

Annual Review of Earth and Planetary Sciences

Droughts, Wildfires, and Forest Carbon Cycling: A Pantropical Synthesis

Paulo M. Brando,^{1,2} Lucas Paolucci,^{2,3}
Caroline C. Ummenhofer,⁴ Elsa M. Ordway,^{5,6,7}
Henrik Hartmann,⁸ Megan E. Cattau,⁹
Ludmila Rattis,^{1,2} Vincent Medjibe,¹⁰ Michael T. Coe,^{1,2}
and Jennifer Balch^{9,11}

¹Woods Hole Research Center, Falmouth, Massachusetts 02540, USA;
email: pbrando@whrc.org

²Instituto de Pesquisa Ambiental da Amazônia (IPAM), Brasília-DF 71503-505, Brazil

³Setor de Ecologia e Conservação, Departamento de Biologia, Universidade Federal de Lavras, 37200-000 Lavras, Minas Gerais, Brazil

⁴Department of Physical Oceanography, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA

⁵Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA

⁶Department of Global Ecology, Carnegie Institution for Science, Stanford, California 94305, USA

⁷Center for Global Discovery and Conservation Science, Arizona State University, Tempe, Arizona 85281, USA

⁸Department of Biogeochemical Processes, Max Planck Institute for Biogeochemistry, 07745 Jena, Germany

⁹Earth Lab, Cooperative Institute for Research in Environmental Sciences (CIRES), University of Colorado Boulder, Boulder, Colorado 80303, USA

¹⁰Commission des Forêts d'Afrique Centrale (COMIFAC), 20818 Yaoundé, République du Cameroun

¹¹Department of Geography, University of Colorado Boulder, Boulder, Colorado 80309, USA

ANNUAL
REVIEWS **CONNECT**

www.annualreviews.org

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

Annu. Rev. Earth Planet. Sci. 2019. 47:555–81

The *Annual Review of Earth and Planetary Sciences* is online at earth.annualreviews.org

<https://doi.org/10.1146/annurev-earth-082517-010235>

Copyright © 2019 by Annual Reviews.
All rights reserved

Keywords

tropical forests, carbon, Amazon, Congo Basin, Southeast Asia, drought, climate change, tree mortality

Abstract

Tropical woody plants store ~230 petagrams of carbon (PgC) in their above-ground living biomass. This review suggests that these stocks are currently

growing in primary forests at rates that have decreased in recent decades. Droughts are an important mechanism in reducing forest C uptake and stocks by decreasing photosynthesis, elevating tree mortality, increasing autotrophic respiration, and promoting wildfires. Tropical forests were a C source to the atmosphere during the 2015–2016 El Niño–related drought, with some estimates suggesting that up to 2.3 PgC were released. With continued climate change, the intensity and frequency of droughts and fires will likely increase. It is unclear at what point the impacts of severe, repeated disturbances by drought and fires could exceed tropical forests’ capacity to recover. Although specific threshold conditions beyond which ecosystem properties could lead to alternative stable states are largely unknown, the growing body of scientific evidence points to such threshold conditions becoming more likely as climate and land use change across the tropics.

- Droughts have reduced forest carbon uptake and stocks by elevating tree mortality, increasing autotrophic respiration, and promoting wildfires.
- Threshold conditions beyond which tropical forests are pushed into alternative stable states are becoming more likely as effects of droughts intensify.

1. INTRODUCTION

Global forests account for approximately 50% of the world’s gross primary productivity (GPP) and store 90% of the total carbon (C) in natural terrestrial ecosystems (Pan et al. 2013). This large C reservoir has apparently grown over the past several decades, contributing to stabilizing the global climate (Houghton et al. 2015). Forests currently remove ~27% of the total anthropogenic C emitted into the atmosphere (Le Quéré et al. 2016). This C removal results, in part, from productivity increases in recovering secondary forests (Kondo et al. 2018) as well as from C accumulation in primary forests (Houghton 2007).

Episodic droughts play an important role in shaping the structure, diversity, and functioning of tropical forests and their capacity to store and cycle C (Brando et al. 2006, Meir et al. 2009, Nepstad et al. 2001). Drought events contribute to tree mortality, alter ecosystem processes, and interfere with plant competition for resources (Lebrija-Trejos et al. 2010, Malhi 2011). Anthropogenic activities increasingly interact with these drought-related effects on tree assemblages as forests become more fragmented and exposed to greater thinning and burning (Nepstad et al. 2008, Nobre et al. 2016). Climate change may interact with and accelerate the effects of anthropogenic and natural disturbances. The resulting disturbance events may occur at a rate too fast for tropical forests to keep pace with (Lewis et al. 2015, Trumbore et al. 2015). In response, tropical forests may undergo large and persistent changes in structure and function. Declines in C stocks and sequestration rates resulting from these structural and functional changes could have major implications for the global climate system. Quantifying and attributing changes in ecosystem properties to different drivers are key to understanding feedbacks between tropical forests and climate.

Here we review the roles of drought–fire interactions in changes to tropical forest C stocks across Amazonia, the Congo Basin, and Southeast Asia (SEA) (**Figure 1**). We focus on processes underpinning drought and fire impacts and interactions that affect the capacity of tropical forests to cycle and store C. Although changes in forest C cycling are occurring across the entire tropics, forests within and across Amazonia, the Congo Basin, and SEA likely respond differently to drought and fire events, given their distinct evolutionary histories and disturbance regimes

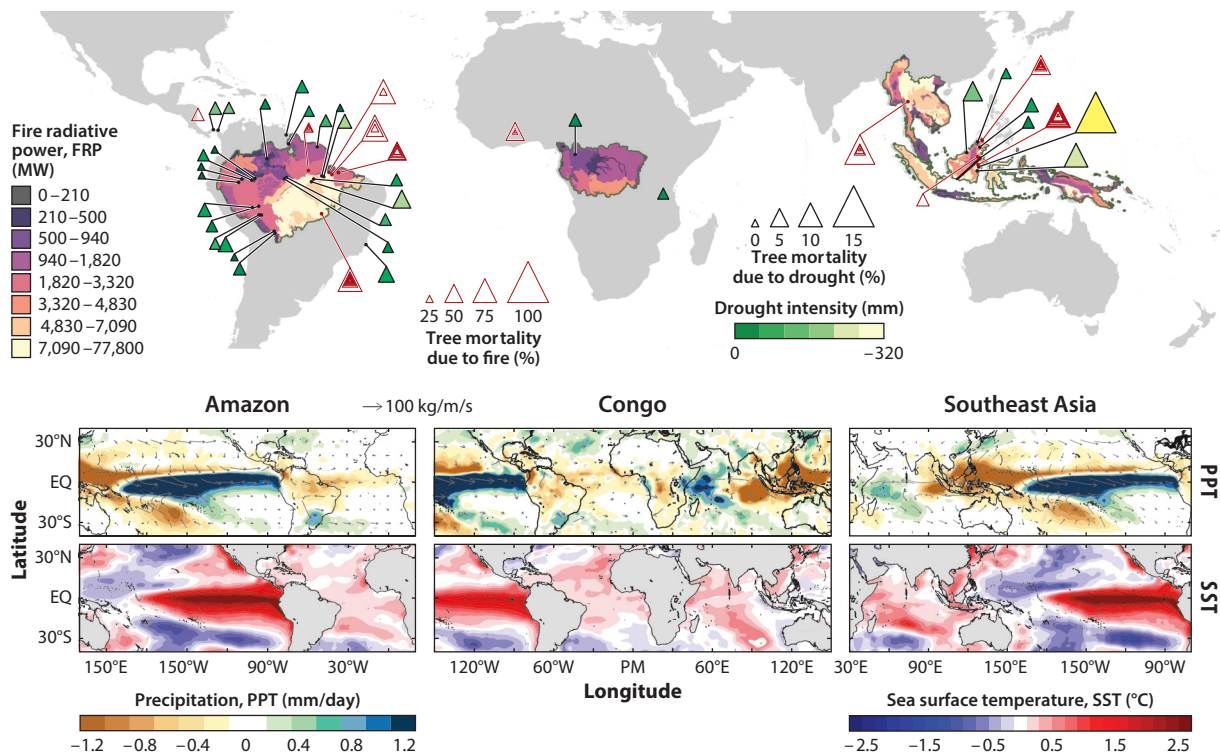


Figure 1

(Top) Boundaries of potential tropical forests of the Amazon Basin, Congo Basin, and SEA; the difference in fire radiative power per eco-region between 2015 and 2014; and drought-induced tree mortality (filled triangles) and fire-induced tree mortality (open triangles) according to different drought intensities, as represented by the maximum climatological water deficit. (Bottom) Climate anomalies for key representative droughts for PPT, vertically integrated moisture transport between the surface and 500 hPa (gray arrows), and SST, represented as the composite anomaly of drought years for that particular tropical forest relative to the long-term climatological average for the period 1979–2016. Analyses are focused on the months for the predominant rainy season for the respective tropical forest—that is, November–April for the Amazon, September–May for the Congo, and December–February for SEA. Data sets used include Climate Prediction Center Merged Analysis Product PPT; specific humidity, zonal, and meridional winds from National Centers for Environmental Prediction/National Center for Atmospheric Research reanalysis (Kistler et al. 2001); and Extended Reconstructed SST v5 (Huang et al. 2017). Abbreviations: PPT, precipitation; SEA, Southeast Asia; SST, sea surface temperature.

(Levine et al. 2016, Seddon et al. 2016, Willis et al. 2018). We therefore highlight potential differences across these systems where possible.

Our review focuses primarily on the remaining moist and wet tropical forests, where data are most widely available (Figure 1). When relevant, we highlight the effects of drought and fire on C cycling in peatland, lowland, and dry forests of the tropics. We generally assume that remaining forests are composed mainly of primary forests; however, we acknowledge that the structure and composition of current forests have been influenced in various ways by a long human history in each region (Lewis et al. 2015) (see the sidebar titled *How Much Tropical Forest Remains?*).

2. CARBON STOCKS AND CYCLING OF PRIMARY TROPICAL FORESTS

The live C stored in moist tropical forests results from the long-term balance between C assimilated during photosynthesis and C lost during respiration and tree mortality. Tropical forests are

HOW MUCH TROPICAL FOREST REMAINS?

The geographic distribution of tropical forests has remained relatively constant since the last ice age, with moist and dry closed-canopy forests covering roughly 10% of Earth's ice-free land surface. Beginning in the 1400s, however, deforestation for timber extraction and the expansion of agricultural production began to affect much of the tropics. In the Amazon, this process was extremely slow until the 1980s, after which point clearing accelerated as pasturelands (primarily) and mechanized agriculture (secondarily) began expanding at the expense of primary forests. In total, about 20% of forests in the Amazon have been cleared. In Southeast Asia, a similar process has occurred and about 40% has been deforested. Since the 1970s, forested areas have declined substantially as logging and industrial agriculture spread, leaving many remaining forests heavily fragmented and degraded. In Africa, deforestation has occurred throughout the nineteenth, twentieth, and twenty-first centuries, associated with shifting cultivation, mining, and timber extraction. Continued agricultural expansion and increased foreign investment in land for the cultivation of major commodity crops, such as soy and oil palm, have raised concerns of accelerated deforestation across tropical Africa. To date, 25% of the region's forests have been cleared, in part to lower demographic pressure, limited accessibility, poor infrastructure, and low-impact logging. Despite extensive deforestation, roughly 1.4 billion ha of tropical forests remain.

estimated to assimilate 40 petagrams of carbon (PgC or 10^{15} g)/year via GPP (Beer et al. 2010) or 30 PgC when we consider the area in **Figure 1**, according to Moderate Resolution Imaging Spectrometer (MODIS)-based estimates. Amazon forests account for the largest fraction of this GPP (53%), followed by African and SEA forests (Zhang et al. 2017). Of the total GPP in tropical forests, roughly 30–40% results in biomass accumulation, while the remainder is respired back to the atmosphere. A smaller fraction of the assimilated C results in stored reserves (e.g., sugars and starch) and can eventually be used for growth or to maintain basic physiological processes. Current estimates of the total GPP accumulating as biomass [net primary productivity (NPP)] from MODIS average 12 PgC/year, although when a larger area is considered, estimates may reach 22 PgC/year. From these totals, Amazon forests account for 53%, while African and SEA forests account for 19% and 28%, respectively (Zhao & Running 2010). Few studies have quantified all NPP components, with current estimates pointing to wood production consuming more NPP ($39\% \pm 10\%$) than leaf ($34\% \pm 6\%$) and fine root production ($27\% \pm 11\%$) (Malhi 2011).

Climate exerts strong controls on the spatial variability of C uptake and productivity of tropical forests. In general, photosynthesis decreases in regions with lower annual total precipitation (e.g., <2,000 mm) and prolonged dry seasons (e.g., >3.5 months). This includes much of the evergreen forests of Africa, southern Amazonia, and SEA. In contrast, areas with greater annual precipitation and short dry seasons often have substantially higher and more constant rates of photosynthesis, such as in parts of central Amazonia and SEA (Guan et al. 2015). The exceptions to these patterns relate to extreme wet regions where high cloud cover and low light availability limit productivity during wet seasons (Lee et al. 2013). In montane systems, low air temperatures can also reduce forest productivity. Despite variability in GPP across the tropics, most high-elevation primary forests average between 20 and 40 megagrams of carbon (MgC or 10^6 g)/ha per year (Malhi 2011). NPP can follow similar spatial patterns to GPP, although differences are common due to the influences of autotrophic respiration on NPP.

In total, tropical forests are estimated to store 390 PgC (Pan et al. 2013), with living woody vegetation accounting for ~230 PgC in their aboveground living biomass (Baccini et al. 2012, Saatchi et al. 2011). Amazon forests store nearly half of these C stocks in woody vegetation, with the remainder split evenly between African and Southeast Asian forests. In general, most

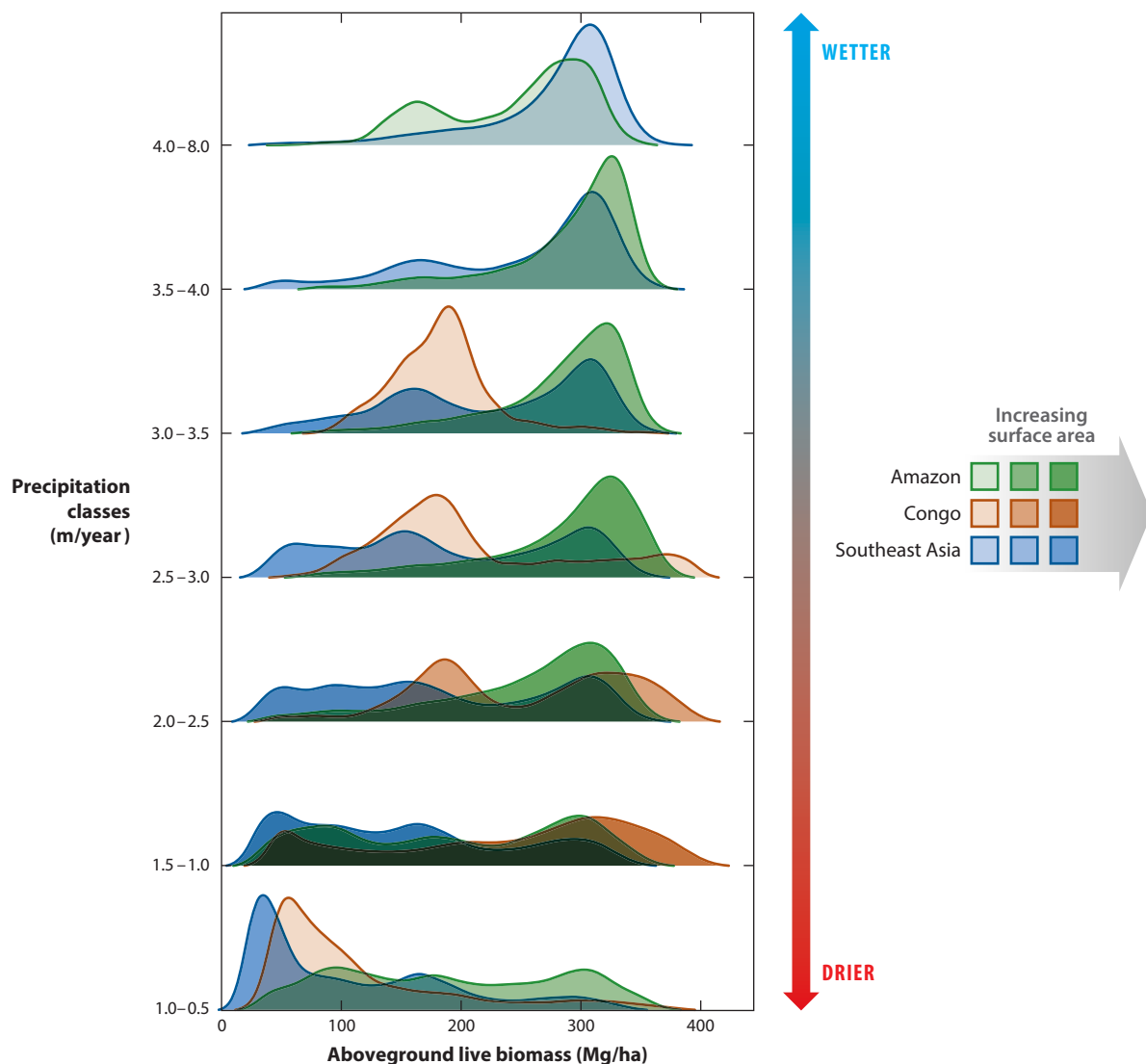


Figure 2

Relative density distributions of aboveground biomass in living woody plants per 1981–2017 mean annual precipitation class for tropical forest in the Amazon, Congo Basin, and Southeast Asia. The color shading is proportional to the number of 30 m × 30 m pixels in each of the relative density plots. Thus, the more solid is the color, the greater number of pixels and larger the area in that precipitation class, while less solid color represents fewer pixels and less area. Figure adapted from Baccini et al. (2012).

forests with high aboveground carbon (AGC) grow in continuously wet regions, such as Borneo (220 MgC/ha), where mortality rates are low and productivity is high (Lewis et al. 2013). Across drier tropical regions, AGC density is lower, particularly when annual precipitation drops below 1,500–2,000 mm (**Figure 2**). Yet, forest productivity and AGC densities can vary within similar climatic regions. Some African forests store substantially greater aboveground live biomass than other tropical regions with similar total annual precipitation (**Figure 2**) but also lower AGC stocks in wetter regions. The large variability in AGC stocks across the tropics results from biotic

and abiotic interactions that differ based on edaphic conditions, C residence time, rooting depth, species and functional diversity, disturbance regimes, anthropogenic influences, and dry-season length (Castanho et al. 2013).

3. INCREASING CARBON STOCKS OF PRIMARY FORESTS

The live C stocks of tropical forests are apparently increasing. Since the 1990s, AGC has accumulated at a rate of ~ 1.2 PgC/year, concentrated in Amazonia (0.42–0.65 PgC/year) and Africa (0.48–0.53 PgC/year), with smaller increases also occurring in SEA (0.12–0.14 PgC/year) (Lewis et al. 2009b, Pan et al. 2013). A widely held hypothesis to explain this growth in C storage relates to increased concentrations of atmospheric carbon dioxide (CO_2) boosting forest productivity (Lewis et al. 2009a). Furthermore, estimates from dynamic global vegetation models suggest that with future increasing concentrations of atmospheric CO_2 , vegetation productivity rates will increase enough to avoid a potential forest dieback (Rammig et al. 2010). However, neither the network of field plots used to estimate forest wood accumulation nor the vegetation models used to represent the forest C fluxes appear to properly capture or represent small- and medium-sized tree mortality events (Trumbore et al. 2015), such as wind-driven treefalls, fires, and insect disturbance. Without accurately accounting for tree mortality, it is possible that the historical and potential future C sink in tropical forests is overestimated (Baccini et al. 2017).

Tree mortality is a key contributor to the recent slowdown in the rates of AGC stock accumulation in Amazonian tropical forests (Brienen et al. 2015). C losses from forest mortality appear to be increasing while tree growth has remained relatively constant (Phillips & Brienen 2017). While many factors likely drive mortality, drought-related tree mortality can lead to substantial changes in the global C cycle (Lewis et al. 2009a) because tropical droughts can be so widespread (Marengo et al. 2012, van der Werf et al. 2010). For example, doubling drought-related mortality of large Amazonian trees (diameter at breast height > 50 cm) across the entire basin (from 1% to 2%) would result in an additional ~ 0.2 PgC necromass, which would be fully committed to the atmosphere over the course of decades or longer. However, plants have several adaptations to cope with droughts that can vary widely in frequency, intensity, and extent across the tropics (see the sidebar titled *How to Define Drought*). This helps to explain why drought-related tree mortality estimates range from 1% to 19% (Phillips et al. 2010) (**Figure 1**).

4. NATURAL DRIVERS OF TROPICAL DROUGHTS

Variations in sea surface temperature (SST) modulate regional hydroclimate and can significantly contribute to tropical droughts. The El Niño–Southern Oscillation (ENSO) originating in the tropical Pacific is the leading mode of interannual variability and is associated with changes in precipitation and temperatures around the world (Ropelewski & Halpert 1987). The Indian Ocean Dipole (IOD) is the Indian Ocean’s leading mode of variability. In its positive phase, the IOD is associated with cool SST in the eastern Indian Ocean and warmer-than-normal conditions in the west. Its positive phase is characterized by reduced convection and dry conditions across SEA, while enhanced convection and wet conditions occur over East Africa (Saji et al. 1999, Webster et al. 1999). The Atlantic Multidecadal Oscillation (AMO) in the North Atlantic describes a slowly varying SST pattern with warm anomalies occurring in a horseshoe pattern (in the tropical and eastern Atlantic, extending northward to Greenland and northwestward into the Labrador Sea) during its warm phase. The AMO has a 60–80-year cycle and extensive impacts on hydroclimatic conditions in the Sahel and North and South America, among other regions (Alexander et al. 2014). These modes interact and modulate rain-bearing climatological features of the tropics,

HOW TO DEFINE DROUGHT

Drought is a complex phenomenon that depends on the combined effect of atmospheric quantities (mostly precipitation but also temperature), storage terms in the ground such as soil moisture, and responses of the natural and human system across a range of timescales (Natl. Acad. Sci. Eng. Med. 2016). Given this complexity, drought can at best be incompletely described by different drought indices (Hartmann et al. 2013). While there are different types of drought (e.g., meteorological, hydrological, agricultural, socioeconomic) (Wilhite & Glantz 1985), here we focus on meteorological drought (a period with an abnormal precipitation deficit) and hydrological drought (depletion of surface or subsurface water supply). Droughts vary in their spatial extent (local to continental scale), timing or seasonality, duration, evolution, and intensity. As highlighted in a recent review of ecological impacts of extreme climatic events, such as droughts and heatwaves (Ummenhofer & Meehl 2017), progress in understanding biophysical interactions across a range of scales has been hampered by limitations in the observational network, both for physical climate system parameters and even more so for long-term ecological monitoring. However, recent advances provide new opportunities for assessing how hydroclimatic extremes modulate ecosystem structure and functioning that arise from better scientific understanding of these events, coupled with technological advances in instrumentation, observing systems, and Earth system models that simulate biogeochemical cycles and interactions with the biosphere at increasing complexity.

such as the intertropical convergence zones (ITCZs) and monsoons, thus affecting regional and local moisture supply to the rainforests.

During El Niño events, anomalously warm SST in the eastern Pacific and related circulation changes over South America disrupt atmospheric moisture transport to the Amazon. This results in rainfall deficits and drought conditions during the wet season, as occurred during the 1982–1983, 1997–1998, and 2015–2016 events (**Figure 1**). ENSO's impact on Amazon hydroclimatic conditions is sensitive to the longitudinal position of maximum warming in the equatorial Pacific (Hill et al. 2011, Tedeschi et al. 2013). Using atmospheric general circulation model experiments with idealized warming along the equatorial Pacific, Hill et al. (2011) showed that the tropical rainfall responses over South America differed depending on whether maximum warming occurred in the eastern versus central Pacific. Experiments with warming in the eastern Pacific, similar to the 1997–1998 El Niño event, resulted in a suppressed monsoon with weakened moisture advection into the South Atlantic Convergence Zone (SACZ). In contrast, when maximum warming occurred further west in the Pacific, the summer monsoon was average or slightly wetter. Dry-season droughts in the Amazon, as during 2005 and 2010 (Lewis et al. 2011, Zeng et al. 2008), were associated with an anomalously warm tropical Atlantic during the positive phase of the AMO, which weakens moisture transport and prolongs the dry season (Marengo et al. 2011).

Annual precipitation in the Congo Basin falls predominantly during the spring and autumn months, following the passage of the ITCZ. The timing and intensity of these rains are modulated by SST in the adjacent Atlantic and Indian Oceans as well as through remote impacts from the Pacific (**Figure 1**). Droughts are more likely to occur in the Congo Basin during periods of warm tropical Atlantic SST and El Niño events and under positive IOD conditions, when there are shifts in the zonal Walker circulation and reduced moisture transport into the continent. Central equatorial Africa, including the Congo Basin, has experienced significant drying trends in recent decades (Asefi-Najafabady & Saatchi 2013, Chambers & Roberts 2014, Hua et al. 2016, Zhou et al. 2014), which means that the basin is getting drier on average and more drought events are occurring. Focusing on the April–June months, Hua et al. (2016) associated this drying with

anomalous Indo-Pacific SST driving a westward extension of the Walker circulation, which resulted in suppressed ascent and reduced low-level moisture transport over the Congo Basin.

Hydroclimatic conditions in SEA are intimately tied to the zonal Walker circulation, with its rising branch over the Indo-Pacific warm pool during normal conditions. Shifts in the Walker circulation occur during El Niño events and the positive phase of the IOD, so that anomalous descent and suppressed convection occur over SEA, while anomalous ascending motion and associated rainfall anomalies (**Figure 1**) are instead seen further east over the Pacific and in the western Indian Ocean.

The impacts of these changes on Southeast Asian hydroclimatic conditions depend on the type of ENSO event. The most severe Indonesian droughts and wildfires are associated with eastern Pacific (or cold-tongue) El Niños and positive IOD events (**Figure 1**) rather than central Pacific (or warm-pool) El Niño events and weak positive or even negative IOD events (Pan et al. 2018). Multidecadal variability associated with the IOD and ENSO drives high- and low-variance periods in tropical SST and Indonesian streamflow (D'Arrigo et al. 2011), making some decades more drought prone than others.

5. PHYSIOLOGICAL TREE RESPONSES TO DROUGHT

Under normal climatic conditions, tropical trees take up and store enough soil water to meet their demands during dry-season months. This allows forests to assimilate nutrients, cool their leaves, and fix C. As drought sets in, most tropical tree species avoid severe water stress by employing several strategies. These include the adjustment of sapwood cell turgor via the buildup of solutes; use of water stored in their trunks (capacitance) to maintain transpiration during water shortages for several days (Santiago et al. 2018); increased thermotolerance of leaves against tissue damage during hot droughts (Allen et al. 2015); and, as drought progresses, shedding of leaves to reduce whole-tree transpiration (Domingues et al. 2018). This multitude of available strategies helps tropical tree species maintain a positive hydraulic safety margin during droughts (Santiago et al. 2018, Santos et al. 2018), whereby plant water potential is maintained at levels that prevent xylem embolism. Trees with deep root systems can access water pools in deeper soil layers and may be able to take up enough water even when soil water content becomes limiting for shallow-rooting trees (Nepstad et al. 1994, Stahl et al. 2013).

6. MECHANISMS OF DROUGHT-INDUCED TREE MORTALITY

During prolonged or severe droughts, mechanisms to tolerate water deficit may fail and the hydraulic system can be damaged. Xylem flow is maintained by evaporation of water in leaves that causes a tension in the xylem, pulling water up the stem (Anderegg et al. 2016). When evaporation rates exceed water uptake by roots, this tension increases and emboli (gas bubbles) in conducting cells may occur that can spread through the xylem and interrupt water transport (Tyree & Sperry 1988). To prevent desiccation of the entire plant, trees have developed a hydraulic architecture that confines most cavitation (i.e., blocking of a xylem vessel or tracheid by an air bubble or cavity is called an embolism) to more expendable and distal organs (Tyree & Ewers 1991). Trees from tropical ecosystems that experience seasonal droughts locate the highest vulnerability to cavitation to low-cost organs such as leaves and branches (Bucci et al. 2016). This mechanism causes partial (i.e., leaf, branch) mortality, as was observed during a recent ENSO-related drought in the central and eastern Amazon (Leitold et al. 2018). Further declines in water availability may cause runaway cavitation in tree stems and ultimately death of the organism via hydraulic failure (McDowell et al. 2008). For instance, precipitation manipulations in tropical forests have shown that a substantial

proportion of living biomass (30–40%) may be lost in response to severe and prolonged drought (Brando et al. 2008, Rowland et al. 2015b).

Large trees tend to be more susceptible to drought-induced mortality than smaller trees (da Costa et al. 2010, Nepstad et al. 2007, Rowland et al. 2015b, Trugman et al. 2018), particularly when increases in air dryness accompany droughts. This likely occurs because the xylem of larger trees experiences greater gravitational forces, which impede water transport and increase risks of cavitation (Brando 2018, Giardina et al. 2018). Larger trees also require substantially longer recovery times to regrow more lost xylem (Trugman et al. 2018).

The initial tree response to drought is stomatal closure to reduce transpiration (Santos et al. 2018). However, this impedes diffusion of CO₂ into the leaves and C assimilation (Chaves et al. 2003), which can ultimately lead to reduced defense capacity against herbivory, slowed phloem transport, and hampered osmoregulation (McDowell et al. 2011). Concurrent elevated temperatures during hot droughts increase C expenditure via elevated respiration rates (Atkin et al. 2005). In addition to drought-induced reductions of photosynthesis, increased respiration rates can push trees to a negative C balance even under conditions with relatively high soil moisture (Zhao et al. 2013). Trees store substantial amounts of carbohydrates (and lipids) in branches, stems, and roots that can be mobilized during periods of low C assimilation to maintain normal functioning, with the age of this C varying between days and many years (Furze et al. 2018, Hartmann & Trumbore 2016). Depletion of C reserves and ensuing C starvation have been proposed as potential mechanisms of drought-induced tree mortality (McDowell et al. 2008), where trees use up their carbohydrate reserves during prolonged drought until requirements of life-maintaining physiological functions cannot be met any longer.

Although C starvation continues to be disputed as a mechanism driving drought-induced tree mortality (Hartmann et al. 2015, Körner 2003), it is clear that a prolonged negative C balance can have profound effects on tree functioning. For example, Adams et al. (2017) found that high levels of xylem damage were more likely to kill trees directly than reserve depletion, although residual carbohydrate concentrations at death and xylem vulnerability were negatively correlated in some species. Carbohydrates are thought to play an important role in the maintenance of xylem water transport, particularly during periods of recovery from severe drought stress (Secchi et al. 2017). Using physiological models, Trugman et al. (2018) documented delayed tree mortality following drought events that results from slow C starvation as trees attempt to regain a positive C balance through the repair and regrowth of drought-damaged xylem over multiple years.

7. COMMUNITY-LEVEL RESPONSES TO DROUGHT

As our understanding of how trees die in response to drought is improving, it remains extremely challenging to quantify drought responses of entire forest ecosystems. When individual trees die, communities can reassemble based on the drought sensitivity of different species and conspecific variation (e.g., tree height) (Engelbrecht et al. 2007). The mortality response to drought is determined by both the composition and structure of the forest. For example, drought may result in high mortality in some species but not others (Breshears et al. 2005) depending on differences in stomatal regulation of water use (Breshears et al. 2009). Furthermore, drought characteristics (e.g., severity, duration, timing) can have substantial impacts on tree physiological responses (McDowell et al. 2018b). Yet, how this affects mortality in different species or plant functional types remains uncertain (Hartmann et al. 2018).

The lack of relevant data for tropical tree species and the complexity of ecological interactions make scaling physiological drought effects from individual trees to forest ecosystems challenging (Hartmann et al. 2018). New forest communities resulting from compositional shifts in response

to drought will likely optimize the use of water, nutrients, and other resources in different ways. As a result, community responses to drought will likely be nonlinear, with different forest ecosystems potentially even achieving different equilibrium states (Trumbore et al. 2015). For instance, small- and medium-sized trees subjected to experimental rainfall exclusion in central Amazonia grew faster after a peak in large-tree mortality (Rowland et al. 2015a), perhaps suggesting a stabilization process and ecosystem-level acclimation to drought.

Over the long run, droughts may select plant communities that are more resistant to water stress. It is possible that ecosystems historically exposed to more frequent droughts and drier climates (e.g., the Congo Basin and southeast Amazon) have tree assemblages that are more adapted to droughts compared to wet forests (Esquivel-Muelbert et al. 2016, Fauset et al. 2012). However, drier forests are climatologically closer to the rainfall threshold that favors savannas over forests, raising the possibility that these forests may ultimately be more vulnerable to increasing temperatures and drought (Hirota et al. 2011, Staver et al. 2011).

8. CARBON CONSEQUENCES OF TROPICAL DROUGHTS

The productivity of many tropical forests is also considered light limited due to persistent cloud cover (Brando et al. 2010). During the initial stages of drought, increased solar radiation reaching the forest canopy can partially offset the negative effects of water stress on photosynthesis (Xing et al. 2018). Such stabilizing mechanisms will most likely fail during severe and widespread droughts. Drought-stressed tropical forests enter a negative C balance when rates of C losses from respiration surpass rates of C assimilation from photosynthesis (Brienen et al. 2015). During the Amazon drought in 2010, for example, Gatti et al. (2014) estimated a net flux of 0.2 PgC from the basin, compared with non-drought years. These results suggest that, while droughts can cause declines in C emissions from heterotrophic respiration (including soil respiration), short-term reductions in forest growth and increases in autotrophic respiration during such events can be large enough to transform the Amazon into a large C source.

Measurements of reduced C uptake (−15%) based on solar-induced chlorophyll fluorescence measurements across the Amazon in 2010 largely support the notion that the negative forest C balance can result from reduced photosynthesis, at least over short timescales (Lee et al. 2013). However, similarly dry conditions in African forests have not resulted in comparable reductions in productivity (Asefi-Najafabady & Saatchi 2013). Instead, a long-term decline in greenness has emerged across wet and moist African forests, likely in response to a multidecadal reduction in precipitation and a trend of increasing air temperature (Zhou et al. 2014). Yet, it remains unclear how these long-term declines in vegetation greenness translate to changes in the C balance of African forests. Lewis et al. (2009b), for instance, found wet and moist African forests to have accumulated AGC during the late 1990s and early 2000s.

In addition to impacts on C uptake and autotrophic respiration over days and months, droughts can have influences on the forest C balance over years or decades via tree mortality (Malhi 2011). As necromass from dead trees decomposes, C is emitted into the atmosphere for decades or longer, depending on wood characteristics (e.g., wood density as well as lignin and cellulose content) and microclimatic conditions (Itoh et al. 2012, Slik 2004, Van Nieuwstadt & Sheil 2005). Between 37% and 50% of the Amazon Basin experienced drought in 2005 and 2010, respectively (Lewis et al. 2011). These droughts committed up to 1.6 PgC to the atmosphere, largely because of increased tree mortality (Feldpausch et al. 2016, Phillips & Brienen 2017). While most of this C will eventually be emitted to the atmosphere (with a small fraction of the remaining C becoming locked in soils for long periods), to our knowledge, no studies have quantified the amount of C remaining in the atmosphere over time. Assuming average recovery rates, we speculate that

most C could be assimilated back into forests within a few years to a decade. However, several processes can slow post-drought recovery, including subsequent disturbances, climate change, liana infestation, and nutrient limitation (Chazdon et al. 2016, Longo et al. 2018, Schwalm et al. 2017).

In 2015–2016, an El Niño event triggered unusually dry climatic conditions over SEA and Amazonia and warm temperatures over the entire pantropical region. This event allowed the scientific community to evaluate how dry-warm conditions affect the C budget of tropical forests based on multiple satellite-based systems, networks of forest monitoring plots, ecophysiological studies, and improved Earth system models (Malhi et al. 2018). Based on measurements of CO₂ and carbon monoxide fluxes provided by the newly launched Orbiting Carbon Observatory 2 mission (Eldering et al. 2017), Liu et al. (2017) estimated net C emissions of 2.3 PgC for the entire tropics and showed that the mechanisms affecting forest C dynamics resulting in net emissions may vary across tropical continents. Net emissions were driven by reduced GPP (–0.9 PgC) in the Amazon, while central Africa had increased emissions from ecosystem respiration (0.6 PgC), and emissions from wildfires (0.5 PgC) resulted in a net increase in emissions in SEA. Furthermore, Luo et al. (2018) used six models to estimate GPP using satellite imagery and found a negative anomaly in pantropical photosynthesis of 1 PgC during the El Niño event, with most GPP reductions occurring in eastern Amazonia and central Africa. Field-based measurements of forest productivity also suggest reduced C uptake during this drought. Using a statistical model parameterized with field-based data, for instance, Rifai et al. (2018) estimated the 2015–2016 El Niño event to have reduced total wood production across the tropics by 8–9%. Precipitation explained a large portion of this reduction, although in Africa and some other parts of the tropics, air temperatures also played key roles by increasing ecosystem respiration. However, the long-term legacies of this drought event in terms of tropical forest C storage and fluxes in C are still unclear.

9. DROUGHT-FIRE INTERACTIONS: CONSEQUENCES FOR THE CARBON CYCLE

9.1. Trees Become Fuel During Droughts and Increase Forest Flammability

Tropical forest fires rarely result in large burned areas when air dryness in the forest understory is low [vapor-pressure deficit (VPD) <0.75 kPa] and fuel moisture content is high (>23%)—two common characteristics of primary tropical forests (Nepstad et al. 2004, Ray et al. 2005). Even when ignited, most wildfires in tropical forests die out during the night, when air and fuel humidity peak. On rare occasions, fire fronts persist during the hottest parts of the day in regions with prolonged dry seasons (e.g., southeast Amazon), although these fires rarely surpass 40 m/h or release more than 300 kW/m (Brando et al. 2014, Cochrane 2003). Trails and nests of leafcutter ants stop similar fire fronts (Carvalho et al. 2012). Forest fires generally burn small areas in normal years—almost exclusively across drier regions (Morton et al. 2013).

Droughts increase forest flammability across tropical forests by directly increasing air dryness. Indirectly, droughts can also change the physiology of tropical trees (Nepstad et al. 2001) and promote shedding of leaves, twigs, and branches during periods of low soil moisture. Eventually, these woody and nonwoody plant debris contribute to the accumulation of fuel loads on the forest floor. By thinning forest canopies, drought-stressed forests also allow more light to reach the forest floor, warming the forest understory and rapidly drying fuels (Cochrane 2003) (**Figure 3**). Deforestation, logging, and forest edge formation intensify forest flammability by damaging canopies and creating even hotter, drier climatic conditions (Cochrane 2003, Nepstad et al. 2008). Once burned, most tropical forests also become more vulnerable to subsequent fire events due to

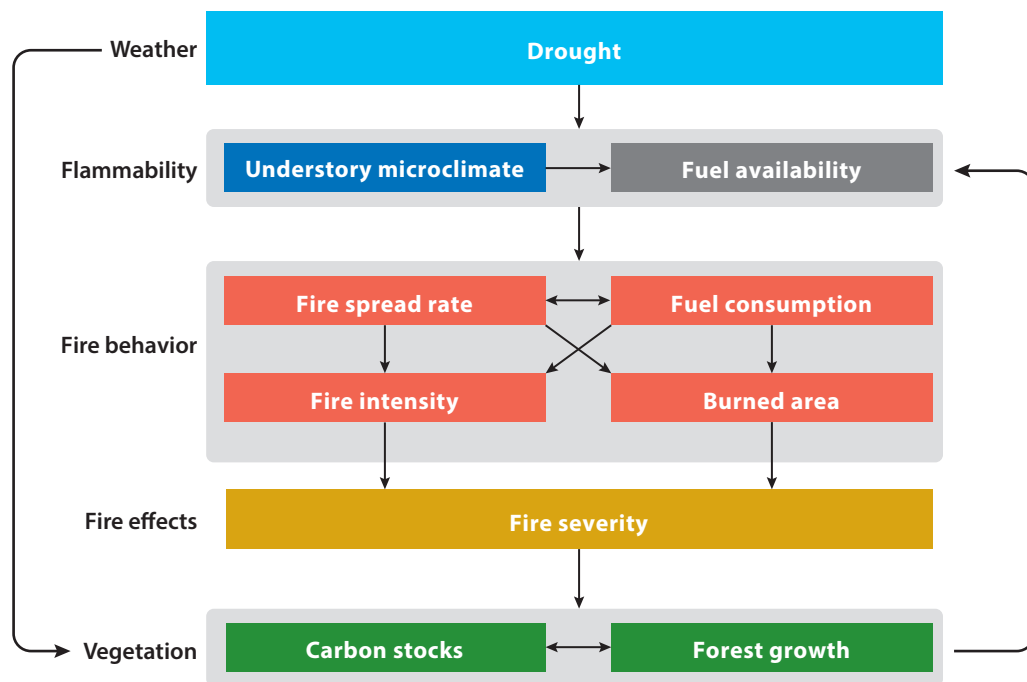


Figure 3

Schematic diagram showing how drought-mediated wildfires impact the carbon (C) stocks and productivity of tropical forests. Droughts can affect vegetation directly through physiological responses, reducing C stocks and forest growth (green). They also affect vegetation by increasing forest flammability (blue) and altering fire behavior (red) and fire effects (yellow). Consequently, more severe fires and lower C stocks and productivity are expected. This fire pathway can cause a positive fire feedback, further increasing fuel load and dryness and consequently fire severity.

increased biomass fuel and drier microclimates (Aragão et al. 2018, Nepstad et al. 2004, Slik & Eichhorn 2003), although high fire frequency diminishes fuel loads in some cases (Balch et al. 2008).

Tropical peatlands and some floodplain forests also tend to become more flammable during droughts through hydrologic changes. By reducing the groundwater depth below critical thresholds (e.g., 40 cm), droughts aerate most peat soils (Usup et al. 2004, Wösten et al. 2008), which can become a major potential fuel load (Page & Hooijer 2016). Land-use change causes additional peat drainage (Putra 2011, Warren et al. 2016), further increasing flammability. Similarly, in Amazon blackwater floodplains, the annual retreat of the waters can be exacerbated by droughts. As a result, large masses of exposed root mats can be combusted by wildfires (Flores et al. 2017).

9.2. How Fire Kills Tropical Trees

Tropical forest trees can be highly vulnerable to fire. Their typically thin bark provides little insulation against heat-induced damage to the vascular cambium, a layer of cells responsible for producing phloem (Michaletz & Johnson 2007). This limits C translocation from leaves to roots, eventually ending fine-root production and causing plant mortality due to hydraulic failure. Because bark thickness increases with tree diameter in most species (Balch et al. 2013), small trees are highly fire sensitive. Among larger, thicker-barked individuals though, the probability of mortality

often increases with increasing fire intensity (Barlow et al. 2012b, Cochrane & Barber 2009). For example, Brando et al. (2014) showed that in southeast Amazonia, an increase of 100 kW/m in fire line intensity increased tree mortality by 10%. Thus, when high-intensity fires occur (e.g., 800 kW/m), very few trees are likely to survive (Barlow & Peres 2008, Barlow et al. 2003). Because droughts can substantially increase fire intensity (Cochrane 2003), mortality rates in burned tropical forests increase during droughts (Aragão et al. 2018) (**Figure 3**), driving aboveground biomass losses of 50% or more in upland forests and >90% in floodplain forests.

Although bark thickness is one of the main predictors of fire-induced tree mortality, this plant trait usually explains less than 50% of post-fire tree death (Brando et al. 2012). Low-intensity fires can kill trees via several mechanisms beyond damage to the vascular cambium. High-intensity fires can cause reduced hydraulic conductivity of the xylem and associated increases in xylem water tensions, driving plant mortality by limiting C assimilation and growth for extended periods of time. In the southeast Amazon, post-fire tree mortality was unusually high within experimentally burned plots, even when trees were not scorched by prescribed fires, probably due to heat-related damage to roots (Brando et al. 2012). In addition to this direct effect, fires can cause increased tree mortality by weakening tree trunks and facilitating associated tree snapping (Silvério et al. 2019). Although tropical wildfires tend to occur in the understory, they can thin the forest canopy by killing a high proportion of the trees (Balch et al. 2015). In response, individual crowns of large trees become more exposed to winds, which can increase the likelihood of trunk snapping and tree uprooting, especially if damaged root mats provide less structural support. These interactions between wildfires and windstorms disproportionately affect large trees (Barlow et al. 2003) and trees along forest edges, where fires tend to be more intense and winds stronger (Brando et al. 2014).

Regionally, post-fire tree mortality varies widely, ranging from 5% to 90% (McDowell et al. 2018a). This high variability partially results from complex factors controlling fire intensity, the most important predictor of fire-induced tree mortality. Fire intensity varies across tropical forests based on different fuel loads, microclimatic conditions, fire season lengths, and unusually dry and warm weather (Nepstad et al. 2001). Tree resistance to fire is another important variable influencing post-fire tree mortality, although it is far less understood across the tropics. Tree species growing in drier regions are expected to grow thicker bark than trees in wetter regions (Brando et al. 2012). Under similar fire regimes, higher post-fire tree mortality would be expected among thinner-barked individuals growing in wetter regions compared to drier tropical forests composed of more thick-barked individuals. In reality, however, fire intensity varies enormously across tropical forests (van der Werf et al. 2008), with the individual contributions for tree mortality of fire intensity and tree species sensitivity to fire remaining poorly quantified. Generally, forest ecosystems most vulnerable to fire are those dominated by trees that have thin bark and higher fire intensity. Exceptions to this pattern, however, are seasonally flooded and peatland forests. In these systems, fire-related damage to tree roots can drive substantial mortality (Flores et al. 2014).

9.3. People and Fire: Ignition, Fuels, and the Understory Microclimate

Tropical forest fires are ignited almost entirely via accidental ignition or by people clearing vegetation, burning agricultural fields and pastureland, or committing arson. Active frontier zones and the transportation networks within them are a major hub of fire activity (Nepstad et al. 1999, Schroeder et al. 2009). Anthropogenic ignitions are increasingly prevalent in vast portions of tropical forests undergoing extensive land-use and land-cover change. Most human activities in the Amazon region started during the 1980s, when large tracts of forest were converted to agricultural fields. In general, instances of lightning-ignited wildfires in closed-canopy forests are much

less common in wet and moist tropical forests, as rains often accompany these events (Cochrane 2003).

Sources of fire ignition tend to decrease over time as an agricultural frontier matures and more intensive land-use practices dominate (Bowman et al. 2009). In parts of the tropics with more developed agricultural systems, the cultivation of mechanized crops has reduced fire activity. However, fire continues to be used to establish cropland and pastureland elsewhere. Even in areas with low deforestation rates, land management practices in previously cleared areas often involve fire, which can readily spread to nearby forests. This spread of wildfire into adjacent forest areas is well documented in the satellite record (Aragão & Shimabukuro 2010).

Land-use and land-cover changes also fundamentally alter fuels and the microclimate at forest edges. After decades of widespread deforestation, nearly 20% of remaining tropical forests lie within 100 m of a forest edge (Brando et al. 2014, Brinck et al. 2017, Haddad et al. 2017). Forest edges allow for greater sunlight and wind penetration, higher air temperatures, increased VPD, and lower soil moisture and relative humidity (Laurance 2000) resulting in very dry accumulated fuels. Native and non-native grasses, often introduced at forest edges, can provide even greater amounts of fine fuels that readily burn (Silverio et al. 2013, Nepstad et al. 2004). Overall, the land-use change effects increased ignitions, greater fuels, and drier conditions interact with drought conditions to increase the likelihood of fire occurrence in tropical forests (Aragão et al. 2018, Chen et al. 2017).

9.4. Fire Effects on Carbon Stocks and Fluxes in Tropical Forests: From Closed-Canopy Amazon Forests to Indonesian Peatlands

C emissions from forest fires depend partially on how much area burns. While fire spread in non-drought years is usually hampered by high fuel and air humidity (Uhl & Kauffman 1990), droughts can create conditions for widespread fires (Nepstad et al. 2001). Brando et al. (2014) estimated increases of 50% in fine fuels and in understory air dryness during the 2007 regional drought in southern Amazonia, when 5–10% of the region's forests burned. Further, during the 1997–1998 El Niño-related drought, understory wildfires burned 39,000 km² of Amazon forests (Alencar et al. 2015, Morton et al. 2013b). Increased burned area also occurred during droughts in other tropical forests, including in the southwestern Amazon, the Congo Basin, and SEA.

To affect such large areas, fire fronts burn for multiple days or even months, fueled by dry and abundant fine and coarse woody debris (Morton et al. 2013). These fire fronts can be reignited during the day or simply move through hot-dry nights in exceptional cases. Windy conditions can also contribute to large burned areas, although the relative role of winds remains poorly understood in the tropics (Silvestrini et al. 2011). In addition to droughts and winds, burned area is strongly influenced by landscape characteristics. Most wildfires burn hot-dry forest edges (Cochrane & Barber 2009b, Nepstad et al. 2001, Numata et al. 2017), although fuel continuity in highly fragmented regions can constrain fire spread (Brando et al. 2014).

C emissions from tropical fires can be divided into two timescales. First, fuels are instantaneously transferred to the atmosphere. Most tropical wildfires combust 20–60 MgC/ha of dead leaves, twigs, and larger woody biomass (Balch et al. 2008, Berenguer et al. 2014, Brando et al. 2016, Cochrane 2003b). Because large areas burn during droughts, emissions from forest fires account for increases in atmospheric C concentrations. For instance, gross C emissions from forest fires (old-growth plus secondary forests) in Amazonia averaged 454 Tg (10¹² g) of CO₂ per year from 2003 to 2015, with large spikes during droughts in 2005, 2007, and 2015. More broadly, during the 1997–1998 El Niño event at least 7,900 km² of forests burned in Indonesia, releasing an estimated 0.81–2.57 PgC to the atmosphere (Lauhon et al. 2002).

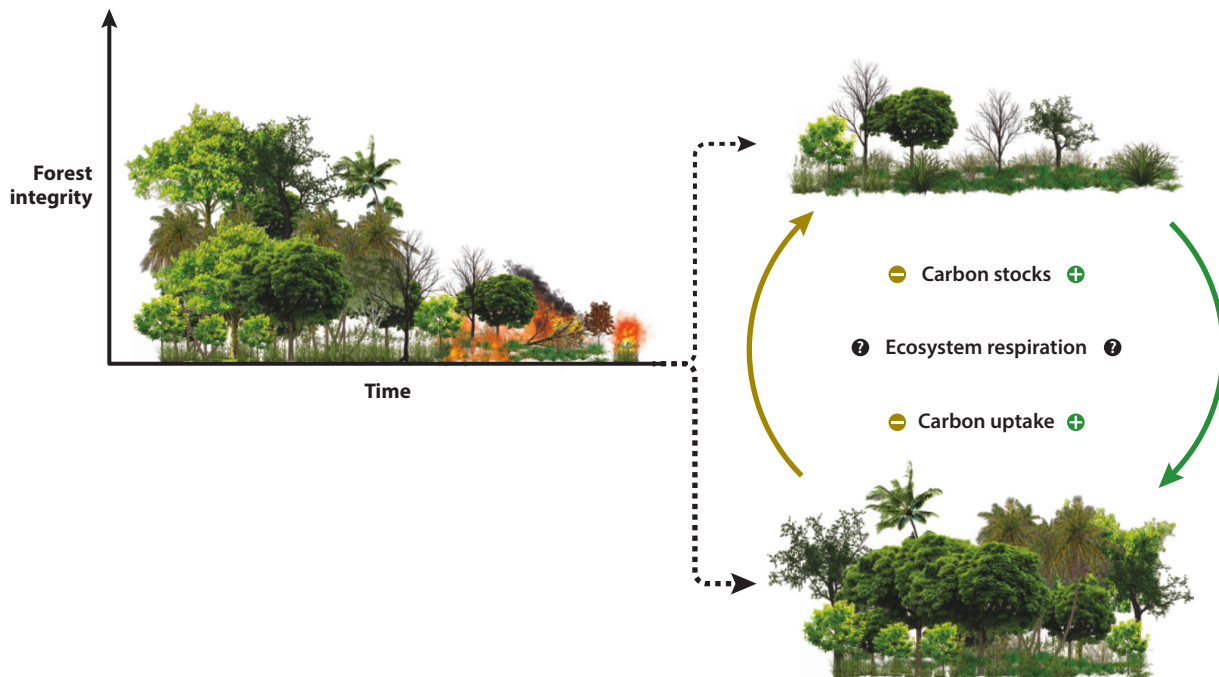


Figure 4

Two potential trajectories of burned tropical forests: full recovery or transition to a new state. With no fundamental changes in climate and/or soil nutrient pools, most burned forests recover biomass within decades and climate-related functions within a few years.

The second timescale of emissions relates to tree mortality from low-intensity fires, which can continue to occur for multiple years. As a result, understory fires release large amounts of C to the atmosphere as dead trees decompose. Not only do such fires commit this C to the atmosphere, but also they affect forest C accumulation (**Figure 4**). Although fires release nutrients over the short term (e.g., phosphorus), repeated high-intensity fires reduce the availability of key nutrients (e.g., soil C and nitrogen) necessary for the growth of surviving trees (Pellegrini et al. 2018). Forest regrowth can partially counterbalance C losses from tree losses after the fires via recruitment and reduced soil respiration (Brando et al. 2016, Metcalfe et al. 2018), although live AGC stocks of burned forests may remain much lower than background levels for several decades (Berenguer et al. 2014, Rappaport et al. 2018, Silva et al. 2018). With fewer trees growing, fire-disturbed areas tend to experience reductions in NPP.

9.5. Disturbing Tropical Peat Forests

Fires in tropical peatlands contribute to their current role as a C source. Emissions from peatland fires in SEA are estimated at 0.12 PgC/year, compared with 0.15 PgC/year from oxidation (Miettinen et al. 2017). Climate and hydrology are important controls on fire activity in tropical peatlands (Stott 2000). In Indonesia, for example, drought conditions associated with ENSO result in increased fire activity (Fuller & Fulk 2001, Spessa et al. 2015, Wooster et al. 2012). During the 2015–2016 El Niño, fires raging across Indonesia from September to November affected more than 15,000 km² of peatland and over that short time period gave rise to an estimated emission of more than 1 million tons of CO₂. Within SEA forests, the most intensive fires in Indonesia

took place in southern Sumatra and southern Kalimantan, although there was high spatial heterogeneity in rainfall (Aldrian & Djamil 2008) and fire occurrence. Research findings also suggest that repeated fires in peatlands can lead to a loss of forest resilience, resulting in a transition to an alternative stable state, particularly when interacting with drainage, logging, or drought (Hoscilo et al. 2011). This can lead to delayed or no recovery of the C released from peat fires.

10. TROPICAL DROUGHTS IN A WARMING WORLD

Although forests are highly resilient to drought-related disturbances, an increase in frequency and intensity of droughts associated with climate change could promote widespread and permanent degradation of tropical forests. However, predictions of changes to droughts differ depending on whether drought is defined using a hydrological variable, such as evapotranspiration, or as a rainfall deficit (Natl. Acad. Sci. Eng. Med. 2016). The role of warming on hydrological drought through increased surface evapotranspiration is well understood. However, several other factors lower the confidence in attribution studies regarding drought; these include uncertainties in land-surface feedbacks, lack of soil moisture observations, non-meteorological factors, and the complexity of defining drought in an attribution context (Natl. Acad. Sci. Eng. Med. 2016).

According to the Intergovernmental Panel on Climate Change Fifth Assessment report confidence terminology (Mastrandrea et al. 2010), the general current state of event attribution science on drought is medium with regard to the (*a*) capabilities of climate models to simulate drought, (*b*) quality and length of the observational record of droughts, and (*c*) understanding of the physical mechanisms that lead to changes in extremes because of climate change (Natl. Acad. Sci. Eng. Med. 2016).

In the tropics, observed and projected changes in drought occurrence are tied to changes in the convergence zones and monsoons. Future increases in precipitation extremes related to the monsoons are very likely in South America, Africa, and SEA, although there is less agreement among models about projected changes in interannual variability (Christensen et al. 2013). ENSO exhibits considerable interdecadal variability in amplitude and spatial pattern in the observed record, with low confidence in El Niño changes in intensity and spatial pattern in a warmer climate. However, ENSO will very likely remain the dominant mode of interannual variability. Twenty-first century changes in moisture availability will likely intensify ENSO-induced rainfall variability on regional scales (Christensen et al. 2013), although this may be region dependent (Seager et al. 2012). Across the Indian Ocean, the recent observed and projected changes in SST resemble a positive phase of the IOD. Furthermore, the skewness between positive and negative IOD events is anticipated to decrease (Cai et al. 2013) and extreme positive IOD events, such as the 1997 event, to occur more often (Cai et al. 2014).

Overall, state-of-the-art climate models project a very likely increase in temperatures over South America in the twenty-first century, with the greatest warming in southern Amazonia (Christensen et al. 2013). The models also agree on an increase in extreme precipitation for South America as well as an extension of the monsoon area and a southward displacement of the SACZ. Both Coupled Model Intercomparison phase 3 and 5 (CMIP3 and CMIP5) models project drier conditions in eastern Amazonia during the dry season (Cook et al. 2012) and wetter conditions in the western Amazon. Despite low confidence in global drought trends, some regions have experienced more intense and longer droughts during the second half of the twentieth century, including northeastern Brazil (Seneviratne et al. 2012).

As to the effect of droughts for the Amazon, the number of consecutive dry days is projected to increase over the course of the twenty-first century, particularly in the east, and soil moisture is projected to decrease, especially in the north (Seneviratne et al. 2012). These projected changes by the end of the twenty-first century are most pronounced for the dry season (June–August). This

is consistent with CMIP3 model simulations, which project an increase in dry-season length and a 70% reduction in rainforest extent by the end of the twenty-first century (Cook & Vizy 2008). Assessing future projections of meteorological drought in the Amazon, Duffy et al. (2015) also found increases in frequency and geographic extent in the eastern Amazon and the opposite in the west, with areas affected by mild and severe droughts likely to double and triple, respectively, by 2100.

Climate model projections disagree on the wet-season changes, with some projecting drier conditions and others predicting wetter conditions, highlighting the low confidence in these projections (Christensen et al. 2013). Projected hydroclimate changes over the Amazon are consistent with ENSO-related effects on mean precipitation, such as the projected decrease in eastern Amazonia precipitation (Christensen et al. 2013, Duffy et al. 2015). The distinct impacts of different types of ENSO (Eastern Pacific versus Central Pacific ENSO) on South American precipitation (Hill et al. 2011, Tedeschi et al. 2013) and their representation in climate models need to be kept in mind.

Most model projections for the twenty-first century do not indicate significant changes in consecutive dry days or soil moisture anomalies for the Congo Basin or SEA (Seneviratne et al. 2012). However, the confidence in projected precipitation changes for Africa for the twenty-first century is medium at best, owing to the modest ability of models to capture the most important phenomena controlling African climate (Christensen et al. 2013). This is likely compounded by the limited observational record, which prohibits robust conclusions from being drawn about trends in drought incidence for much of Africa and Asia, including the Congo Basin and SEA.

While projections suggest an increase in mean and extreme precipitation of the South Asian monsoon, model agreement over the Maritime Continent particularly is low, as mesoscale and submesoscale systems play a prominent role in this area due to the complex topography, interaction between ocean and land, and large diurnal variability, which challenge global climate models (Jourdain et al. 2013). Some studies propose a decrease in precipitation over the Maritime Continent, consistent with a high-confidence projected IOD-like warming pattern during July–October, while confidence for changes in ENSO frequency or intensity is lower (Christensen et al. 2013). No obvious trends in extreme precipitation over SEA have been observed apart from an increase in the ratio of wet- to dry-season rainfall in eastern Indonesia (Aldrian & Djamil 2008).

In addition to large-scale patterns in SST, droughts across the tropics can be exacerbated by deforestation (Nobre et al. 2016, Silvério et al. 2015). In some tropical regions, one-third of the regional rainfall can result from large trees transferring soil water to the atmosphere (Nepstad et al. 1994). Cutting down trees and replacing them with pasturelands or croplands can reduce water available for this local recycling process and affect rainfall patterns, especially in areas of widespread deforestation (e.g., >40%) (Nobre et al. 2016). Additionally, losses of forest cover can amplify diurnal temperature variation and increase mean and maximum temperatures (Alkama & Cescatti 2016), with implications for hydroclimatic conditions during droughts and heat waves. In southeastern and western Amazonia, large-scale deforestation has already altered the regional climate, with the onset of the wet season occurring three weeks later (Fu et al. 2013). It is possible that similar processes could occur in other parts of the tropics. However, in SEA the high moisture convergence from ocean to land could outweigh such effects.

11. THE FUTURE OF TROPICAL FORESTS

Increased frequency and intensity of droughts may change the structure, composition, and function of many tropical forests in the coming decades (Trumbore et al. 2015). Combined with rapid deforestation and increased burning in the tropics, more frequent and intense droughts and associated wildfires could drastically reduce forest C stocks. A shift of tropical forests from being a

net C sink to a net C source in the near future would likely result from these changes (Lewis et al. 2015, Trumbore et al. 2015), which would have important consequences for the global C cycle.

Despite the large uncertainties in future climate projections for the tropics (especially Africa and SEA), increased air temperature is likely to increase evapotranspiration rates and create more extreme events. Modeling tropical forest ecosystem responses to these events requires explicit representation of physiological processes, including plant hydraulic failure, drought-induced C starvation, and changes in plant productivity in response to CO₂ fertilization. The development of such models for tropical systems, however, has been limited by a lack of data on these physiological properties and how they relate to tree mortality in the tropics (Barlow et al. 2012a, Malhi et al. 2014). As a result, Earth system models project a wide range of future outcomes for tropical forests, from strongly increased to strongly decreased capacity of tropical forests to store C in the future (Malhi et al. 2014). The high variability among simulations makes confident projections of the future of tropical forest C stocks and fluxes highly uncertain. Better characterizations of forest responses to mounting stressors (e.g., forest fragmentation, wildfires, droughts, and windstorms), including tree mortality events and post-mortality recovery, are required to reduce uncertainties.

It is unclear whether or when the impacts of severe, repeated disturbances by drought and fires could exceed tropical forests' capacity to recover (Davidson et al. 2012). Current research cannot properly identify specific threshold conditions beyond which ecosystem properties could lead to alternative stable states. Yet, the growing body of scientific evidence points to such threshold conditions becoming more likely across the tropics with climate and land use change. A major cause for concern is that forest responses to fire and drought can be abrupt and catastrophic (Brando et al. 2014, Nepstad et al. 2007). Focused field observations, experiments, and improved numerical models are critical for significantly improved understanding of tropical forest responses to future perturbations related to changing climate and drought and fire frequency and intensity.

SUMMARY POINTS

1. Drought-fire impacts are significantly greater along forest edges.
2. Recent droughts have temporarily changed tropical forests from a net carbon (C) sink to a net C source on timescales varying from at least a few months to a few years.
3. It is still unclear how long drought legacies can persist. A better understanding of the recovery time of drought-disturbed forests is required.
4. Knowing the full impacts of drought-fire interactions on the C dynamics of tropical forests is limited by a lack of mechanistic understanding of drought- and fire-induced tree mortality.
5. Droughts are likely to become more frequent and intense across the tropics in the near future, but climate models still project such events with limited confidence, especially in the Congo Basin (because of a lack of high-quality observations for comparison) and SEA (because of the complexities in monsoon drivers).

FUTURE ISSUES

1. Growing demands for tropical agricultural commodities are likely to increase sources of fire ignition and negative impacts on forests.

2. Complex interactions among disturbances such as drought, fires, blowdowns, and forest fragmentation combined with a changing climate will drive much of the variability in carbon stocks of the remaining tropical forests in the near future.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

P.M.B. acknowledges financial support from the National Science Foundation (NSF) Macrosystems and the National Council for Scientific and Technological Development (productive grant). Use of the following data sets is gratefully acknowledged: National Centers for Environmental Prediction/National Center for Atmospheric Research reanalysis; Climate Prediction Center Merged Analysis Product; and NOAA Extended Reconstructed SST v5 data provided by the National Oceanic and Atmospheric Administration Office of Oceanic and Atmospheric Research, Earth System Research Laboratory Physical Sciences Division, Boulder, Colorado, USA, through their website <https://www.cdc.noaa.gov>. C.C.U. acknowledges financial support through NSF AGS-1602455 as well as the Early Career Scientist Endowed Fund and the George E. Thibault Early Career Scientist Fund at Woods Hole Oceanographic Institution. The authors are thankful for thoughtful comments from R. Houghton and R. Birdsey.

LITERATURE CITED

- Adams HD, Zeppel MJ, Anderegg WR, Hartmann H, Landhäusser SM, et al. 2017. A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nat. Ecol. Evol.* 1(9):1285–91
- Aldrian E, Djamil YS. 2008. Spatio-temporal climatic change of rainfall in East Java Indonesia. *Int. J. Climatol.* 28(4):435–48
- Alencar AA, Brando PM, Asner GP, Putz FE. 2015. Landscape fragmentation, severe drought, and the new Amazon forest fire regime. *Ecol. Appl.* 25(6):1493–505
- Alexander MA, Kilbourne KH, Nye JA. 2014. Climate variability during warm and cold phases of the Atlantic Multidecadal Oscillation (AMO) 1871–2008. *J. Mar. Syst.* 133:14–26
- Alkama R, Cescatti A. 2016. Biophysical climate impacts of recent changes in global forest cover. *Science* 351:600–4
- Allen CD, Breshears DD, McDowell NG. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6(8):129
- Anderegg WRL, Klein T, Bartlett M, Sack L, Pellegrini AFA, et al. 2016. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *PNAS* 113:5024–29
- Aragão LEOC, Anderson LO, Fonseca MG, Rosan TM, Vedovato LB, et al. 2018. 21st century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nat. Commun.* 9(1):536
- Aragão LEOC, Shimabukuro YE. 2010. The incidence of fire in Amazonian forests with implications for REDD. *Science* 328(5983):1275–78
- Asefi-Najafabady S, Saatchi S. 2013. Response of African humid tropical forests to recent rainfall anomalies. *Philos. Trans. R. Soc. B* 368(1625):20120306

- Atkin OK, Bruhn D, Hurry VM, Tjoelker MG. 2005. *Evans Review No. 2: the hot and the cold: unravelling the variable response of plant respiration to temperature. Funct. Plant Biol.* 32(2):87–105
- Baccini A, Goetz SJ, Walker WS, Laporte NT, Sun M, et al. 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nat. Clim. Change* 2(3):182–85
- Baccini A, Walker W, Carvalho L, Farina M, Sulla-Menashe D, Houghton RA. 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. *Science* 358(6360):230–34
- Balch JK, Brando PM, Nepstad DC, Coe MT, Silv rio D, et al. 2015. The susceptibility of southeastern Amazon forests to fire: insights from a large-scale burn experiment. *BioScience* 65(9):893–905
- Balch JK, Massad TJ, Brando PM, Nepstad DC, Curran LM. 2013. Effects of high-frequency understory fires on woody plant regeneration in southeastern Amazonian forests. *Philos. Trans. R. Soc. B* 368(1619):20120157
- Balch JK, Nepstad DC, Brando PM, Curran LM, Portela O, et al. 2008. Negative fire feedback in a transitional forest of southeastern Amazonia. *Glob. Change Biol.* 14(10):2276–87
- Barlow J, Parry L, Gardner TA, Ferreira J, Arag o LEOC, et al. 2012a. The critical importance of considering fire in REDD+ programs. *Biol. Conserv.* 154:1–8
- Barlow J, Peres CA. 2008. Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philos. Trans. R. Soc. B* 363(1498):1787–94
- Barlow J, Peres CA, Lagan BO, Haugaasen T. 2003. Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecol. Lett.* 6:6–8
- Barlow J, Silveira JM, Mestre LAM, Andrade RB, D’Andrea GC, et al. 2012b. Wildfires in bamboo-dominated Amazonian forest: impacts on above-ground biomass and biodiversity. *PLOS ONE* 7(3):e33373
- Beer C, Reichstein M, Tomelleri E, Ciais P, Jung M, et al. 2010. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* 329(5993):834–38
- Berenguer E, Ferreira J, Gardner TA, Arag o LEOC, De Camargo PB, et al. 2014. A large-scale field assessment of carbon stocks in human-modified tropical forests. *Glob. Change Biol.* 20(12):3713–26
- Bowman DMJS, Balch JK, Artaxo P, Bond WJ, Carlson JM, et al. 2009. Fire in the Earth system. *Science* 324(5926):481–84
- Brando P. 2018. Tree height matters. *Nat. Geosci.* 11:390–91
- Brando PM, Balch JK, Nepstad DC, Morton DC, Putz FE, et al. 2014. Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *PNAS* 111(17):6347–52
- Brando PM, Goetz SJ, Baccini A, Nepstad DC, Beck PSA, Christman MC. 2010. Seasonal and interannual variability of climate and vegetation indices across the Amazon. *PNAS* 107(33):14685–90
- Brando PM, Nepstad DC, Balch JK, Bolker B, Christman MC, et al. 2012. Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Glob. Change Biol.* 18(2):630–41
- 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. *Philos. Trans. R. Soc. B* 363(1498):1839–48
- Brando PM, Oliveria-Santos C, Rocha W, Cury R, Coe MT. 2016. Effects of experimental fuel additions on fire intensity and severity: unexpected carbon resilience of a neotropical forest. *Glob. Change Biol.* 22(7):2516–25
- Brando PM, Ray D, Nepstad D, Cardinot G, Curran LM, Oliveira R. 2006. Effects of partial throughfall exclusion on the phenology of *Coussarea racemosa* (Rubiaceae) in an east-central Amazon rainforest. *Oecologia* 150(2):181–89
- Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, et al. 2005. Regional vegetation die-off in response to global-change-type drought. *PNAS* 102(42):15144–48
- Breshears DD, Myers OB, Meyer CW, Barnes FJ, Zou CB, et al. 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Front. Ecol. Environ.* 7(4):185–89
- Brienen RJW, Phillips OL, Feldpausch TR, Gloor E, Baker TR, et al. 2015. Long-term decline of the Amazon carbon sink. *Nature* 519(7543):344–48

- Brinck K, Fischer R, Groeneveld J, Lehmann S, De Paula MD, et al. 2017. High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. *Nat. Commun.* 8:14855
- Bucci SJ, Goldstein G, Scholz FG, Meinzer FC. 2016. Physiological significance of hydraulic segmentation, nocturnal transpiration and capacitance in tropical trees: paradigms revisited. In *Tropical Tree Physiology: Adaptations and Responses in a Changing Environment*, ed. G Goldstein, LS Santiago, pp. 205–25. Cham, Switz.: Springer
- Cai W, Santoso A, Wang G, Weller E, Wu L, et al. 2014. Increased frequency of extreme Indian Ocean Dipole events due to greenhouse warming. *Nature* 510:254–58
- Cai W, Zheng X-T, Weller E, Collins M, Cowan T, et al. 2013. Projected response of the Indian Ocean Dipole to greenhouse warming. *Nat. Geosci.* 6:999–1007
- Carvalho KS, Alencar A, Balch J, Moutinho P. 2012. Leafcutter ant nests inhibit low-intensity fire spread in the understory of transitional forests at the Amazon's forest-savanna boundary. *Psyche J. Entomol.* 2012:780713
- Castanho A, Coe MT, Costa MH, Malhi Y, Galbraith D, Quesada CA. 2013. Improving simulated Amazon forest biomass and productivity by including spatial variation in biophysical parameters. *Biogeosciences* 10(4):2255–72
- Chambers JQ, Roberts DA. 2014. Ecology: drought in the Congo Basin. *Nature* 509:34–37
- Chaves MM, Maroco JP, Pereira JS. 2003. Understanding plant responses to drought from genes to the whole plant. *Funct. Plant Biol.* 30(3):239–64
- Chazdon RL, Broadbent EN, Rozendaal DMA, Bongers F, Zambrano AMA, et al. 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Sci. Adv.* 2(5):e1501639
- Chen Y, Morton DC, Andela N, van der Werf GR, Giglio L, Randerson JT. 2017. A pan-tropical cascade of fire driven by El Niño/Southern Oscillation. *Nat. Clim. Change* 7(12):906–11
- Christensen JH, Kumar KK, Aldrian E, An SI, Cavalcanti IFA, et al. 2013. Climate phenomena and their relevance for future regional climate change. 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*, ed. TF Stocker, D Qin, G-K Plattner, SK Tignor, J Allen et al., pp. 1217–308. Cambridge, UK: Cambridge Univ. Press
- Cochrane MA. 2003. Fire science for rainforests. *Nature* 421(6926):913–19
- Cochrane MA, Barber CP. 2009. Climate change, human land use and future fires in the Amazon. *Glob. Change Biol.* 15(3):601–12
- Cook B, Zeng N, Yoon JH. 2012. Will Amazonia dry out? Magnitude and causes of change from IPCC climate model projections. *Earth Interact.* 16:1–27
- Cook KH, Vizy EK. 2008. Effects of twenty-first-century climate change on the Amazon rain forest. *J. Clim.* 21(3):542–60
- da Costa ACL, Galbraith D, Almeida S, Portela BTT, da Costa M, et al. 2010. Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest. *New Phytol.* 187(3):579–91
- D'Arrigo R, Abram N, Ummenhofer C, Palmer J, Mudelsee M. 2011. Reconstructed streamflow for Citarum River, Java, Indonesia: linkages to tropical climate dynamics. *Clim. Dyn.* 23:451–62
- Davidson EA, de Araújo AC, Artaxo P, Balch JK, Brown IF, et al. 2012. The Amazon basin in transition. *Nature* 481(7381):321–28
- Domingues TF, Ometto JPHB, Nepstad DC, Brando PM, Martinelli LA, Ehleringer JR. 2018. Ecophysiological plasticity of Amazonian trees to long-term drought. *Oecologia* 187:933–40
- Duffy PB, Brando P, Asner GP, Field CB. 2015. Projections of future meteorological drought and wet periods in the Amazon. *PNAS* 112(43):13172–77
- Eldering A, Wennberg PO, Crisp D, Schimel DS, Gunson MR, et al. 2017. The Orbiting Carbon Observatory-2 early science investigations of regional carbon dioxide fluxes. *Science* 358(6360):eaam5745
- Engelbrecht BM, Comita LS, Condit R, Kursar TA, Tyree MT, et al. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447(7140):80
- Esquivel-Muelbert A, Baker TR, Dexter KG, Lewis SL, ter Steege H, et al. 2016. Seasonal drought limits tree species across the Neotropics. *Ecography* 40(5):618–29

- Fauset S, Baker TR, Lewis SL, Feldpausch TR, Affum-Baffoe K, et al. 2012. Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecol. Lett.* 15(10):1120–29
- Feldpausch TR, Phillips OL, Brienens RJ, Gloor E, Lloyd J, et al. 2016. Amazon forest response to repeated droughts. *Glob. Biogeochem. Cycles* 30:964–82
- Flores BM, Holmgren M, Xu C, van Nes EH, Jakovac CC, et al. 2017. Floodplains as an Achilles' heel of Amazonian forest resilience. *PNAS* 114(17):4442–46
- Flores BM, Piedade MTF, Nelson BW. 2014. Fire disturbance in Amazonian blackwater floodplain forests. *Plant Ecol. Divers.* 7(1–2):319–27
- Fu R, Yin L, Li W, Arias PA, Dickinson RE, et al. 2013. Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *PNAS* 110:18110–15
- Fuller DO, Fulk M. 2001. Burned area in Kalimantan, Indonesia mapped with NOAA-AVHRR and Landsat TM imagery. *Int. J. Remote Sensing* 22(4):691–97
- Furze ME, Trumbore S, Hartmann H. 2018. Detours on the phloem sugar highway: stem carbon storage and remobilization. *Curr. Opin. Plant Biol.* 43:89–95
- Gatti LV, Gloor M, Miller JB, Doughty CE, Malhi Y, et al. 2014. Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements. *Nature* 506(7486):76–80
- Giardina F, Konings AG, Kennedy D, Alemohammad SH, Oliveira RS, et al. 2018. Tall Amazonian forests are less sensitive to precipitation variability. *Nat. Geosci.* 11:405–9
- Guan K, Pan M, Li H, Wolf A, Wu J, et al. 2015. Photosynthetic seasonality of global tropical forests constrained by hydroclimate. *Nat. Geosci.* 8(4):284–89
- Haddad NM, Holt RD Jr., Fletcher RJ, Loreau M, Clobert J. 2017. Connecting models, data, and concepts to understand fragmentation's ecosystem-wide effects. *Ecography* 40(1):1–8
- Hartmann DL, Klein Tank AMG, Rusticucci M, Alexander LV, Brönnimann S, et al. 2013. Observations: atmosphere and surface. 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*, ed. TF Stocker, D Qin, G-K Plattner, SK Tignor, J Allen, et al., pp. 159–254. Cambridge, UK: Cambridge Univ. Press
- Hartmann H, McDowell NG, Trumbore S. 2015. Allocation to carbon storage pools in Norway spruce saplings under drought and low CO₂. *Tree Physiol.* 35:243–52
- Hartmann H, Schuldt B, Sanders TGM, Macinnis-Ng C, Boehmer HJ, et al. 2018. Monitoring global tree mortality patterns and trends. Report from the VW symposium 'Crossing scales and disciplines to identify global trends of tree mortality as indicators of forest health.' *New Phytol.* 217(3):984–87
- Hartmann H, Trumbore S. 2016. Understanding the roles of nonstructural carbohydrates in forest trees from what we can measure to what we want to know. *New Phytol.* 211:386–403
- Hill KJ, Taschetto AS, England MH. 2011. Sensitivity of South American summer rainfall to tropical Pacific Ocean SST anomalies. *Geophys. Res. Lett.* 38(1):L01701
- Hirota M, Holmgren M, van Nes EH, Scheffer M. 2011. Global resilience of tropical forest and savanna to critical transitions. *Science* 334(6053):232–35
- Hoscilo A, Page SE, Tansey KJ, Rieley JO. 2011. Effect of repeated fires on land-cover change on peatland in southern Central Kalimantan, Indonesia, from 1973 to 2005. *Int. J. Wildland Fire* 20(4):578–88
- Houghton RA. 2007. Balancing the global carbon budget. *Annu. Rev. Earth Planet. Sci.* 35(1):313–47
- Houghton RA, Byers B, Nassikas AA. 2015. A role for tropical forests in stabilizing atmospheric CO₂. *Nat. Clim. Change* 5(12):1022–23
- Hua W, Zhou L, Chen H, Nicholson SE, Raghavendra A, Jiang Y. 2016. Possible causes of the Central Equatorial African long-term drought. *Environ. Res. Lett.* 11(12):124002
- Huang B, Thorne PW, Banzon VF, Boyer T, Chepurin G, et al. 2017. Extended Reconstructed Sea Surface Temperature, Version 5 (ERSSTv5): upgrades, validations, and intercomparisons. *J. Clim.* 30:8179–205
- Itoh A, Nanami S, Harata T, Ohkubo T, Tan S, et al. 2012. The effect of habitat association and edaphic conditions on tree mortality during El Niño-induced drought in a Bornean dipterocarp forest. *Biotropica* 44(5):606–17
- Jourdain NC, Gupta AS, Taschetto AS, Ummenhofer CC, Moise AF, Ashok K. 2013. The Indo-Australian monsoon and its relationship to ENSO and IOD in reanalysis data and the CMIP3/CMIP5 simulations. *Clim. Dyn.* 41(11–12):3073–102

- Kistler R, Kalnay E, Collins W, Saha S, White G, et al. 2001. The NCEP–NCAR 50-year reanalysis: monthly means CD-ROM and documentation. *Bull. Am. Meteorol. Soc.* 82:247–68
- Kondo M, Ichii K, Patra PK, Poulter B, Calle L, et al. 2018. Plant regrowth as a driver of recent enhancement of terrestrial CO₂ uptake. *Geophys. Res. Lett.* 45(10):4820–30
- Körner C. 2003. Carbon limitation in trees. *J. Ecol.* 91:4–17
- Lauhon LJ, Gudiksen MS, Wang D, Lieber CM. 2002. Epitaxial core-shell and core-multishell nanowire heterostructures. *Nature* 420(6911):57–61
- Laurance WF. 2000. Do edge effects occur over large spatial scales? *Trends Ecol. Evol.* 15(4):P134–35
- Le Quéré C, Andrew RM, Canadell JG, Sitch S, Korsbakken JI, et al. 2016. Global carbon budget 2016. *Earth Syst. Sci. Data* 8(2):605–49
- Lebrija-Trejos E, Meave JA, Poorter L, Pérez-García EA, Bongers F. 2010. Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. *Perspect. Plant Ecol. Evol. Syst.* 12(4):267–75
- Lee JE, Frankenberg C, van der Tol C, Berry JA, Guanter L, et al. 2013. Forest productivity and water stress in Amazonia: observations from GOSAT chlorophyll fluorescence. *Proc. R. Soc. B* 280(1761):20130171
- Leitold V, Morton DC, Longo M, dos-Santos MN, Keller M, Scaranello M. 2018. El Niño drought increased canopy turnover in Amazon forests. *New Phytol.* 219(3):959–71
- Levine NM, Zhang K, Longo M, Baccini A, Phillips OL, et al. 2016. Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. *PNAS* 113(3):793–97
- Lewis SL, Brando PM, Phillips OL, van der Heijden GMF, Nepstad D. 2011. The 2010 Amazon drought. *Science* 331(6017):554
- Lewis SL, Edwards DP, Galbraith D. 2015. Increasing human dominance of tropical forests. *Science* 349(6250):827–32
- Lewis SL, Lloyd J, Sitch S, Mitchard ETA, Laurance WF. 2009a. Changing ecology of tropical forests: evidence and drivers. *Annu. Rev. Ecol. Evol. Syst.* 40(1):529–49
- Lewis SL, Lopez-Gonzalez G, Sonké B, Affum-Baffoe K, Baker TR, et al. 2009b. Increasing carbon storage in intact African tropical forests. *Nature* 457(7232):1003–6
- Lewis SL, Sonké B, Sunderland T, Begne SK, Lopez-Gonzalez G, et al. 2013. Above-ground biomass and structure of 260 African tropical forests. *Philos. Trans. R. Soc. B* 368(1625):20120295
- Liu J, Bowman KW, Schimel DS, Parazoo NC, Jiang Z, et al. 2017. Contrasting carbon cycle responses of the tropical continents to the 2015–2016 El Niño. *Science* 358(6360):eaam5690
- Longo M, Knox RG, Levine NM, Alves LF, Bonal D, et al. 2018. Ecosystem heterogeneity and diversity mitigate Amazon forest resilience to frequent extreme droughts. *New Phytol.* 219:914–31
- Luo X, Keenan TF, Fisher JB, Jiménez-Muñoz J-C, Chen JM, et al. 2018. The impact of the 2015/2016 El Niño on global photosynthesis using satellite remote sensing. *Philos. Trans. R. Soc. B* 373(1760):20170409
- Malhi Y. 2011. The productivity, metabolism and carbon cycle of tropical forest vegetation. *J. Ecol.* 100(1):65–75
- Malhi Y, Gardner TA, Goldsmith GR, Silman MR, Zelazowski P. 2014. Tropical forests in the Anthropocene. *Annu. Rev. Environ. Resour.* 39:125–59
- Malhi Y, Rowland L, Aragão LEOC, Fisher RA. 2018. New insights into the variability of the tropical land carbon cycle from the El Niño of 2015/2016. *Philos. Trans. R. Soc. B* 373:20170298
- Marengo JA, Tomasella J, Alves LM, Soares WR, Rodriguez DA. 2011. The drought of 2010 in the context of historical droughts in the Amazon region. *Geophys. Res. Lett.* 38(12):L12703
- Marengo JA, Tomasella J, Soares WR, Alves LM, Nobre CA. 2012. Extreme climatic events in the Amazon basin. *Theor. Appl. Climatol.* 107(1–2):73–85
- Mastrandrea MD, Field CB, Stocker TF, Edenhofer O, Ebi KL, et al. 2010. *Guidance note for lead authors of the IPCC Fifth Assessment Report on consistent treatment of uncertainties*. Product prepared for IPCC Cross-Working Group Meeting on Consistent Treatment of Uncertainties, Jasper Ridge, CA, July 6–7
- McDowell NG, Allen CD, Anderson-Teixeira K, Brando P, Brien R, et al. 2018a. Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytol.* 219:851–69
- McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol. Evol.* 26:523–32

- McDowell NG, Michaletz ST, Bennett KE, Solander KC, Xu C, et al. 2018b. Predicting chronic climate-driven disturbances and their mitigation. *Trends Ecol. Evol.* 33(1):15–27
- McDowell NG, Pockman WT, Allen CD, Breshears DD, Cobb N, et al. 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytol.* 178(4):719–39
- Meir P, Brando PM, Nepstad D, Vasconcelos S, Costa ACL, et al. 2009. The effects of drought on Amazonian rain forests. *Geophys. Monogr. Ser.* 186:429–49
- Metcalf DB, Rocha W, Balch JK, Brando PM, Dougherty CE, Malhi Y. 2018. Impacts of fire on sources of soil CO₂ efflux in a dry Amazon rain forest. *Glob. Change Biol.* 24(8):3629–41
- Michaletz ST, Johnson EA. 2007. How forest fires kill trees: a review of the fundamental biophysical processes. *Scand. J. For. Res.* 22(6):500–15
- Miettinen J, Hooijer A, Vernimmen R, Liew SC, Page SE. 2017. From carbon sink to carbon source: extensive peat oxidation in insular Southeast Asia since 1990. *Environ. Res. Lett.* 12(2):024014
- Morton DC, Le Page Y, DeFries R, Collatz GJ, Hurtt GC. 2013. Understorey fire frequency and the fate of burned forests in southern Amazonia. *Philos. Trans. R. Soc. B* 368(1619):20120163
- Natl. Acad. Sci. Eng. Med. 2016. *Attribution of Extreme Weather Events in the Context of Climate Change*. Washington, DC: Natl. Acad. Press
- Nepstad DC, Carvalho G, Barros AC, Alencar A, Capobianco JP, et al. 2001. Road paving, fire regime feedbacks, and the future of Amazon forests. *For. Ecol. Manag.* 154:395–407
- Nepstad DC, de Carvalho CR, Davidson EA, Jipp PH, Lefebvre P, et al. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372:666–69
- Nepstad DC, Lefebvre P, Lopes da Silva U, Tomasella J, Schlesinger P, et al. 2004. Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. *Glob. Change Biol.* 10:704–17
- Nepstad DC, Stickler CM, Soares-Filho B, Merry F. 2008. Interactions among Amazon land use, forests and climate: prospects for a near-term forest tipping point. *Philos. Trans. R. Soc. B* 363(1498):1737–46
- 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(9):2259–69
- Nepstad DC, Verssimo A, Alencar A, Nobre C, Lima E, et al. 1999. Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* 398(6727):505–8
- Nobre CA, Sampaio G, Borma LS, Castilla-Rubio JC, Silva JS, Cardoso M. 2016. Land-use and climate change risks in the Amazon and the need of a novel sustainable development paradigm. *PNAS* 113(39):10759–68
- Numata I, Silva SS, Cochrane MA, d'Oliveira MV. 2017. Fire and edge effects in a fragmented tropical forest landscape in the southwestern Amazon. *For. Ecol. Manag.* 401:135–46
- Page SE, Hooijer A. 2016. In the line of fire: the peatlands of Southeast Asia. *Philos. Trans. R. Soc. B* 371(1696):20150176
- Pan X, Chin M, Ichoku CM, Field RD. 2018. Connecting Indonesian fires and drought with the type of El Niño and phase of the Indian Ocean Dipole during 1979–2016. *J. Geophys. Res. Atmos.* 123:7974–88
- Pan Y, Birdsey RA, Phillips OL, Jackson RB. 2013. The structure, distribution, and biomass of the world's forests. *Annu. Rev. Ecol. Evol. Syst.* 44(1):593–622
- Pellegrini AFA, Ahlström A, Hobbie SE, Reich PB, Nieradzik LP, et al. 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* 553:194–98
- Phillips OL, Brienen RJW. 2017. Carbon uptake by mature Amazon forests has mitigated Amazon nations' carbon emissions. *Carbon Balance Manag.* 12(1):1–9
- Phillips OL, van der Heijden G, Lewis SL, López-González G, Aragão LEOC, et al. 2010. Drought-mortality relationships for tropical forests. *New Phytol.* 187(3):631–46
- Putra EI. 2011. The effect of the precipitation pattern of the dry season on peat fire occurrence in the Mega Rice Project area, Central Kalimantan, Indonesia. *Tropics* 19(4):145–56
- Rammig A, Jupp T, Thonicke K, Tietjen B, Heinke J, et al. 2010. Estimating the risk of Amazonian forest dieback. *New Phytol.* 187(3):694–706

- Rappaport DI, Morton DC, Longo M, Keller M, Dubayah R, dos-Santos MN. 2018. Quantifying long-term changes in carbon stocks and forest structure from Amazon forest degradation. *Environ. Res. Lett.* 13(6):065013
- Ray D, Nepstad D, Moutinho P. 2005. Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. *Ecol. Appl.* 15(5):1664–78
- Rifai SW, Girardin CAJ, Berenguer E, del Aguila-Pasquel J, Dahlsjö CAL, et al. 2018. ENSO drives interannual variation of forest woody growth across the tropics. *Philos. Trans. R. Soc. B* 373(1760):20170410
- Ropelewski CF, Halpert MS. 1987. Global and regional scale precipitation patterns associated with the El Niño/Southern Oscillation. *Mon. Weather Rev.* 115(8):1606–26
- Rowland L, da Costa AC, Galbraith DR, Oliveira RS, Binks OJ, et al. 2015a. Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* 528:119–22
- Rowland L, Lobo-do-Vale RL, Christoffersen BO, Melém EA, Kruijt B, et al. 2015b. After more than a decade of soil moisture deficit, tropical rainforest trees maintain photosynthetic capacity, despite increased leaf respiration. *Glob. Change Biol.* 21:4662–72
- Saatchi SS, Harris NL, Brown S, Lefsky M, Mitchard ETA, et al. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. *PNAS* 108(24):9899–904
- Saji NH, Goswami BN, Vinayachandran PN, Yamagata T. 1999. A dipole mode in the tropical Indian Ocean. *Nature* 401(6751):360
- Santiago LS, De Guzman ME, Baraloto C, Vogenberg JE, Brodie M, et al. 2018. Coordination and trade-offs among hydraulic safety, efficiency and drought avoidance traits in Amazonian rainforest canopy tree species. *New Phytol.* 218(3):1015–24
- Santos VAHFD, Ferreira MJ, Rodrigues JVFC, Garcia MN, Ceron JVB, et al. 2018. Causes of reduced leaf-level photosynthesis during strong El Niño drought in a Central Amazon forest. *Glob. Change Biol.* 24:4266–79
- Schroeder W, Alencar A, Arima E, Setzer A. 2009. The spatial distribution and interannual variability of fire in Amazonia. *Amazon. Glob. Change* 186:43–60
- Schwalm CR, Anderegg WRL, Michalak AM, Fisher JB, Biondi F, et al. 2017. Global patterns of drought recovery. *Nature* 548(7666):202–5
- Seager R, Naik N, Vogel L. 2012. Does global warming cause intensified interannual hydroclimate variability? *J. Clim.* 25:3355–72
- Secchi F, Pagliarani C, Zwieniecki MA. 2017. The functional role of xylem parenchyma cells and aquaporins during recovery from severe water stress. *Plant Cell Environ.* 40(6):858–71
- Seddon AWR, Macias-Fauria M, Long PR, Benz D, Willis KJ. 2016. Sensitivity of global terrestrial ecosystems to climate variability. *Nature* 531(7593):229–32
- Seneviratne SI, Nicholls N, Easterling D, Goodess CM, Kanae S, et al. 2012. Changes in climate extremes and their impacts on the natural physical environment. In *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation: Special Report of the Intergovernmental Panel on Climate Change*, ed. CB Field, pp. 109–230. Cambridge, UK: Cambridge Univ. Press
- Silva CVJ, Aragão LEOC, Barlow J, Espirito-Santo F, Young PJ, et al. 2018. Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics. *Philos. Trans. R. Soc. B* 373:20180043
- Silvério DV, Brando PM, Balch JK, Putz FE, Nepstad DC, et al. 2013. Testing the Amazon savannization hypothesis: fire effects on invasion of a neotropical forest by native cerrado and exotic pasture grasses. *Philos. Trans. R. Soc. B* 368(1619):20120427
- Silvério DV, Brando PM, Bustamante MMC, Putz FE, Marra DM, et al. 2019. Fire, fragmentation, and windstorms: a recipe for tropical forest degradation. *J. Ecol.* 107(2):656–67
- Silvério DV, Brando PM, Macedo MN, Beck PS, Bustamante M, Coe MT. 2015. Agricultural expansion dominates climate changes in southeastern Amazonia: the overlooked non-GHG forcing. *Environ. Res. Lett.* 10(10):104015
- Silvestrini RA, Soares-Filho BS, Nepstad D, Coe M, Rodrigues H, Assunção R. 2011. Simulating fire regimes in the Amazon in response to climate change and deforestation. *Ecol. Appl.* 21(5):1573–90

- Slik JWF. 2004. El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. *Oecologia* 141(1):114–20
- Slik JWF, Eichhorn KAO. 2003. Fire survival of lowland tropical rain forest trees in relation to stem diameter and topographic position. *Oecologia* 137(3):446–55
- Spessa AC, Field RD, Pappenberger F, Langner A, Englhart S, et al. 2015. Seasonal forecasting of fire over Kalimantan, Indonesia. *Nat. Hazards Earth Syst. Sci.* 15(3):429–42
- Stahl C, Hérault B, Rossi V, Burban B, Bréchet C, Bonal D. 2013. Depth of soil water uptake by tropical rainforest trees during dry periods: Does tree dimension matter? *Oecologia* 173(4):1191–201
- Staver AC, Archibald S, Levin SA. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334(6053):230–32
- Stott P. 2000. Combustion in tropical biomass fires: a critical review. *Prog. Phys. Geogr.* 24(3):355–77
- Tedeschi RG, Cavalcanti IF, Grimm AM. 2013. Influences of two types of ENSO on South American precipitation. *Int. J. Climatol.* 33(6):1382–400
- Trugman AT, Detto M, Bartlett MK, Medvigy D, Anderegg WRL, et al. 2018. Tree carbon allocation explains forest drought-kill and recovery patterns. *Ecol. Lett.* 21(10):1552–60
- Trumbore S, Brando P, Hartmann H. 2015. Forest health and global change. *Science* 349(6250):814–18
- Tyree MT, Ewers FW. 1991. The hydraulic architecture of trees and other woody plants. *New Phytol.* 119(3):345–60
- Tyree MT, Sperry JS. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiol.* 88(3):574–80
- Uhl C, Kauffman JB. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* 71(2):437–49
- Ummenhofer CC, Meehl GA. 2017. Extreme weather and climate events with ecological relevance: a review. *Philos. Trans. R. Soc. B* 372(1723):20160135
- Usup A, Hashimoto Y, Takahashi H, Hayasaka H. 2004. Combustion and thermal characteristics of peat fire in tropical peatland in Central Kalimantan, Indonesia. *Tropics* 14(1):1–19
- van der Werf GR, Dempewolf J, Trigg SN, Randerson JT, Kasibhatla PS, et al. 2008. Climate regulation of fire emissions and deforestation in equatorial Asia. *PNAS* 105(51):20350–55
- van der Werf GR, Randerson JT, Giglio L, Collatz GJ, Mu M, et al. 2010. Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997–2009). *Atmos. Chem. Phys.* 10(23):11707–35
- Van Nieuwstadt MGL, Sheil D. 2005. Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *J. Ecol.* 93:191–201
- Warren M, Froliking SE, Dai Z, Kurnianto S. 2016. Impacts of land use, restoration, and climate change on tropical peat carbon stocks in the 21st century: implications for climate mitigation. *Mitig. Adapt. Strateg. Glob. Change* 22:1041–61
- Webster PJ, Moore AM, Loschnigg JP, Leben RR. 1999. Coupled ocean–atmosphere dynamics in the Indian Ocean during 1997–98. *Nature* 401(6751):356–60
- Wilhite DA, Glantz MH. 1985. Understanding: the drought phenomenon: the role of definitions. *Water Int.* 10(3):111–20
- Willis KJ, Jeffers ES, Tovar C. 2018. What makes a terrestrial ecosystem resilient? *Science* 359(6379):988–89
- Wooster MJ, Perry GLW, Zoumas A. 2012. Fire, drought and El Niño relationships on Borneo (Southeast Asia) in the pre-MODIS era (1980–2000). *Biogeosciences* 9(1):317–40
- Wösten JH, Clymans E, Page SE, Rieley JO, Limin SH. 2008. Peat–water interrelationships in a tropical peatland ecosystem in Southeast Asia. *Catena* 73(2):212–24
- Xing D, Xu X, Wu Y, Liu Y, Wu Y, et al. 2018. Leaf tensity: a method for rapid determination of water requirement information in *Brassica napus* L. *J. Plant Interact.* 13(1):380–87
- Zeng N, Yoon J-H, Marengo JA, Subramaniam A, Nobre CA, et al. 2008. Causes and impacts of the 2005 Amazon drought. *Environ. Res. Lett.* 3(1):014002
- Zhang Y, Xiao X, Wu X, Zhou S, Zhang G, et al. 2017. A global moderate resolution dataset of gross primary production of vegetation for 2000–2016. *Sci. Data* 4:170165

- Zhao J, Hartmann H, Trumbore S, Ziegler W, Zhang Y. 2013. High temperature causes negative whole-plant carbon balance under mild drought. *New Phytol.* 200(2):330–39
- Zhao M, Running SW. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science* 329(5994):940–43
- Zhou L, Tian Y, Myneni RB, Ciais P, Saatchi S, et al. 2014. Widespread decline of Congo rainforest greenness in the past decade. *Nature* 509(7498):86–90

Contents

Big Time <i>Paul F. Hoffman</i>	1
Unanticipated Uses of the Global Positioning System <i>Kristine M. Larson</i>	19
Dynamics in the Uppermost Lower Mantle: Insights into the Deep Mantle Water Cycle Based on the Numerical Modeling of Subducted Slabs and Global-Scale Mantle Dynamics <i>Takashi Nakagawa and Tomoeiki Nakakuki</i>	41
Atmospheric Escape and the Evolution of Close-In Exoplanets <i>James E. Owen</i>	67
The Sedimentary Cycle on Early Mars <i>Scott M. McLennan, John P. Grotzinger, Joel A. Hurowitz, and Nicholas J. Tosca</i>	91
New Horizons Observations of the Atmosphere of Pluto <i>G. Randall Gladstone and Leslie A. Young</i>	119
The Compositional Diversity of Low-Mass Exoplanets <i>Daniel Jontof-Hutter</i>	141
Destruction of the North China Craton in the Mesozoic <i>Fu-Yuan Wu, Jin-Hui Yang, Yi-Gang Xu, Simon A. Wilde, and Richard J. Walker</i>	173
Seawater Chemistry Through Phanerozoic Time <i>Alexandra V. Turchyn and Donald J. DePaolo</i>	197
Global Patterns of Carbon Dioxide Variability from Satellite Observations <i>Xun Jiang and Yuk L. Yung</i>	225
Permeability of Clays and Shales <i>C.E. Neužil</i>	247
Flood Basalts and Mass Extinctions <i>Matthew E. Clapham and Paul R. Renne</i>	275
Repeating Earthquakes <i>Naoki Uchida and Roland Bürgmann</i>	305

Soil Functions: Connecting Earth's Critical Zone <i>Steven A. Banwart, Nikolaos P. Nikolaidis, Yong-Guan Zhu, Caroline L. Peacock, and Donald L. Sparks</i>	333
Earthquake Early Warning: Advances, Scientific Challenges, and Societal Needs <i>Richard M. Allen and Diego Melgar</i>	361
Noble Gases: A Record of Earth's Evolution and Mantle Dynamics <i>Sujoy Mukhopadhyay and Rita Parai</i>	389
Supraglacial Streams and Rivers <i>Lincoln H Pitcher and Laurence C. Smith</i>	421
Isotopes in the Water Cycle: Regional- to Global-Scale Patterns and Applications <i>Gabriel J. Bowen, Zhongyin Cai, Richard P. Fiorella, and Annie L. Putman</i>	453
Marsh Processes and Their Response to Climate Change and Sea-Level Rise <i>Duncan M. FitzGerald and Zoe Hughes</i>	481
The Mesozoic Biogeographic History of Gondwanan Terrestrial Vertebrates: Insights from Madagascar's Fossil Record <i>David W. Krause, Joseph J.W. Sertich, Patrick M. O'Connor, Kristina Curry Rogers, and Raymond R. Rogers</i>	519
Droughts, Wildfires, and Forest Carbon Cycling: A Pantropical Synthesis <i>Paulo M. Brando, Lucas Paolucci, Caroline C. Ummenhofer, Elsa M. Ordway, Henrik Hartmann, Megan E. Cattau, Ludmila Rattis, Vincent Medjibe, Michael T. Coe, and Jennifer Balch</i>	555
Exoplanet Clouds <i>Christiane Helling</i>	583

Errata

An online log of corrections to *Annual Review of Earth and Planetary Sciences* articles
may be found at <http://www.annualreviews.org/errata/earth>