to a lesser extent, southern Africa (0.2 Pg C) and southeast Asia (0.2 Pg C). The Amazonian anomaly is consistent with a drought-related decrease in photosynthesis inferred from the SIF observations, and the Asian anomaly seems predominantly associated with fires. These fires were less intense and extensive than SE Asia's substantial fire emissions in 1997/ 98, partially because conditions were not as dry for a prolonged period this time. The African source is the most puzzling as there was a limited indication of strong drought affecting photosynthesis, but high temperatures may have increased plant and soil respiration. Except for this large tropical African source, the analysis of Gloor et al. [7] is broadly consistent with a previously published inversion analysis based primarily on satellite data [22], once the different baselines in the two studies are factored out.

Rödenbeck et al. [8] provide a longer-term perspective on interactions between ENSO, climate anomalies and the carbon cycle. By employing a limited subset of atmospheric observations that stretch back several decades, they present a carbon anomaly analysis spanning the period 1957-2017. They demonstrate a strong correlation between ENSO, temperature anomalies and tropical carbon emissions. A potentially important indicator of tropical carbon cycle instability would be if the sensitivity of the CO2 anomaly to the temperature anomaly increased over time. They find a long-term pattern of increasing sensitivity until the early 2000s, followed by decreasing sensitivity. However, they suggest that these trends are partially explained by a shifting spatial pattern of where El Niño's impacts are greatest. Their analysis suggests the key carbon anomaly regions tend to be eastern Amazonia and south-central Africa, a pattern confirmed in the 2015/16 event. This is consistent with the more data-rich but shorter-term analysis by Gloor et al. [7].

5. Biosphere models

Land surface models (LSMs) provide an opportunity to test the sensitivity of the global or regional carbon and water cycle responses to anomalies in temperature and drought that arise from El Niño events. An analysis of 16 LSMs, driven with common atmospheric driver data, demonstrates that the ensemble mean of all the LSMs was able to reproduce the main observed patterns of interannual variability in the land carbon sink [11], when compared to carbon inversion flux estimates and some remote sensing estimates. These model simulations suggest that the reduction in gross primary production (i.e. canopy photosynthesis) was the main driver of the decreasing carbon sink across all tropical regions during the 2015/16 El Niño. This disagrees with a previously published inversion study that attributed the decrease to higher respiration fluxes in Africa and greater fire emissions in Asia [22]. However, there was a very high range of responses between LSMs, and the agreement between the LSMs and inversion studies varies depending on the El Niño event studied. Considering Amazonia alone, both van Schaik et al. [23] and Bastos et al. [11] provide similar estimates of the reductions in total Amazonian photosynthesis during the 2015/16 El Niño event, which also fit within the ranges described by inversion modelling and chlorophyll fluorescence (approx. 0.9–1.5 Pg C yr⁻¹ [7,19,22]).

The modelling results reinforce two important issues: (i) studies of vegetation responses to an El Niño with any individual model may be subject to strong structural or parametric bias and (ii) across LSMs there remains high variance in their capacity to accurately simulate vegetation responses to El Niño events. Emerging observational constraints on ecosystem behaviour, documented in this theme issue and elsewhere (e.g. [24-28]), may provide more and better benchmarks, thereby improving model structures and calibrations to increase their predictive fidelity in future such inter-comparisons.

6. Field studies of ecophysiology and carbon dynamics

Given the high variance in modelled simulation of the impacts of the El Niño on vegetation carbon dynamics, it is vital to further inform and test model structure against in situ ecophysiological field studies. An understanding of the physiological responses of tropical forests to El Niño events can be obtained using an array of techniques currently available to field ecologists. These include, but are not restricted to, monitoring tree mortality and growth, monitoring tree carbon assimilation with measurements of photosynthesis and stomatal conductance, estimating changes in tree transpiration using sap flow, monitoring carbon release in the form of heterotrophic and/or autotrophic respiration, and measuring net canopy-atmosphere fluxes through eddy covariance flux towers.

Many of the detailed process studies during this El Niño were focused on the Amazon region. However, the Global Ecosystems Monitoring (GEM) network (gem.tropicalforests.ox.ac.uk) attempts to provide a pantropical analysis of forest carbon dynamics and ecophysiology. Rifai et al. [24] report an analysis of tree growth from sites across Amazonia, Africa and Borneo. They report sharp declines in tree growth in response to the El Niño, driven by increases in soil water deficit and atmospheric water vapour deficit. If stem growth is taken as an indicator of changes in total forest carbon production, then, by extrapolation, the Amazon forest dominated the global signal of reduced productivity during the 2015/16 El Niño, and also generally dominates the total interannual variation in the productivity of the

tropics. Variation in southeast Asia was a secondary factor and there was a negligible net signal from tropical Africa. This field-observed Amazon signal is consistent with the global atmospheric inversion and biospheric modelling estimates [7,8,11] but the negligible effect in tropical Africa is not. Stem growth alone may, however, not be a good indicator of whether total carbon assimilation (GPP) was reduced during this period, due to the well-established decoupling between patterns of tree growth and canopy photosynthetic processes [29]. Forthcoming studies from the GEM network will provide a more complete examination of the tropical forest carbon budget during the El Niño, including examination of respiration. A detailed study of an eastern Amazonian site by Santos et al. [30] reported that tropical Amazonian trees suffered up to a 28% reduction in photosynthesis driven by stomatal closure during the 2015/16 El Niño. This is broadly consistent with the decline in woody growth in eastern Amazonia reported by Rifai et al. [24].

What is critical to interpreting changes in the signals from any of these variables over time is a clear understanding of which El Niño-mediated changes in climate are responsible for the observed variation in tree growth and carbon cycling. Brum et al. [25] find that atmospheric water vapour deficit (VPD), rather than changes in soil moisture and precipitation, is the key driver of increasing dry season transpiration during the 2015/16 El Niño in a site in eastern Amazonia. Fontes et al. [28] find sharp drops in water flux through trees, associated with drops in both leaf and xylem safety margins. Both studies nonetheless report that several tropical Amazonian species did not downregulate transpiration in response to the extreme El Niño dry season, in agreement with previous results from a long-term drought experiment in the Amazon [31]. This suggests that trees may be prioritizing carbon production at the expense of risking great hydraulic damage. The largest trees were found to be responsible for the greatest proportion of transpiration flux [25] and were also shown to have the greatest change in mortality rate as a consequence of drought [27]. Shenkin et al. [27] found a relationship between drought-induced mortality rates and tree heights in Amazonian trees, but a weaker relationship with crown exposure, suggesting a limited role for atmospheric demand and a strong impact of water supply on the risk of death. Rather unexpectedly, the drought-induced mortality signal was buffered in logged forests during El Niño events, plausibly because of decreased competition for water and other resources in these forests. Hence, results from Brum et al. [25] and Shenkin et al. [27] suggest that it is possible for stand thinning (due to prior mortality, logging or disturbance) to limit hydraulic risk and mortality rates in tropical forests.

These ecophysiological observations and insights can lead to improvement in the model representation of key processes. Eller et al. [32] address a key model structural issue in LSMs through designing a new stomatal optimization of xylem model, which optimizes stomatal conductance to maximize plant carbon gain, while simultaneously minimizing plant hydraulic damage. Incorporating this plant hydraulic scheme into an LSM creates two new insights into modelling El Niño events. First, it demonstrates that the sensitivity of the vegetation to atmospheric drought or soil drought can vary between tropical sites, even within the same continent. Second, it also demonstrates that if plant hydraulics were incorporated into LSMs it is plausible that the humid tropical regions would be simulated as being more sensitive, in terms of carbon loss, to El Niño events. In coupling a hydrology model to a vegetation model, van Schaik et al. [23] demonstrate that shifts in net biome production across different regions are driven by shifts in the climate drivers controlling GPP. They simulate that the regions with the greatest reductions in GPP during the 2015/16 El Niño are controlled largely by negative soil moisture anomalies, contrasting with the site-specific results of Brum et al. [25], but consistent with the pan-tropical tree growth study of Rifai et al. [24]

7. Fire

A significant component of the tropical carbon source anomaly during El Niño events may come from fires. Data from the Global Fire Emissions Database (GFED4.1; see www.globalfiredata.org) suggest a positive anomaly of +0.3 Pg C in 2015 and a negative anomaly of -0.1 Pg C in 2016, with the fire signal dominated by southeast Asia [11]. This is a much smaller anomaly than reported for 1997/98, when peat fires resulted in large emissions from southeast Asia [33] The intensity of the drought and fire season was weaker in that region this time round, apparently because some early 2016 rains damped the drought before it reached critical fire threshold values. However, much uncertainty remains both in mapping tropical forest fires (many of which can be cryptic understorey fires at time of occurrence) and estimating their immediate and long-term carbon emissions. The 2015/16 El Niño provided an opportunity to understand in detail the magnitude and mechanisms of carbon emission associated with tropical forest fires.

This issue contains three studies exploring the long- and short-term impacts of fires in Amazonia in relation to El Niño. Eastern Amazonia was the region most heavily impacted by the 2015/16 El Niño [10,15] and experienced extensive wildfire leaking from farms in both intact and previously logged forests. Withey et al. [34] present a detailed study of the core of this affected region, where 1 million hectares of (predominantly primary) forest experienced fire. There appeared to be no difference in emissions between forest types (primary or secondary) and no strong proxy for fire emission could be found, indicating that substantial challenges remain for predicting fire emissions using models. Crucially, their detailed estimates indicate carbon emissions around 2.5 times greater than estimated for the same region from global satellite-based fire databases such as GFED, suggesting that the fire-associated carbon emissions may be greatly underestimated from these global fire products, especially when they damage but do not completely eliminate the forest.

Berenguer et al. [35] demonstrate that fire can have some positive impacts on forest growth, with burned trees experiencing greater growth-related increases in carbon stocks post fire. Most probably this is a consequence of reduced competition following the mortality of competing trees, particularly given that this phenomenon was strongest in the low wood density trees, which are likely to be more reliant on high resource availability. Despite these short-term increases in growth, fire was found to have an overwhelming negative impact on forest carbon storage. Silva et al. [36] track the impacts of Amazonian forest fires for several decades after fire events: they find that fires reduced forest biomass by around 25% on average and shifted forests into an alternative state with different forest dynamics. Importantly, this shift into a new stable state was driven by delayed mortality of large, high wood density trees, from which the forests did not recover even multiple decades after the drought. Firerelated shifts in forest structure and the losses of the largest trees have substantial consequences, as slow growth means they are unlikely to re-establish before the next large fire if El Niño or other drought events become more frequent. This will result in permanent reductions in the carbon storage and carbon and water cycling capacities of Amazonian forest.

As with the ground-based ecophysiology studies in this issue, fire data, particularly from field studies of fire impacts, appear to be heavily biased towards Amazonia. However, there is a strong case for ensuring we have better data on fire emissions and ground-based fire impact data from southeast Asia. The El Niño-associated emissions from Indonesia and Papua were estimated to be between 0.3 and 0.6 Pg C [20], respectively. However, there are also large uncertainties on the figure presented in this study caused by (i) using different satellite products for estimating CO emissions (e.g. the Infrared Atmospheric Sounding Interferometer (IASI) versus the MOPITT data); (ii) using CO products for emissions estimation versus using global satellite fire observation data (e.g. the Global Fire Assimilation System GFED); (iii) uncertainties in the spatial extent and depth of peat, the key driver of carbon emission during fire in southeast Asia. Given the magnitude of fire emissions, particularly from southeast Asia, and our limited understanding of what controls them, improving our understanding of how to monitor them and predict them using models (e.g. [11]) should be a priority for future research.

8. Short- and long-term predictability

A pivotal question is to what degree the short-term response of tropical ecosystems to the El Niño, the focus of this theme issue, gives us insights into the long-term resilience or vulnerability of these ecosystems. The remote sensing analysis of Anderson et al. [21] suggests that Amazonian forests are becoming increasingly sensitive to droughts, either as a direct consequence of repeated droughts, or because the sequential droughts occur in the context of an increasingly warmer regional climate. At the scale of the global carbon cycle, however, the inversion model analyses of Rödenbeck et al. [8] and Gloor et al. [7] show no overall trend of increasing sensitivity of tropical carbon emissions to climate perturbations.

Meir et al. [26] use the results of their long-term drought experiment in eastern Amazonia to directly test the relationship between short-term responses and long-term vulnerability. Short-term responses are dominated by ecophysiological processes (e.g. trees closing their stomata to reduce water loss and suppressing photosynthesis as a consequence). Longerterm responses, by contrast, are dominated by tree demography (death of large trees, in particular, reduction of forest sap wood area as a consequence, changes in forest structure and recruitment of more drought-tolerant species). They find that some processes (e.g. total ecosystem water use) are quite predictable from the short-term to long-term response. Other processes, in particular the specific patterns and mechanism of tree mortality, are much less predictable from short-term responses.

9. Conclusion

Having reviewed the main results across this theme issue, we revisit the aims set out at the start of this synthesis.

(a) How good is our integrated understanding of the Earth System?

The papers in this theme issue showcase the broad array of techniques and tools that can now be applied to tackle key Earth System Science questions, including an expanding array of space-borne sensors, a new generation of integrated global climate and carbon cycle datasets, and global networks of atmospheric observations, intensive field studies and long-term monitoring. We find that broadly these diverse tools paint a consistent picture of what happened to the terrestrial carbon cycle over the El Niño: there was a decreased land carbon sink (i.e. a positive carbon cycle anomaly) in the tropics (e.g. [6,8,11]), this appears predominantly driven by a water stress-associated decline in photosynthesis (e.g. [7,18,19,23]), with additional contributions from ecosystem respiration and fire [11,20,34]. At the largest scale the tropical carbon cycle returned to its pre-El Niño state after the event [7,8], although fire and drought leave long-term consequences in terms of tree mortality and forest structure that can play out for decades after the initial stress event [36], and can increase ecosystem sensitivity to future stress events [21].

There are caveats in this picture, however. Climate datasets suffer from poor data availability and process representation in many tropical land regions, and care needs to be taken in their application to drive models [15]. Process-focused field studies are heavily weighted towards the Americas (e.g. [25,30,35]) and there is a need to bring in more data and analyses from other parts of the tropics. It seems likely that global fire products underestimate carbon emissions from tropical forest fires [34], and the longer-term carbon cycle effects of drought and fire are poorly monitored and poorly represented in biosphere models. Another issue, simpler to address, is the need to employ a consistent baseline time period to enable comparison between studies. The studies reported in this theme issue employ a range of baselines, and it is anticipated that a future outcome from the synthesis will be a combined study that applies a consistent baseline.

(b) Do particular regions dominate the carbon cycle response signal?

Multiple strands of data, including climate observations, field studies, remote sensing and atmospheric observations, point to eastern Amazonia as the region most responsive to the El Niño, and dominating in its contribution to the interannual variability of the tropical carbon cycle (e.g. [7,8,10,18,24]). In the 2015/16 El Niño, southern Africa also seems to have played a substantial role [7], whereas the contribution from southeast Asia was much weaker than in 1997/98, as the fire signal there was weaker at this time [20]. The role of central Africa is less clear, with some studies suggesting it plays a substantial role, whereas other studies suggest not. This pattern partially validates the present weighting of studies towards Amazonia but also highlights the need for more research and monitoring in tropical and southern Africa in particular.

(c) What are the key processes that drive the response of the tropical carbon sink?

A range of evidence suggests that the decline of photosynthesis in response to drought stress plays a dominant role in explaining the decline in the tropical carbon sink during El Niño. This is consistent with field observations of plant ecophysiology and growth. The fire contribution is thought to be relatively small, on the order of 0.3 Pg C [11], but it is possible that this could increase substantially if the effects of cryptic sub-canopy fires are taken into account [34]. Ecosystem respiration responses appear to be smaller in contribution, but this could be because respiration appears as a residual in many studies (photosynthesis can be directly estimated by remote sensing approaches such as SIF, but respiration cannot). No study in this theme issue reports field measurements of respiration response to the El Niño: such data exist, and it is hoped that subsequent papers will provide a more rounded picture of the tropical carbon cycle that includes direct measurements of respiration.

(d) What does the El Niño response tell us about the sensitivity or proximity of a tropical forest tipping point?

The studies presented here give insights into the potential of a tropical forest carbon cycle feedback in three ways: through studies over multi-decadal time periods that can identify shifting sensitivity (e.g. [8]), through identification of key mechanisms that drive the interannual variability (e.g. [11,23,24]) and through examination of longer-term response to the initial stress or disruption event [26,36]. In combination, these studies begin to sketch out the mechanisms and paths of causality that could drive a tropical forest dieback. The immediate short-term response appears to be mainly through a decline in photosynthesis or a fire event. The short-term decline in photosynthesis may not have long-term consequences, and there is little evidence of consistently increasing carbon cycle sensitivity over time. However, if the decline in photosynthesis is associated with increased mortality in the long term (either in response to a single drought or to repeated drought) and changes in forest structure, this can have long-term consequences. Fire events are almost always associated with immediate and longer-term mortality, and their associated carbon emissions are likely to have been underestimated. Hence mortality, whether through fire or drought, is the key pathway that mediates between short-term response and long-term degradation. The drivers and patterns of tree mortality in the tropics remain unclear and warrant further investigation as a priority for research.

In summary, this paper and the accompanying theme issue showcase and evaluate the wide array of approaches and technologies that were available to monitor the terrestrial carbon cycle during the 2015/2016 El Niño. They demonstrate that substantial progress has been made in approaching a comprehensive understanding that drives the interannual variability of the biosphere carbon budget. We thank all those who have contributed to the collective effort, and hope that these studies will stimulate further research and synthesis to address important questions about the future of the biosphere carbon cycle.

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References

- 1. Lenton TM, Held H, Kriegler E, Hall JW, Lucht W, Rahmstorf S, Schellnhuber HJ. 2008 Tipping elements in the Earth's climate system. Proc. Natl Acad. Sci. USA **105**, 1786 – 1793. (doi:10.1073/pnas.0705414105)
- 2. Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ. 2000 Acceleration of global warming due to carboncycle feedbacks in a coupled climate model. Nature **408**, 184 – 187. (doi:10.1038/35041539)
- Malhi Y, Aragão LE, Galbraith D, Huntingford C, Fisher R, Zelazowski P, Sitch S, McSweeney C, Meir P. 2009 Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. Proc. Natl Acad. Sci. USA 106, 20 610 – 20 615. (doi:10.1073/pnas.0804619106)
- Rasmusson EM, Wallace JM. 1983 Meteorological aspects of the El Niño/Southern Oscillation. Science 222. 1195 – 2020. (doi:10.1126/science.222.4629.1195)
- 5. Keeling CD, Revelle R. 1985 Effects of El-Nino southern oscillation on the atmospheric content of carbon-dioxide. Meteoritics 20, 437-450.
- 6. Betts RA, Jones CD, Knight JR, Keeling RF, Kennedy JJ, Wiltshire AJ, Andrew RM, Aragao LEOC. 2018 A successful prediction of the record CO₂ rise associated with the 2015/2016 El Niño. Phil. Trans. R. Soc. B 373, 20170301. (doi:10.1098/rstb.2017.0301)
- 7. Gloor E et al. 2018 Tropical land carbon cycle responses to 2015/16 El Niño as recorded by atmospheric greenhouse gas and remote sensing data. Phil. Trans. R. Soc. B 373, 20170302. (doi:10. 1098/rstb.2017.0302)
- Rödenbeck C, Zaehle S, Keeling R, Heimann M. 2018 History of El Niño impacts on the global carbon cycle 1957-2017: a quantification from atmospheric CO2 data. Phil. Trans. R. Soc. B 373, 20170303. (doi:10.1098/rstb.2017.0303)
- 9. Wang W et al. 2013 Variations in atmospheric CO₂ growth rates coupled with tropical temperature. Proc. Natl Acad. Sci. USA 110, 13 061-13 066. (doi:10.1073/pnas.1219683110)
- 10. Jimenez JC, Barichivich J, Mattar C, Takahashi K, Santamaría-Artigas A, Sobrino JA, Malhi Y. 2018 Spatio-temporal patterns of thermal anomalies and drought over tropical forests driven by recent extreme climatic anomalies. Phil. Trans. R. Soc. B **373**, 20170300. (doi:10.1098/rstb.2017.0300)
- 11. Bastos A et al. 2018 Impact of the 2015/2016 El Niño on the terrestrial carbon cycle constrained by bottomup and top-down approaches. Phil. Trans. R. Soc. B 373, 20170304. (doi:10.1098/rstb.2017.0304)
- 12. Friend AD, White A. 2000 Evaluation and analysis of a dynamic terrestrial ecosystem model under preindustrial conditions at the global scale. Global Biogeochem. Cycles 14, 1173-1190. (doi:10.1029/ 1999GB900085)

- 13. Phillips OL et al. 1998 Changes in the carbon balance of tropical forests: evidence from long-term plots. Science 282, 439-442. (doi:10.1126/science. 282.5388.439)
- 14. Palmer Pl. 2018 The role of satellite observations in understanding the impact of El Niño on the carbon cycle: current capabilities and future opportunities. Phil. Trans. R. Soc. B 373, 20170407. (doi:10.1098/ rstb.2017.0407)
- 15. Burton C, Rifai S, Malhi Y. 2018 Inter-comparison and assessment of gridded climate products over tropical forests during the 2015/2016 El Niño. Phil. Trans. R. Soc. B 373, 20170406. (doi:10.1098/rstb.2017.0406)
- 16. Jung M, Reichstein M, Schwalm CR, Huntingford C, Sitch S. 2017 Compensatory water effects link yearly global land CO₂ sink changes to temperature. Nature **541**, 516. (doi:10.1038/nature20780)
- 17. Poulter B, Hattermann F, Hawkins ED, Zaehle S, Sitch S, Restrepo-Coupe N, Heyder U, Cramer W. 2010 Robust dynamics of Amazon dieback to climate change with perturbed ecosystem model parameters. Glob. Change Biol. 16, 2476-2495. (doi:10.1111/j.1365-2486.2009.02157.x)
- 18. Luo X et al. 2018 The impact of the 2015/2016 El Niño on global photosynthesis using satellite remote sensing. Phil. Trans. R. Soc. B 373, 20170409. (doi:10.1098/rstb.2017.0409)
- 19. Koren G et al. 2018 Widespread reduction in suninduced fluorescence from the Amazon during the 2015/2016 El Niño. Phil. Trans. R. Soc. B 373, 20170408. (doi:10.1098/rstb.2017.0408)
- 20. Nechita-Banda N et al. 2018 Monitoring emissions from the 2015 Indonesian fires using CO satellite data. Phil. Trans. R. Soc. B 373, 20170307. (doi:10. 1098/rstb.2017.0307)
- 21. Anderson LO, Ribeiro Neto G, Cunha AP, Fonseca MG, Mendes de Moura Y, Dalagnol R, Wagner FH, Aragão LEOC. 2018 Vulnerability of Amazonian forests to repeated droughts. Phil. Trans. R. Soc. B **373**, 20170411. (doi:10.1098/rstb.2017.0411)
- 22. Liu J et al. 2017 Contrasting carbon cycle responses of the tropical continents to the 2015-2016 El Niño. Science 358, 191. (doi:10.1126/science.aam5690)
- 23. van Schaik E, Killaars L, Smith NE, Koren G, van Beek LPH, Peters W, van der Laan-Luijkx IT. 2018 Changes in surface hydrology, soil moisture, and gross primary production in the Amazon during the 2015/2016 El Niño. Phil. Trans. R. Soc. B 373, 20180084. (doi:10.1098/rstb.2018.0084)
- 24. Rifai SW et al. 2018 ENSO Drives interannual variation of forest woody growth across the tropics. Phil. Trans. R. Soc. B **373**, 20170410. (doi:10.1098/rstb.2017.0410)
- 25. Brum M, Gutiérrez López J, Asbjornsen H, Licata J, Pypker T, Sanchez G, Oliveira RS. 2018 ENSO effects

- on the transpiration of eastern Amazon trees. Phil. Trans. R. Soc. B 373, 20180085. (doi:10.1098/rstb. 2018.0085)
- 26. Meir P, Mencuccini M, Binks O, da Costa AL, Ferreira L. Rowland L. 2018 Short-term effects of drought on tropical forest do not fully predict impacts of repeated or long-term drought: gas exchange versus growth. Phil. Trans. R. Soc. B 373, 20170311. (doi:10.1098/rstb.2017.0311)
- 27. Shenkin A, Bolker B, Peña-Claros M, Licona JC, Ascarrunz N, Putz FE. 2018 Interactive effects of tree size, crown exposure and logging on droughtinduced mortality. Phil. Trans. R. Soc. B 373, 20180189. (doi:10.1098/rstb.2018.0189)
- 28. Fontes CG et al. 2018 Dry and hot: the hydraulic consequences of a climate change-type drought for Amazonian trees. Phil. Trans. R. Soc. B 373, 20180209. (doi:10.1098/rstb.2018.0209)
- 29. Malhi Y et al. 2015 The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. Glob. Change Biol. 21, 2283 - 2295. (doi:10.1111/gcb.12859)
- 30. Santos V, Ferreira M, Rodrigues J, Garcia M, Ceron J, Nelson BW, Saleska SR. 2018 Causes of reduced leaf-level photosynthesis during strong El Niño drought in a Central Amazon forest. Glob. Change *Biol.* **24**, 4266 – 4279. (doi:10.1111/gcb.14293)
- 31. da Costa AC et al. 2018 Stand dynamics modulate water cycling and mortality risk in droughted tropical forest. Glob. Change Biol. 24, 249-258. (doi:10.1111/qcb.13851)
- 32. Eller CB et al. 2018 Modelling tropical forest responses to drought and El Niño with a stomatal optimization model based on xylem hydraulics. Phil. Trans. R. Soc. B 373, 20170315. (doi:10.1098/rstb. 2017.0315)
- 33. Page SE, Siegert F, Rieley JO, Boehm H-DV, Jaya A, Limin S. 2002 The amount of carbon released from peat and forest fires in Indonesia during 1997. *Nature* **420**, 61–65. (doi:10.1038/nature01131)
- 34. Withey K et al. 2018 Quantifying the immediate carbon emissions from El Niño-mediated wildfires in humid tropical forests. Phil. Trans. R. Soc. B 373, 20170312. (doi:10.1098/rstb.2017.0312)
- 35. Berenguer E, Malhi Y, Brando P, Nunes Cordeiro A, Ferreira J, França F, Chesini Rossi L, Maria Moraes de Seixas M, Barlow J. 2018 Tree growth and stem carbon accumulation in human-modified Amazonian forests following drought and fire. Phil. Trans. R. Soc. B 373, 20170308. (doi:10.1098/rstb.2017.0308)
- 36. Silva CVJ et al. 2018 Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics. Phil. Trans. R. Soc. B 373, 20180043. (doi:10.1098/rstb.2018.0043)