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Climate extremes and the carbon cycle

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The terrestrial biosphere is a key component of the global carbon cycle and its carbon balance is strongly influenced by climate. Continuing environmental changes are thought to increase global terrestrial carbon uptake. But evidence is mounting that climate extremes such as droughts or storms can lead to a decrease in regional ecosystem carbon stocks and therefore have the potential to negate an expected increase in terrestrial carbon uptake. Here we explore the mechanisms and impacts of climate extremes on the terrestrial carbon cycle, and propose a pathway to improve our understanding of present and future impacts of climate extremes on the terrestrial carbon budget.

For the past five decades terrestrial ecosystems have been absorbing 25–30% of anthropogenic carbon dioxide (CO_2) emissions[1], with much of this uptake occurring via carbon accumulation in forest biomass and soils[2]. Proposed mechanisms for this net carbon sink due to enhanced vegetation growth include CO_2 and nitrogen fertilization, and gradually increasing growing season length in northern regions. Overall, this terrestrial sink mitigates the anthropogenic increase of atmospheric CO_2 levels, and provides a negative feedback in the climate/carbon-cycle system[3]. It is essential to investigate to what extent, for how long and in which ecosystems this net CO_2 absorption and negative feedback will continue.

To address these questions, coupled carbon–climate model experiments have been set up[4], the most recent being the Coupled Model Intercomparison Project (CMIP5), whose results are used in the current Intergovernmental Panel on Climate Change (IPCC) assessment. In the CMIP5 comparison, state-of-the-art Earth system models incorporate a mechanistic description of the carbon cycle coupled with climate. In all of these models, the combined effect of CO_2, climate change and (in fewer models) nitrogen deposition leads to increased vegetation productivity, fostering enhanced carbon sinks in temperate and boreal regions and the above-mentioned negative feedback on climate change. Future projections of ecosystem responses and thus feedback strength are, however, highly uncertain[3,4]. Recent studies indicate that the occurrence of extreme events, for instance heatwaves, droughts or storms, and the associated disturbances can partially offset carbon sinks or even cause net losses in carbon stocks, thereby releasing CO_2 to the atmosphere[5–8]. Because extreme events can trigger immediate and time-lagged responses of ecosystems, such as mortality, fires or insect infestations[9,10], their effects on carbon fluxes and stocks are nonlinear. Thus, even a small shift in the frequency or severity of climate extremes could substantially reduce carbon sinks and may result in sizeable positive feedbacks to climate warming.

In this Perspective, we investigate the diverse impacts of climate extremes on the carbon cycle of terrestrial ecosystems. We start with a conceptual treatment of climate extremes from an impact point of view, analyse key ecosystem mechanisms triggered by climate extremes and make a first attempt to estimate the susceptibility of the carbon cycle in different ecosystem types. Finally, based on a set of metrics on the magnitude of extremes calculated from multi-temporal Earth observation data and Earth system model simulations, we provide a first estimate of the relative magnitude of carbon-cycle deviations caused by climate extremes over the past 30 years.

We propose that climate extremes have the potential to significantly affect the carbon cycle regionally and globally. To obtain reliable estimates of the sign and magnitude of future carbon-cycle feedbacks, a better understanding and descriptions of both the occurrence of climate extremes themselves and the ecosystem carbon-cycle processes that are triggered by climate extremes need to be achieved. To this end, we advocate a new generation of ecosystem manipulation experiments dedicated to studying extreme events, targeted long-term carbon-cycle observations, and an emphasis on high-resolution climate and biosphere modelling.

Climate extremes and the biosphere

The study of climate and weather extremes has a long history in climatology and hydrology. This research has led to a commonly applied statistical framework for defining climate extremes[11,12]. Yet such definitions of extremes, based on climate statistics alone, are not necessarily well suited for assessing the impact on ecosystems and their carbon cycle, as illustrated in the following thought experiment. Consider a year with precipitation of, say, 499 mm—this observation is regarded as a statistical extreme, if for the past 100 years annual precipitation has always been between 500 mm and 510 mm (although with considerable seasonal variation), despite the fact that this difference of 1–11 mm or 0.2–2% is negligible in terms of its ecosystem impact. Similarly in the real world, if monthly winter temperatures at high latitudes typically vary between $-30\,^{\circ}C$ and $-40\,^{\circ}C$, a month with $-25\,^{\circ}C$ again is extreme according to the climatological definition, but is far below any critical threshold for inducing an ecosystem response.

A specific definition of climate extremes relevant for terrestrial ecosystems is thus needed, where the extremeness in the expected response, not only in meteorological drivers, is considered. Accordingly, it has been suggested that an extreme climatic event should be defined as "an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or functions well outside the bounds of

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what is considered typical or normal variability"[13]. This definition is general enough to include meteorological constellations that are not extreme for a single variable but are extreme for a combination of variables (a multivariate extreme or compound event[12,14]), such as a combined heatwave and drought, or a drought followed by extreme precipitation.

To emphasize the impact perspective further, we restate this definition of biosphere-relevant climate extremes as "conditions where an ecosystem function (such as carbon uptake) is higher or lower than a defined extreme percentile during a defined time period and over a certain area, traceable to single or multivariate anomalous meteorological variables". As a consequence of this definition, the identification and detection of extremes is first focused on ecosystem diagnosis, and then requires the attribution of an extreme ecosystem impact to immediate and lagged effects of meteorological variables (also see "Carbon-cycle extremes in the satellite period" section).

There is clear evidence that extreme events not only affect the carbon cycle concurrently (for example, by reducing vegetation productivity or destroying carbon stocks during fire events), but can initiate lagged responses. For example, one year after an anomalously warm season, soil heterotrophic respiration was enhanced in a grassland, offsetting net ecosystem carbon uptake[15]; soil frost increased the sensitivity of heterotrophic respiration to summer drought in a forest[16]; and increased tree mortality was measured after severe droughts in many instances[17–19]. Lagged and legacy effects of extreme events on ecosystem carbon cycling are poorly understood, and can potentially involve multiple synergistic and antagonistic mechanisms operating in parallel at different levels of organization and timescales, for which a hierarchical response framework has been suggested[20]. These mechanisms include (1) diminished plant resistance to abiotic stress (for example, via antioxidants, osmolytes or changes in membrane stability), pests and pathogens (for example, via altered secondary metabolites) and their effects on plant performance; (2) changes in the amount, quality and timing of litter and rhizodeposition; (3) effects on soil physical and chemical characteristics (soil organic matter fractions, aggregate stability, hydrophobicity[21]); and (4) shifts in plant, microbial and animal species composition (for example, increased fungi, because fungi are more drought-resistant than bacteria[22]) and associated changes in carbon and nitrogen cycling, which feed back to (1)–(3)[23].

Future research should address such mechanisms in integrated studies at the ecosystem scale, and provide a mechanistic basis for projecting effects of extreme meteorological constellations on the carbon cycle. In addition to the above-mentioned mechanisms at ecosystem level, we also envisage lagged effects in societal and economic systems with substantial lagged responses in the carbon cycle, for example if increasing food prices caused by low yields, combined with risk of wind throw, were to encourage conversion of forests to croplands or grasslands.

Ecosystem-dependent processes and impacts

Climate extremes induce a suite of interconnected effects, all of which have the potential to alter the carbon balance of ecosystems profoundly on different timescales (Fig. 1). This is illustrated by the effect of heatwaves and dry spells: this type of climate extreme has a direct effect on CO_2 fluxes, because both photosynthesis and respiration respond to warmer temperature and soil moisture limitation. Moreover, these factors work synergistically at the leaf, ecosystem and the regional scales as follows. Drought leads to stomatal closure by plants, decreasing leaf transpiration and evaporative cooling, aggravating the effect of high air temperatures

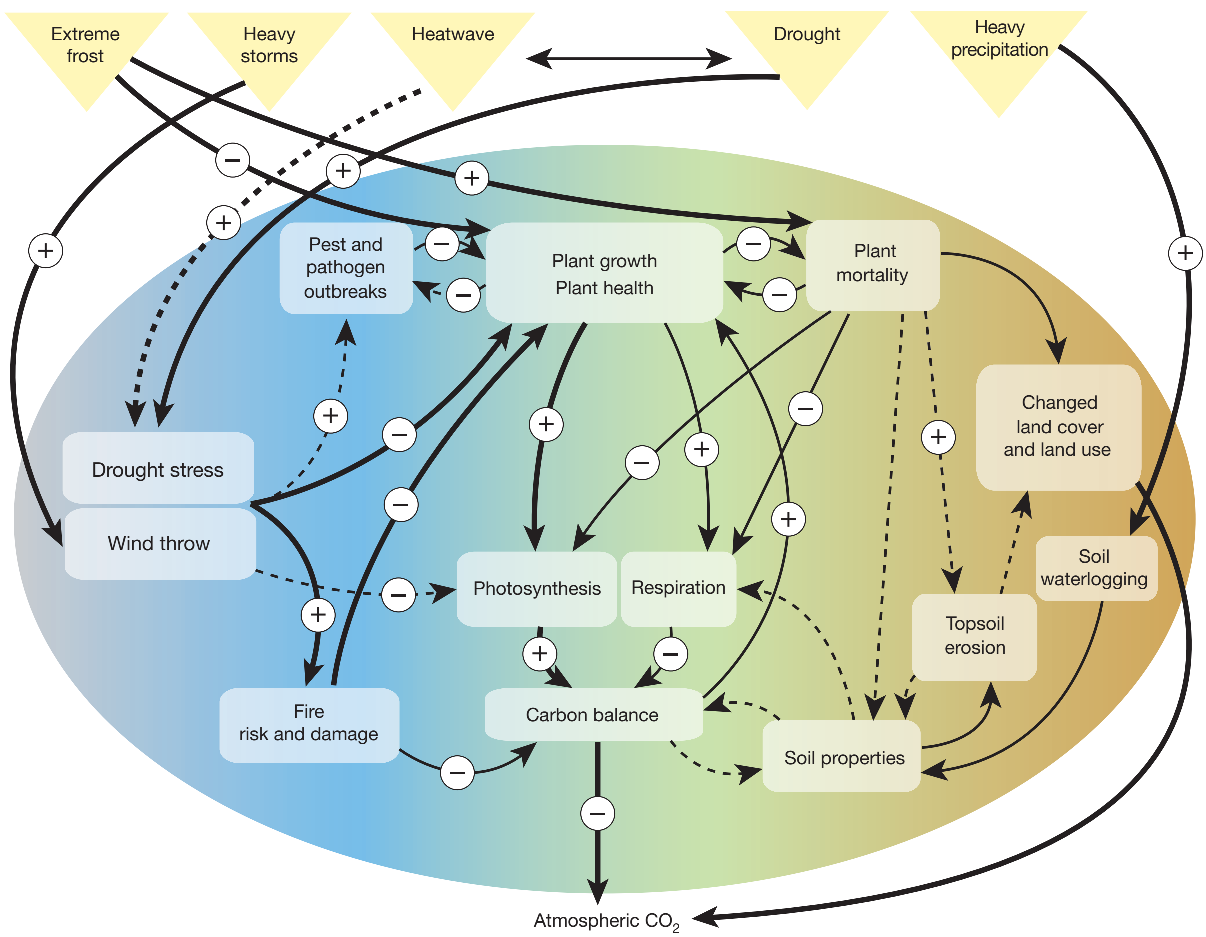

Figure 1 | Processes and feedbacks triggered by extreme climate events. The extreme events considered are droughts and heatwaves, heavy storms, heavy precipitation and extreme frost. Solid arrows show direct impacts; dashed arrows show indirect impacts. The relative importance of the impact relationship is shown by arrow width (broader arrows are more important).

(and strong short-wave radiation)[24]. Similarly, at the regional scale, soil moisture–temperature feedbacks can lead to a higher likelihood of heatwaves under dry soil conditions[25].

Moreover, soil drought, meaning more negative soil water potential and low soil hydraulic conductivity, usually leads to a higher vapour-pressure gradient between leaves and the atmosphere, causing a stress on the hydraulic system of plants that is further exacerbated by high temperatures. Consequently, high tension in the xylem can trigger embolism and partial failure of hydraulic transport in the stem, and can even be a contributory factor to mortality. This mechanism is currently regarded as a dominant cause of tree mortality under drought[10,26], interdependent with other postulated mechanisms related to the carbohydrate metabolism and insect infestations. In this respect, plant mortality can be a lagged effect of heat and drought that has impacts on the carbon balance for decades at least, and can lead to changing vegetation cover with associated feedbacks to local and regional hydrology and climate. Further effects of drought stress include an increase of fire risk and—as a delayed response—pathogen and pest outbreaks, the latter also being related to the sensitivity of ecosystems to heavy storms and wind-throw-related mortality in forests (Fig. 1).

Although the mechanisms triggered by different climate extremes can be described in conceptual terms as in the section above, their specific impact is highly dependent on ecosystem type. We summarize in Table 1, and the following section, specific anticipated effects of climate extremes for forests, peatlands, grasslands and croplands.

Forests and peatlands

Forests are characterized by the large biomass carbon stocks per square metre, which are vulnerable to wind throw, (ice-)storms, frost, drought, fire and pathogen or pest outbreaks. Moreover, given that trees take a long time to regrow, recovery times for forest biomass lost through extreme events are particularly long. Hence, the effects of climate extremes on the carbon balance in forests are both immediate and lagged, and potentially long-lasting. The impact of a climate extreme depends partially on events that have happened years before. Thus, assessing the net effect of climate extremes on forest carbon stocks requires a clearly defined time horizon during which immediate and lagged losses or gains can be assessed. In addition, any climate mitigation policy that relies on long-term carbon storage in forest biomass and the forest soil must guard against the likelihood of loss of accumulated carbon stocks in the face of future extreme events.

Although forests are potentially susceptible to all types of extreme event (Table 1), globally, drought is the most widespread factor affecting the carbon balance. For instance, during the European 2003 heatwave, precipitation (and soil moisture) deficit rather than temperature was the main factor reducing the water and carbon fluxes in the temperate and Mediterranean forest ecosystems[27,28]. Severe and recurrent droughts have been identified as a major contributing factor in the recently accelerated rates of tree decline and mortality of forests[17,29–31]. Beyond the most extensively studied mid-latitude forest belts, drought is also a relevant driver of the physiology and carbon cycling of the highly productive tropical

Table 1 | How forest, grasslands and croplands are affected by climate extremes

Land-cover type	Extremes	Key impact mechanisms	Examples of documented highly susceptible regions	Scientific understanding of future occurrence[12]	Scientific understanding of carbon-cycle impact
Forest	Storms	• Wind throw transforms carbon stock from living biomass to dry, dead wood • Wind throw increases risk of fires and pathogen outbreaks	The Amazon[38], North America[36,37], central Europe[35]	Low	Medium
	Drought Heat	• Water availability affects plant physiology, phenology and carbon allocation patterns • Increased tree mortality, fire risk and susceptibility to pathogens • Shifts in vegetation composition (impacts are large and delayed owing to the longevity of trees)	Central Europe[27,28], western North America[31], the Amazon[30,32]	Low to medium Medium to high	Low Low
	Fire	• Tree mortality has a large, fast impact on large carbon stocks in forests	Western North America[76], southeastern Asia[7], the Mediterranean[77], the circum-boreal areas[39], the Amazon[78]	Low	Low
	Ice storm and frost	• Physical damage can include destruction of whole forest • Xylem embolism and desiccation[79]	China[80], North America[81,82]	Medium to high (for cold temperatures)	Low
Grasslands	Drought Heat	• Species composition shifts (especially combined with additional pressure such as overgrazing) • Degradation and desertification (especially combined with overgrazing) • Erosion (combined with heavy precipitation or storms)	North America[83,84], Europe[85], central Asia[86]	Low to medium Medium to high	Medium Low
Croplands	Storms	• Wind erosion and soil displacement with unclear consequences for the carbon cycle • Direct crop damage	China[87], North America[88]	Low	Low
	Heavy precipitation (including hail)	• Erosion causing loss and displacement of soil and hence carbon • Erosion affecting the soil's long-term productive capacity • Crop damage or failure caused by hail and waterlogging of soils and subsequent anaerobic conditions • Crop lodging, that is, the permanent displacement of cereal stems from the vertical • Increase of pests and pathogens	The tropics[89], North America[90], Australia[91], the Mediterranean[92], western Europe[52], east Asia[93]	Medium to high (low for hail)	Low
	Drought and heat	• Reduced growth or complete crop failure	Europe[5,34,93], North America[94], China[95]	Low to medium	Medium
	Extreme cold	• Reduced growth • Complete winter-crop failure, especially during spring frosts (combined with drought stress)	North America[96], south Australia[97], Europe[98]	Medium to high	Low

forests[26]. Amazonian forests were estimated to have lost 1.6 petagrams (10^{15} g) of carbon (Pg C) and 2.2 Pg C following the severe droughts of 2005 and 2010, respectively (refs 30 and 32). Soil conditions and rooting patterns play an important part in resilience and resistance[33].

Heavy storms and tropical cyclones regularly lead to severe forest damage, resulting in the loss of major limbs and foliage and widespread mortality[6]. Storms are considered to be the most important natural disturbance affecting European forests[34]—the Lothar superstorm reduced the European standing forest biomass stocks in 1999 by about 16 teragrams (10^{12} g) of carbon (Tg C), corresponding to approximately 30% of the net biome production in Europe[35]. Similarly, (sub-)tropical forests are vulnerable to wind-storm mortality and tropical-cyclone-driven mortality[36,37]. A single squall line propagating across Amazonia in January 2005 caused widespread forest tree mortality, and threw to the ground the equivalent of 23% of the basin-wide mean annual biomass accumulation[38].

Around half of the average annual flux of 2.0 Pg C yr^{-1} globally emitted by fires between 1997 and 2009 were from forest ecosystems, with 20% from deforestation and degradation fires in tropical forest, 16% from woodland fires, and 15% from (mostly extra-tropical) forest fires during the MODIS satellite era (2001–2009)[39]. Fires and pest outbreaks can be facilitated by climate extremes in subtropical, Mediterranean and boreal forests and woodlands, but a direct link is not always easy to prove, because many factors, including direct human action, can trigger pests and fires. Nevertheless, climate anomalies associated with El Niño episodes have been shown to cause extreme fire events in tropical forests, affecting Amazon rainforest[40] and tropical southeast Asia, the latter contributing 66% of the atmospheric CO_2 growth rate anomaly during the 1997–1998 event[41].

Peatlands have large carbon stocks, as forests do, but they are below ground and are mostly preserved by their high water table, which limits decomposition. Tropical peatlands contain approximately 90 Pg C worldwide and are particularly susceptible to drought and fires[42]. Northern peatlands contain 500 Pg C (ref. 43) and are susceptible to hydrological extremes, such as droughts and heavy rainfall, which in combination can lead to both losses of carbon by decomposition and immediate CO_2 release and by export of dissolved organic carbon, by which a quarter of net ecosystem production can be lost[44].

In summary, forest (and woodland) ecosystems are potentially susceptible to all climate extremes, with a plethora of important processes and indirect effects, as indicated in Fig. 1. With both large carbon stocks (standing biomass) and carbon fluxes being strongly affected by extremes, forest is the most sensitive biome to climate extremes. Yet many processes (for example, mortality) do not lead to immediate release of carbon to the atmosphere, but rather to a committed release via decomposition (Box 1, Fig. 2). If extremes are followed by fast regrowth and in each recovery cycle carbon with increased residence times is generated (for example, by subsurface transport or charcoal formation), the whole process can be carbon neutral, or potentially can even lead to increased long-term sinks, though this has not yet been demonstrated.

Grasslands and savannas

Grasslands are susceptible to drought, whereas in contrast to forests, other extremes (for example, storms) play a smaller, if not negligible, part. Fire is often an intrinsic factor in grasslands and savannahs, and cannot be considered an extreme. It does, however, contribute to the suppression of trees in woody savannas (such as Miombo) and hence the suppression of build-up of high above-ground carbon stocks. Marcolla *et al.*[45] showed strong acclimation of a grassland to the interannual variability of climate, leading to a dampening of the interannual variability of the carbon balance in an Alpine grassland. Grasslands are also characterized by the high recovery potential of plant growth, as observed both in managed and in unmanaged grasslands[46,47], although the timing of the drought event may be a crucial factor in this regard[48]. Overall, this high resilience distinguishes grasslands clearly from forests and explains why, on a global scale, grasslands often prevail in climates where extremely dry years can occur. However, once degradation feedbacks come into play, where drought triggers loss of vegetation and heavy rain causes subsequent erosion, more frequent extreme events may contribute to desertification of semi-arid to arid grassland, in particular when (over-)grazing is an additional pressure.

Croplands

There are at least three characteristics in which croplands differ from other ecosystems with respect to carbon-cycle responses to climate extremes. First, cropland systems are entirely managed, and management interventions can react on short timescales (for example, irrigation). Second, under annual cropping, the soil–vegetation system is reset regularly through harvest and agricultural management such as tillage, manure/residue management and irrigation. Third, type and duration of crop cover are highly variable, and the soil can be bare for an extended period of time. Consequently, the response to extremes is highly modulated by human intervention both immediately and over longer periods (for example, by changing cultivars or cultivation practice)[49,50].

Thus, the nature and extent of human interventions present one of the greatest uncertainties in assessing the impact of extremes on the carbon balance of croplands[50]. Side effects will also very probably result from active interventions by farmers. Increased irrigation may enhance root biomass production, microbial activity and erosion rates, leading to increased or decreased soil organic carbon stocks. Regular harvesting and soil treatment makes long-term biological legacy effects of climate extremes more

BOX 1

Carbon processes triggered by climate extremes

Some extremes produce a direct biogeochemical signal in the atmosphere (Fig. 2, orange arrows), and may first be detected as regional anomalies in atmospheric CO_2 concentrations, analogous to a pollution plume. Globally, such signals are diluted by atmospheric mixing, but if large enough may still be detected as part of an annual growth anomaly.

In other cases, the effect of a climate extreme is essentially to alter the turnover rate of terrestrial carbon pools, leading to prolonged release of CO_2 to the atmosphere (see Fig. 1 for mechanisms) as a legacy from the extreme. For example, after a peak in mortality induced by wind throw or extreme drought, dead wood will take decades to decay. Such losses, often referred to as ‘committed CO_2 emissions’, may contribute to discrepancies between detected biosphere carbon-cycle anomalies and atmospheric CO_2 signals.

Although they may be less obvious, climate extremes may also trigger processes that decrease the turnover rate of some carbon pools and lead to additional long-term sequestration in these pools. A well-known example is the creation of charcoal during fire, which generally persists longer in soils than does the usual litter input[99].

Transport processes of particulate or dissolved organic carbon outside the ecosystem, either towards the subsurface or laterally into lake and river systems, have recently been shown to move relevant amounts of carbon[59]. These processes can lead to both stabilization and destabilization of carbon, that is, they may decrease or increase turnover times. Indirect effects on biogeochemical cycling in lakes (such as stimulation of turnover) add to the complexity induced by the landscape-scale lateral processes, and the connection between ecosystems. The net effect of these transport processes on the carbon balance remains unclear.

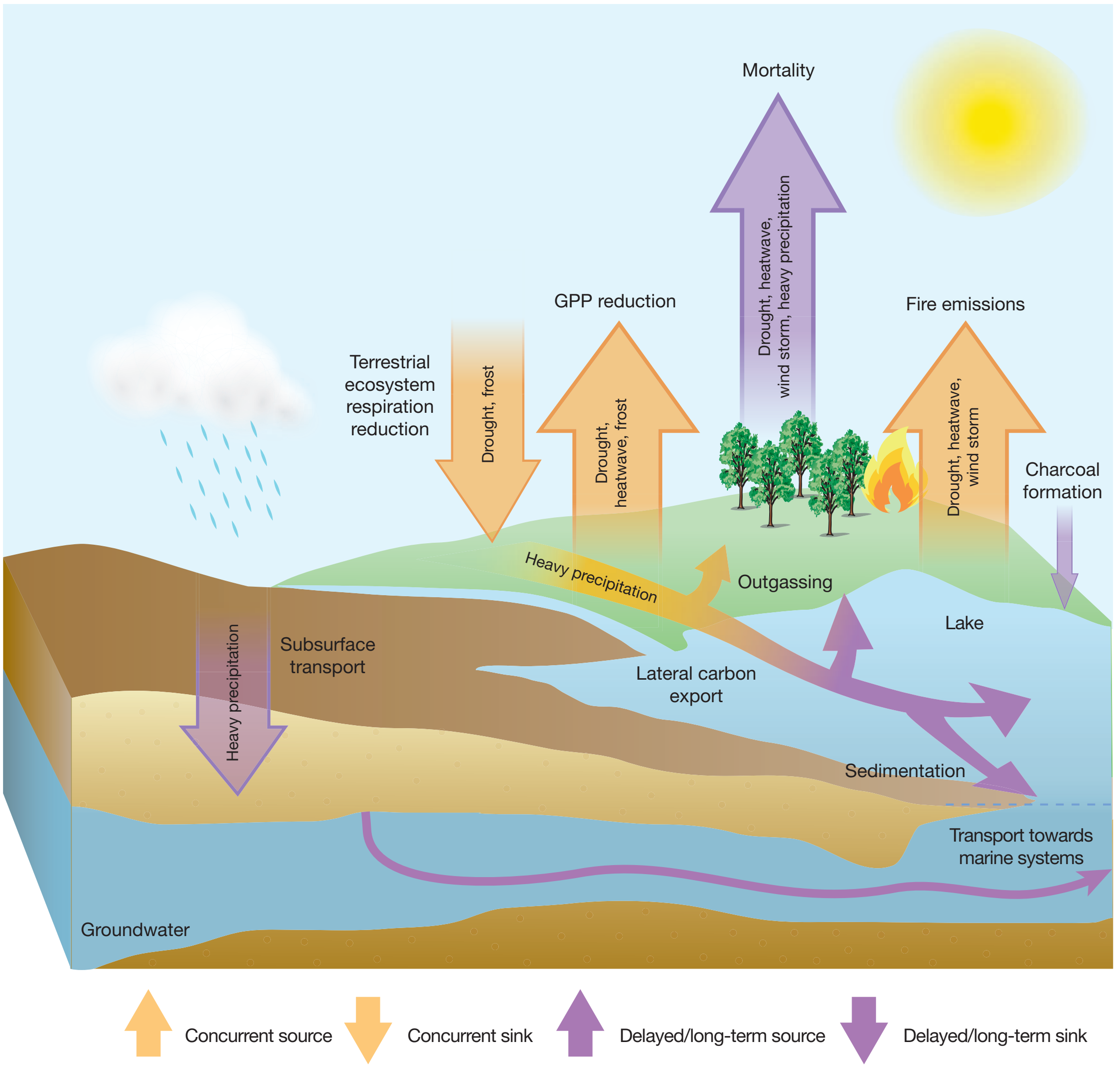

Figure 2 | Overview of how carbon flows may be triggered, or greatly altered, by extreme events. Emphasis is on the potential contrast between the concurrent and delayed signal in the atmosphere. Concurrent effects mean that the carbon signal can be found in the atmosphere while the climate extreme is occurring. Delayed and long-term signals occur either well after the extreme event has occurred, or are too small compared to the background short-term variability to be immediately detectable. The concurrency and signal strengths involved with lateral transport probably depend on the transport distance, which is indicated by the colour gradient (from orange to purple). All concurrent fluxes can also be delayed, given the mechanisms and causal chains depicted in Fig. 1 and discussed in the main text. Sources and sinks are meant relative to conditions without extremes.

unlikely than in forests or grasslands, but the legacy effect due to the impacts of pathogen population dynamics cannot be excluded in croplands. In addition, during a critical phase of its development, crop species can be vulnerable to a very specific stressor, which is otherwise unimportant during the rest of the year. For instance, rice pollen can become sterile if air temperature passes a 37 °C threshold during the short pollination phase in spring[51]. In general, the impact of an extreme event is a crop-specific function of the timing of the extreme, in relation to the sensitivity of the plant during its growth stage[52]. Note also that crop yield can be decoupled from the carbon balance in the face of extreme climate conditions. For instance, a very high carbon uptake caused by an exceptionally warm winter did not induce high yield at a wheat site in Belgium, because of unfavourable weather conditions during the grain maturation stage[53].

Carbon-cycle extremes in the satellite period

Satellites enable us to evaluate the state of land vegetation. For instance, the fraction of absorbed photosynthetically active radiation (fAPAR) often serves as a spatiotemporal indicator for vegetation activity. In tandem with global networks of station measurements of land–atmosphere exchange fluxes of CO_2 (refs 54 and 55) (that is, the FLUXNET initiative), modern machine-learning methods allow us to translate fAPAR into robust estimators for gross primary productivity (GPP). Today these continuous global data streams form a natural basis on which to examine the past three decades and to quantify the impacts of climate extremes on the carbon cycle across the world's ecosystems.

Zscheischler *et al.*[56] followed this impact-oriented search strategy and inventoried three decades of extremes in fAPAR anomalies with an emphasis on large spatiotemporally contiguous events. Using a 10% threshold to define fAPAR extremes, they estimated that the associated decrease in global GPP amounts on average to 2.7 $Pg\,C\,yr^{-1}$ during the period 1982–2011 (using the fifth and first percentiles, the GPP decreases are 1.9 $Pg\,C\,yr^{-1}$ and 0.7 $Pg\,C\,yr^{-1}$, respectively). Regionally, the most pronounced reduction of GPP (64 $Tg\,C\,yr^{-1}$) was observed in Northern Asia (following the IPCC nomenclature for regions[12]). Further, the most vulnerable regions to extremes are eastern Africa (55 $Tg\,C\,yr^{-1}$), eastern Asia (53 $Tg\,C\,yr^{-1}$), northeastern Brazil (53 $Tg\,C\,yr^{-1}$) and central North America (47 $Tg\,C\,yr^{-1}$). An analogous analysis of the CMIP5 model runs[4] over the same period results in a global decrease of GPP due to extremes of 9.60 $Pg\,C\,yr^{-1}$ at the tenth percentile (5%: 6.56 $Pg\,C\,yr^{-1}$; 1%:

2.28 Pg C yr^{-1}) averaged over all model runs. This higher sensitivity of GPP from models compared to Earth observation data could arise from model bias and (in tropical regions) from the difficulty of obtaining good fAPAR data from satellite observations and a consequent underestimation of GPP interannual variability in the satellite–FLUXNET data produced[57].

Attributing the observed fAPAR extremes over the past 30 years to anomalies in either temperature and/or water availability, or to fire events yields the strongest association with drought[56]. Globally, from the hundred largest negative fAPAR extremes identified from satellite measurements between 1982 and 2011, 56 events are explainable by water scarcity, 14 by extreme high temperatures and 10 by exceptionally large fires (note, however, that of the hundred largest events only 43 fall in the time frame where state-of-the-art fire data are available, that is, 1997–2010). Thirty-five negative fAPAR extreme events could not be attributed to a particular driver. A regional exploration reveals systematic associations of negative fAPAR extremes with high water deficits in Africa, India and south-western Russia (Fig. 3a). Associations with both high temperatures and water deficit are found over Australia, North America and South America. Some of the remaining fAPAR extreme events, not attributable to temperature or drought, might be caused by large-scale wind throw, by biotic events such as pest outbreaks or by a complex response to multivariate extremes (extremes not manifested in individual variables but in their uncommon coincidence). The total impact of extreme, spatiotemporally contiguous fAPAR anomalies on GPP is most strongly influenced by the spatial extent at which ecosystems have been affected by regionally extreme climate conditions (Fig. 3b). In contrast, the maximum intensity and the duration of each regional GPP anomaly are of secondary relevance.

It has been proposed that the size distribution of disturbance events in terrestrial ecosystems scales with a power law, like multiple other processes that are governed by phenomena of self-organized criticality[58]. Scrutinizing the distributions of spatiotemporally integrated GPP extremes supports this contention. Zscheischler *et al.*[56] found that the magnitude of GPP extremes (fifth percentile) follows a power law with an exponent of α lying in the remarkably narrow range of 1.74 ± 0.02 across all vegetated continents (Fig. 3c). These values of α are consistent with previous estimates for the spatial extent of disturbance events in tropical and subtropical forests[58]. On the one hand, the convergence of these macro properties points towards a coherent description and scaling of extremes in the global carbon cycle. On the other hand, we can also

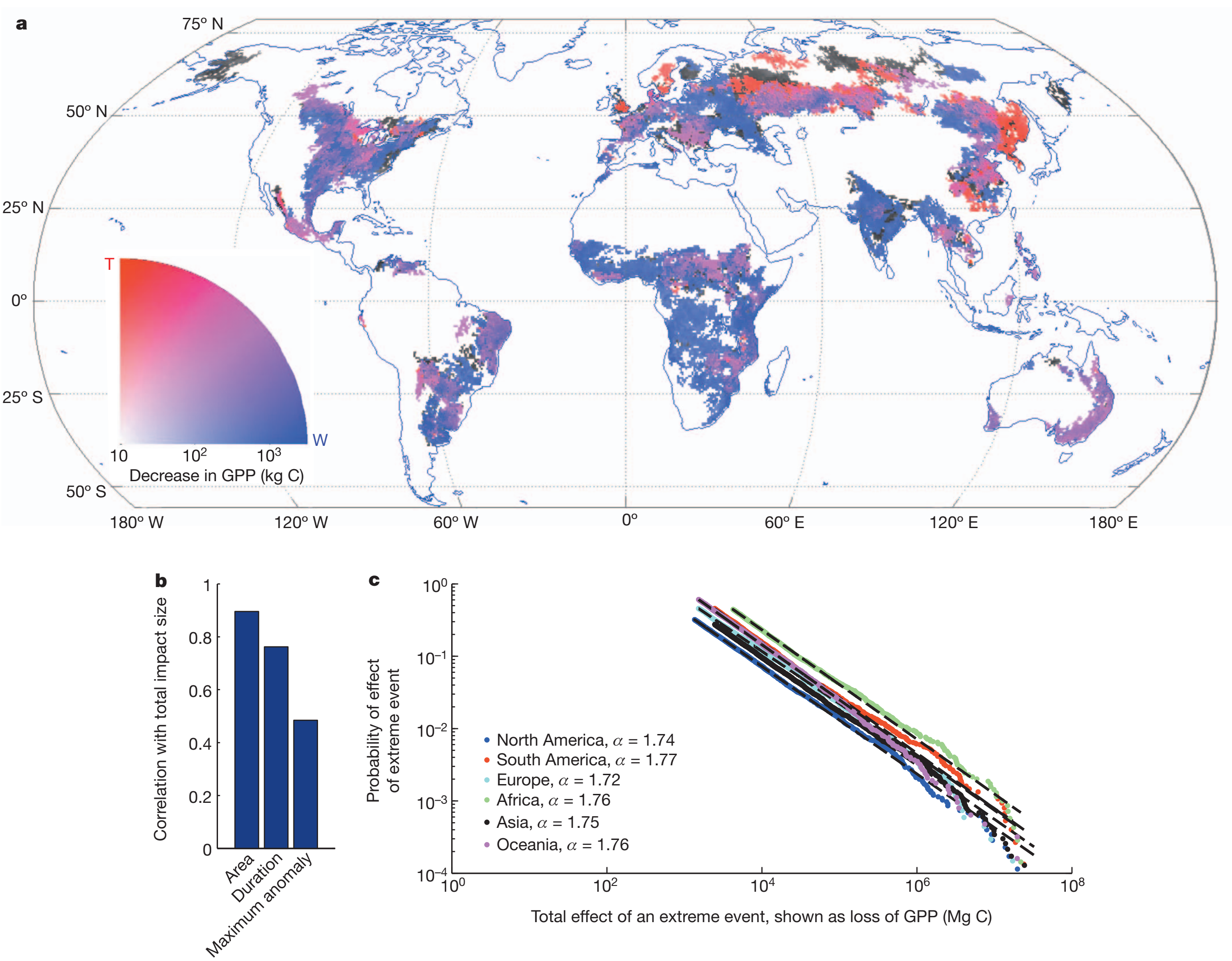

Figure 3 | Global impact of extreme events on the carbon cycle. **a**, Global distribution of extreme events impacting the terrestrial carbon cycle, defined as contiguous regions of extreme anomalies of fAPAR (lower first percentile) during the period 1982–2011 following the nomenclature of ref. 56. The hundred largest events on each continent are shown, along with whether they can be associated with water scarcity (blue, W), extreme high temperatures (red, T), both (pink) or neither (grey). The colour reflects the intensity of the extreme event in terms of integrated loss of GPP, as indicated in the inset. **b**, Correlation of spatiotemporally integrated event impact size with maximum spatial extent (‘Area’), duration (‘Duration’) and maximum intensity (‘Maximum anomaly’). **c**, Size distribution of spatiotemporally integrated event impacts, following a power law with similar scaling exponents across all continents. α is the scaling exponent.

differentiate between different continents: Africa and South America are most likely to be hit by an extreme GPP impact of a given magnitude (Fig. 3c).

Spatiotemporal context and quantification

Detecting spatially and temporally contiguous extreme impacts in the carbon cycle and attributing them to climate extremes is naturally limited by data availability. Especially, the quantification and attribution of effects of extreme events on the carbon balance strongly depends on whether the considered time frame also captures lagged responses, and other carry-over effects as well as ecosystem recovery processes (see also Box 1 and Figs 1 and 2). Clearly, the spatial scale of integration affects the quantification of impacts of climate extremes on the carbon cycle, for example, when the climate extreme causes a transfer of carbon from one ecosystem to another. Inland waters are only recently considered as important sources or sinks of carbon following extreme events.

Carbon stored in lakes and rivers originates from soils and wetlands, with a smaller contribution from autochthonous net ecosystem production. In particular, heavy precipitation events may cause substantial lateral transfers of particulate and dissolved organic carbon from terrestrial to aquatic ecosystems, where it may be partly respired and partly buried[9], leading to an increased carbon sequestration. Aquatic systems are estimated to be the second most important ecosystem in terms of carbon sequestration, ranking above croplands and grassland in Europe[59]. Further, erosion in general transports carbon from one system to a neighbouring one, where the imported carbon may be accumulated and turned over, and may potentially also cause carbon mobilization of autochthonous carbon pools[60].

Coming to grips with carbon-cycle extremes

As shown above, climate extremes trigger anomalous pulses in the carbon cycle, which can temporarily offset carbon sinks (see references in Table 1) and create CO_2 concentration signals detectable by large-scale atmospheric observations if the spatial extent of the affected region is large enough[61]. The analysis by Zscheischler *et al.* (ref. 56 and the above section) indicates that anomalies in vegetation CO_2 uptake induced by climate extremes add up to an average signal of global relevance, that is, of similar magnitude to that of the terrestrial carbon sink[1]. Yet, on a global scale, the global growth rate of atmospheric CO_2 indicates that the land and oceans have continued to take up CO_2 with nearly the same relative strength as in the past[62]. This suggests that negative impacts of climate extremes on the global terrestrial carbon sink have so far not been increasing or decreasing disproportionately, so that on a larger scale the net biome production[63] (that is, the large-scale carbon balance including uptake, respiration, fire emissions, leaching, lateral transport and harvests) remains in the long term a constant fraction of anthropogenic CO_2 emissions. The terrestrial biosphere is the largest contributor to the year-to-year variability of the atmospheric CO_2 growth rate, but its relation to climate variability is not fully understood, leaving interannual residuals ranging between $-2\,\mathrm{Pg\,C\,yr^{-1}}$ and $+2\,\mathrm{Pg\,C\,yr^{-1}}$ when trying to close the global carbon balance[1]. The effects of climate extremes on the carbon cycle have the potential to explain part of this residual variation. However, simple relationships between CO_2 growth rates and climate extremes are not necessarily expected, because of the above-mentioned lag and legacy effects involving 'committed' CO_2 emissions—regionally distinct constellations of climate variables causing carbon extremes, and differences in the response of ecosystems modulated by management.

Overall, the most pressing question is to what extent the coupling between increasing climate extremes[12] and induced CO_2 losses to the atmosphere might offset or even outweigh ecosystem carbon uptake arising from gradually increasing CO_2 concentration, prolonged extratropical growing season length and nitrogen deposition. Available observations and state-of-the-art modelling efforts are insufficient to provide definitive answers. Observational records of climate impacts on ecosystems and the carbon cycle are often too short and not widespread enough to provide sufficient context to interpret and mechanistically understand rare events. Continued simultaneous site-level observations of climate variables, together with carbon and water cycles, such as those being carried out in a global observation network (FLUXNET[64]) and global satellite-based observation of atmosphere and biosphere states, remain pivotal in this context. However, these should be more strongly complemented with longer time series from archived impacts, for instance in tree rings[65] or sediments[66].

Moreover, we need targeted assessments in regions where impacts of climate extremes have occurred, emphasizing the impact-oriented perspective proposed in this study. Nearly real-time information on the biosphere from satellite remote sensing and observation networks should enable rapid-response scientific campaigns to study after-effects and post-disturbance trajectories resulting from climate extremes. In particular, improved and repeated carbon state observations (such as biomass) from space would provide unprecedented information. Better mobilization of satellite imaging capabilities (that is, pointing satellites to an area affected by extremes, fast access to satellite data as for tsunami alerts[67]) and online data processing and distribution of flux tower and atmospheric station data[68] will also offer the research community new tools with which to study carbon extremes and provide information needed for policy-making. Given the importance of drought, we strongly advocate stronger integration of carbon-related and hydrological observations and modelling efforts. More extensive high-quality soil moisture networks are critically important to better sample droughts in the affected regions[69].

Apart from long-term and 'fast-response' observations, it is also particularly important that future event-based manipulation experiments specifically test for thresholds and tipping points[70,71] of ecologically relevant processes that can trigger long-lasting changes. In current manipulation experiments, these nonlinearities are rarely tested for or identified[72]. To considerably improve our mechanistic understanding of ecosystem responses to extreme events, it is crucial to perform increasingly standardized sets of measurements that permit calculation of common metrics to help us deal with the enormous variation in manipulation intensities, timing, return frequencies and duration in a coherent manner[73]. Comparison of heatwave experiments requires quantification of the manipulation as experienced by the biota in terms of temperature as well as physiological water availability. Furthermore, a comprehensive approach with relevant impact measurements made at different plant and ecosystem levels (for example, stress hormones, allocation patterns, changes in vegetation community, as well as responses of soil processes) would substantially increase the value of future experiments. In addition, targeted and rapid response studies taking advantage of naturally occurring extremes (which can be further modified experimentally) should be considered. Following our global analysis, where we find tropical regions strongly affected by climate extremes (Fig. 3), we suggest that future emphasis should be placed on the tropical biomes.

Despite remarkable progress over the past decade, climate models still do not realistically simulate most climate extremes, because their designs are optimized to represent the long-term transient changes in the Earth system[74]. Correspondingly, there also remain large uncertainties in projections of changes in biosphere-relevant climate extremes[12] (Table 1). However, given that droughts and related hydrological processes seem to be the dominant regional trigger for carbon-cycle extremes, an improved representation of drought dynamics in climate models will be crucial. More realistic representation of atmospheric dynamics and particularly convective processes and cloud formation[75] as well as soil hydrology[69] will be required. Although recent emphasis has been on building Earth system models that integrate climate and biogeochemical cycles, higher-resolution modelling efforts and improved physics should provide the basis for better projections of future climate extremes and their consequences for Earth's carbon cycle.

Knowledge gained from new observations and experiments oriented towards climate extremes will enable the most important internal ecosystem feedbacks to be included and appropriately parameterized in terrestrial biosphere models. Given that nutrient cycles modulate the response of carbon fluxes to extreme events, global carbon-cycle modellers should aim for multi-element modelling (carbon, nitrogen, phosphorus). As in climate models, this will require the adoption of higher spatial process resolution in carbon-cycle models. Biological adaptation and the role of biodiversity also remain particularly unclear, and thus are hardly considered in state-of-the-art Earth system models. One would expect adaptation and functional biodiversity to dampen the effect of climate extremes on the carbon cycle, but this has not been sufficiently established to justify their inclusion in currently operational global models.

The same is true for land management effects and their relation with climate extremes. The lateral and vertical transport of carbon out of the ecosystem into the hydrosphere (groundwater, rivers, lakes) during precipitation extremes calls for more strongly landscape-oriented land surface models, where parts of the landscape are intimately coupled (see Box 1 and Fig. 2). We suggest that coupling between the carbon and water cycles requires urgent attention, including how the carbon state variables feed back to the water cycle (such as soil organic carbon effects on infiltration and water-holding capacity), thus affecting susceptibility to meteorological drought.

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