Shifting from a fertilization-dominated to a warming-dominated period

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Carbon dioxide and nitrogen fertilization effects on ecosystem carbon sequestration may slow down in the future because of emerging nutrient constraints, climate change reducing the effect of fertilization, and expanding land use change and land management and disturbances. Further, record high temperatures and droughts are leading to negative impacts on carbon sinks. We suggest that, together, these two phenomena might drive a shift from a period dominated by the positive effects of fertilization to a period characterized by the saturation of the positive effects of fertilization on carbon sinks and the rise of negative impacts of climate change. We discuss the evidence and processes that are likely to be leading to this shift.

Humans strongly fertilize the planet, and human activities are resulting in increasing atmospheric concentrations of carbon dioxide (CO₂) and nitrogen (N) inputs to ecosystems. This leads to increased availability of biospheric carbon (C) and N, and enhanced organismal metabolism. Furthermore, warming is lengthening the growing seasons in the Northern Hemisphere. This causes enhanced plant growth, which is a driver of C sinks but is not sufficient alone: there must also be ecosystem compartments where C is retained before being cycled back to the atmosphere, and plants must allocate C to these long-lived compartments. In fact, the magnitude of C sinks and their duration depend both on the rate of increase of C inputs and on the residence time of the C being taken up by ecosystems. Changes in these two processes will affect the future evolution of sinks—and thus of atmospheric CO₂ and climate. For instance, if the input to land C pools from primary productivity slows down and eventually saturates (for example, because of changing nutrient constraints on plant productivity), and if the residence time of excess C remains constant, sinks will slowly decrease and eventually disappear. If, instead, the C residence time becomes shorter (for example, in the case of increased biomass mortality or an increasing allocation of C to short-lived pools such as fine roots and leaves), then ecosystems lose part of their sink capacity even if their productivity continues to increase. Examples of this occur when disturbances such as fire lead to the long-term reduction of forest biomass and soil C, or to the exposure to decomposition of previously protected soil C. In the case of an irreversible disturbance not followed by a recovery of C stocks, there is not only an initial source of CO₂ to the atmosphere, but there is the replacement of a slow turnover system with a faster one that reduces the sink capacity in the long term; an example is the conversion of forest lands to croplands. Changes in residence time are a function of changes in land use/management and disturbances, changes in C allocation and decomposition, and changes in ecosystem structure. Past, current and future changes in land C sinks thus result from the interplay between an overall change in productivity and/or changes in the residence times of C in ecosystem pools. Both productivity and residence times respond to changing CO₂, climate and nutrient availability.

Current evidence suggests that land C storage and therefore land C sinks are increasing at a global scale, and that human-induced CO₂ and N fertilization and warming (and changes in other climate variables) play a key role in this increase. This land sink has grown rapidly in the past five decades, consistent with the rapid increase in CO₂ emissions from fossil fuel use and with the recorded land use change. At a local scale, estimates from long-term flux tower records show that gross primary productivity (GPP) and net ecosystem production (NEP) have increased by 1% annually from 1995 to 2011 across 23 forests in Europe and the USA. Satellite observations show a widespread greening trend in 25–50% of vegetated areas during the last 30 years as compared to only 4% of the areas showing decreased greenness. Some studies on forest inventories also report increasing C storage in intact tropical and other forests. Attribution studies suggest that increasing atmospheric CO₂ is the most likely factor associated with the increasing strength of the C sink. This is the case for the flux tower sites in Europe and the USA and also for global greening trends, where factorial simulations with global ecosystem models suggest that CO₂ fertilization explains 70% (a 4.7–9.5% increase in global mean leaf area index) of the observed trend in greening; N deposition contributed 9%, climate change 8%, and land-cover change 4%. The relatively small global effect of climate change is because the effects of climate regionally oppose each other whereas the CO₂ fertilization effect is more uniform and consistent across biomes. Analyses of forest inventory data have also concluded that the current increase in biomass C stocks in European and North American forests can only be explained with a contribution of rising CO₂ increasing productivity. These data, together with results from short-term experiments on elevated CO₂ nutrient fertilization and warming, despite their shortcomings, support the theory of enhanced productivity in response to elevated CO₂. The fact that the global residual land sink has increased in the past...
three decades, that long-term flux towers show increases of NEP, and that remote sensing and forest inventory data show an increased sink in most regions, suggests that the residence time of excess C has not been reduced significantly over the past decades with a magnitude sufficient to offset productivity-induced C storage.

However, there are now indications that these trends of increasing sinks may be slowing down. Here, we point out these indications and the likely underlying limitations for fertilization enhancement of C sinks: limitations by key nutrients such as P; reduced sensitivity to warming; negative responses to $T_{\text{min}}$, and heatwaves; droughts, fires, land use changes and their legacy; harvests; and climatic and human disturbances leading to reductions of C residence times. This discussion finally leads us to hypothesize that a long-term weakening of the natural land sink relative to fossil fuel CO2 emissions may be driving the start of an anthropogenic transition from a vegetation-fertilization-dominated period to a period dominated by nutrient and climate constraints on further plant growth, and larger climate change impacts.

**Indications of a slowing down of trends of increasing sinks**

All over the world, and particularly in northern latitudes, the difference between the annual minimum and maximum concentrations of CO2 (the amplitude) has been increasing since the 1960s. This seems to be due mainly to increasing plant growth in the north. The strong seasonality of GPP and ecosystem respiration causes a larger average CO2 amplitude in northern high latitudes than in low latitudes. The analyses of these long-term atmospheric CO2 concentration records from the stations at Mauna Loa in Hawaii and Point Barrow in Alaska show that the sensitivity of the annual peak-to-peak amplitude of CO2 for an increase of 1 ppm CO2 decreased to 0 in 2015, while the sensitivity per °C warming decreased to 0 in the early 1990s and is now negative, particularly in northern latitudes (Fig. 1a–d). These trends suggest that terrestrial ecosystems are responding at a declining rate to the continued increase of atmospheric CO2 (known as the fertilization effect), and, likewise, that the positive effects of warming in the high latitudes leading to higher rates of C uptake are also declining.

Between the first and the last 20 years of the Mauna Loa record (used as two end points, which helps to filter quasi-decadal variability), the ratio of the residual land sink to land-use and fossil-fuel emissions decreased from 0.34 ± 0.08 to 0.28 ± 0.05 ($P = 0.09$), suggesting a slightly decreased efficiency of natural ecosystems to absorb emissions (Table 1). This decline in the efficiency of land sinks

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**Fig. 1 | CO2 and temperature sensitivity of annual amplitude (AMP).** a–d. Data from the Mauna Loa (a,c) and Point Barrow (b,d) stations. AMP is the difference between the annual minimum and maximum atmospheric concentrations of CO2. To conduct these sensitivity analyses, we used monthly average atmospheric CO2 concentration for Mauna Loa (1958–2015) and Point Barrow (1974–2015) observatories, provided by the Scripps Institution of Oceanography (Scripps CO2 program) and by NOAA, Earth System Research Laboratory and Global Monitoring Division (http://www.esrl.noaa.gov/gmd), respectively. We calculated CO2 AMP as the difference in CO2 concentration between the month with the highest CO2 concentration and the month with the lowest CO2 concentration within the same year. We also downloaded global land monthly average temperature record from the Complete Berkeley Dataset (http://berkeleyearth.org/land-and-ocean-data/) and the Northern Hemisphere land–ocean monthly average temperature from the NASA GISS surface temperature database (http://data.giss.nasa.gov/gistemp/). For both temperature data sets, we calculated spring (March–May) and summer (June–August) temperatures. We then fitted generalized least-squares (GLS) models in which the response variable was AMP and the predictor variables were mean annual CO2 concentrations and spring and summer temperatures, while accounting for temporal autocorrelation for lag 1. We ran these models repeatedly for a timespan moving window of 10 years from the beginning to the end of the time series of each observatory. For every timespan window of 10 years analysed, we extracted the model estimates for CO2 (that is, sensitivity of AMP to increasing CO2) and for spring and summer temperatures (that is, sensitivity of AMP to warming). We then used these estimates as response variables in fitted GLS models (correcting for temporal autocorrelation) to calculate the trends in the sensitivities of CO2 and temperature. For Mauna Loa we used temperature data from the Berkeley data set (global), while for Point Barrow we used NASA GISS (Northern Hemisphere). Dots represent the sensitivity of the annual CO2 amplitude to annual CO2 concentration and temperature using 10-year windows. Solid lines indicate significant trends and dashed lines marginally significant trends. Thin dashed lines indicate zero sensitivity. Shaded areas represent 95% confidence interval of the slope.
occurred despite the Pinatubo eruption (which caused a short-lived increase in C sinks). Although C sinks are still increasing, the combined land–ocean CO₂ sink flux per unit of excess atmospheric CO₂ above preindustrial levels has declined by a third over 1959–2012²⁵, implying that CO₂ sinks increased more slowly than excess CO₂. Using a very simple C–climate model²⁷, this slower increase has been attributed to slower-than-exponential CO₂ emissions growth (~35% of the trend), accidents of history causing short-lived increases of sinks such as volcanic eruptions (~25%), sink responses to climate change (~20%), and nonlinear responses to increasing CO₂, mainly oceanic (~20%)²⁸.

An analysis of tree-ring δ¹³C and growth over the last 40 years at 47 sites covering all major types of forest biomes (including boreal, wet temperate, Mediterranean, semi-arid and tropical) also shows that tree growth at those sites did not increase significantly, despite an increase in atmospheric CO₂ concentrations of over 50 ppm and a 20.5% increase in intrinsic water-use efficiency²⁴. This suggests that other factors are countering the potential growth benefits of a CO₂-rich world at many of the studied sites²⁹. Similar results were reported for tropical trees³⁰ and there are also other studies based on forest inventories that suggest a declining sink rate in European forests³¹ and tropical intact forests³², as well as a decline in the biomass accumulation of Amazon forests³³. This decline could possibly be explained by higher night-time temperatures in the tropics driving higher ecosystem respiration³⁴ and increased biomass mortality³⁵. A weakening temperature control on the interannual variations of spring C uptake across northern lands in the past 17 years has also been reported³⁶, and it has been suggested that it is attributable to the declining temperature response of spring net primary productivity (NPP) rather than to changes in heterotrophic respiration or in atmospheric transport patterns. Reduced chilling during dormancy and emerging light limitation are possible mechanisms contributing to the loss of NPP response to warming. Furthermore, the legacy effects of land use changes have a limited duration and therefore need to be taken into account in this consideration of saturation and even reversal of C sinks. A remaining question is whether this is due to stalling productivity or a reduction in residence times in regions where C sinks may be slowing down.

Ecological studies have not fully proved the universality of the CO₂ fertilization effect, whereas several studies have documented the negative effects on ecosystem C storage due to warming and drought (Fig. 2). The impacts of warming and drought on terrestrial ecosystems are negative when the increased evaporative demand and the decreased soil water availability increase drought stress effect and mortality. In the tropics, there is also the negative impact of the likely rise of temperatures above the optimum that decreases GPP and NPP. In fact, optimum temperatures²⁴ are close to current values for tropical forests. In mid-latitudes and boreal regions, additional possible negative impact comes from increased fire risk in dry seasons, although fire risks would not necessarily increase with warming²⁵. In the boreal and arctic regions, with large soil C stocks, warming increases soil respiration and soil C loss from frozen C stocks. For one degree of warming, about 30 Pg of soil C are now estimated to be released into the atmosphere—or about 2–3 times as much as is emitted annually due to human-related activities. These losses are largely driven by the losses of C in these sensitive boreal and arctic regions²⁶,²⁷. Loss of permafrost C can only be partially compensated for by beneficial temperature increases on tree growth in boreal forests, woody encroachment and longer growing seasons due to strong warming in those regions.

The two largest and most vulnerable C stocks are: (1) tropical forest biomass vulnerable to drought³⁸ and rising temperature³⁹ (although this is controversial⁴⁰), and (2) the boreal and arctic soil C stocks vulnerable to warming and thawing⁴¹. Tropical forest biomass and soil C hold about 400 Pg C, while tropical peatlands in Southeast Asia, vulnerable to fire, hold about 100 Pg C³⁷. Frozen C stocks are about 1,600 Pg, among which 130–160 Pg is vulnerable to climate-induced loss⁴²,⁴³. Compared to these large and potentially vulnerable C pools, temperate forest biomass holds only 41 Pg C and pan-boreal forests 50 Pg C³⁸. Thus the plausible loss of 10% of tropical forest biomass, or 37–174 Pg C by 2100 at 1200 high-latitude frozen C³⁷, represents an amount of C comparable with the implausible loss of 100% of temperate and boreal forest biomass.

All this observational data suggests a decrease in the efficiency of C sinks to remove excess atmospheric CO₂, albeit with a continued increase in the magnitude of sinks. Together with the experimental evidence of the effects of rising atmospheric CO₂ on plant growth also often showing saturation of the CO₂ fertilization effect³⁴,³⁵, the data suggests there are limits to the buffering capacity of the biosphere. The evidence all points to a slowdown of CO₂ and N fertilization effects on ecosystem C sequestration, and a rapid emergence of negative ecosystem impacts from global climate change that might drive a shift from a period dominated by fertilization to another characterized by saturated fertilization and strong climate change. That is, the impacts of warming on the land sinks are likely to be larger in the future than the benefits from CO₂ fertilization because of nutrient and climate constraints, management and disturbances that reduce the increase in C stocks and thus the sequestration potential.

**Likely limitations for enhancement of carbon sinks**

The availability of nutrients such as P or K, a reduced sensitivity to CO₂ increase and warming, negative responses to Tₘₐₚ and heatwaves, drought, air pollution, and fire, land use changes, harvests, and climatic and human disturbances that lead to reductions of residence times are examples of factors likely to limit the enhancement of carbon sinks (Fig. 3).

**Key nutrients.** The anthropogenic increase in CO₂ and atmospheric N deposition are not matched by a similar increase in the inputs of other key nutrients such as P and/or K. A simple mass-balance approach of the NPP-based and C-stock-based demands indicates that limited P availability and the corresponding N:P imbalances will result in a smaller CO₂ removal by terrestrial ecosystems during this century than currently predicted by biogeochemical and Earth system models (ESMs)⁴⁴,⁴⁵. Changes in mineralization with climate change, and other processes governing the recycling of nutrients, are a large source of uncertainty in the amount of nutrients available for the accumulation of new biomass⁴⁶. However, an increasing biological P demand is likely to outpace exogenous P inputs.

<table>
<thead>
<tr>
<th>Mean (Pg C yr⁻¹) fossil fuel emissions, land-use change emissions, residual land sink, and the ratio of the residual land sink to land use and fossil fuel emissions, in the 1960s-1970s and in the past 20 years</th>
<th>Fossil fuel emissions</th>
<th>Land-use change emissions</th>
<th>Residual land sink</th>
<th>Ratio of residual land sink to total emissions</th>
</tr>
</thead>
<tbody>
<tr>
<td>1960–1979</td>
<td>3.88 (0.14)</td>
<td>1.44 (0.35)</td>
<td>1.71 (0.49)</td>
<td>0.32 (0.08)</td>
</tr>
<tr>
<td>1996–2015</td>
<td>8.42 (0.35)</td>
<td>1.50 (0.35)</td>
<td>2.68 (0.57)</td>
<td>0.28 (0.05)*</td>
</tr>
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Standard deviations for the four five-year windows of each period are given in parentheses. The change in the ratio of residual land sink to emissions is significant at “P = 0.09” (t-test). Data previously published⁴².
suggested that an accelerated cycling of existing P pools will be critical to sustain productivity and C sinks. An increase in the amount of new P from weathering is also possible under conditions of strong warming, but the effects of climatic warming on P dynamics are even less known. Thus, the changes in the future availability of P are uncertain, but current evidence suggest an overall shortage of P which will act as a limiting factor to meet the increasing demand for plant growth. A better understanding of the factors that regulate exchanges between pools of ‘available’ and ‘unavailable’ soil P is needed. Furthermore, a better quantification of how N limitation restricts C sinks from CO₂ fertilization—both by limiting NPP increase and by resulting in a lower wood allocation as plants are forced to allocate below ground to obtain N for NPP—is also warranted.

Reduced sensitivity to warming and negative responses to T_{min} and heatwaves. Warming is lengthening the growing seasons in the northern latitudes but the apparent response of leaf unfolding to climatic warming (expressed in days of advance of leaf unfolding per °C warming) has decreased by 40% from 1980 to 2013 for deciduous forests in Europe. The reduction in sensitivity is likely to be partly attributable to reduced winter chilling and other mechanisms (such as photoperiod limitation) that may become ultimately limiting when leaf unfolding occurs too early in the season, together resulting in a slowdown in the advance of spring tree phenology.

Furthermore, the satellite-derived normalized difference vegetation index (NDVI), an indicator of vegetation greenness, is negatively correlated with T_{min} in boreal regions of the Northern Hemisphere. Similar patterns were detected in maps of terrestrial net CO₂ exchange obtained from a relatively high-resolution atmospheric inversion. In addition, the analysis of the long-term records of atmospheric CO₂ concentration from the Point Barrow station (71° N) in Alaska suggests that the peak-to-peak amplitude of CO₂ increased by 28±11% for a +1 °C anomaly in T_{min} from May to September over land north of 51° N, but decreased by 34±14% for a +1 °C anomaly in T_{min}. This asymmetry is especially important because temperature data for the past century shows faster warming at night (T_{max}) than during the day (T_{min}), although this effect is uncertain for the future given strong aerosol reductions as suggested by RCP scenarios. These multiple lines of evidence suggest that asymmetric diurnal-nocturnal warming is an important process affecting terrestrial ecosystems. Higher nocturnal temperatures enhance night respiration, with important implications for C cycling.

Severe regional heatwaves are also likely to become more frequent in a changing climate (Fig. 3), and their negative impact on terrestrial C sequestration may thus also become important. For example, the 2003 drought and heatwave decreased European GPP by 30%, which resulted in a strong anomalous net source of CO₂ (0.5 Pg C yr⁻¹) to the atmosphere; this effect is the equivalent of reversing four years of net ecosystem C sequestration in the European continent. Heatwaves are often co-occurring with droughts in mid-latitudes, which may explain some of the impacts. The summer of 2003 was characterized by both dry and hot conditions. For the C cycle, it is more likely that it was the drought conditions that affected the net C anomalies.

Droughts. A number of major droughts in mid-latitudes might have also contributed to the weakening of the growth rate of terrestrial C sinks in recent decades. These large-scale droughts have reduced seasonal NPP in these areas and weakened the terrestrial C sink. However, summer productivity losses can be offset by productivity gains in spring and autumn, so the response of NPP to drought depends on the timing of drought during the growing season, and on ecosystem properties of resistance to drought (for example, deep rooting and efficient stomatal controls). There is an inherent difficulty in quantifying droughts and a wide likelihood range of drought projections, but there are regions where drought is consistently expected to increase. In other regions, wide likelihood range should not be equated with low drought risk, since potential scenarios include large drought increases in key agricultural and ecosystem regions. In fact, vulnerability of tree mortality and forest die-off to hotter and drier conditions is expected to increase. Beyond the signs of drought-induced constrains on land C sinks in mid-latitudes, tropical regions (particularly the Amazon) have been subject to unprecedented levels of drought over the past decade with an associated reduction in the growth of C sinks.

Fire, land use changes, harvests, and climatic and human disturbances lead to reductions of residence times. Human-caused climate change and elevated CO₂ can also shorten residence times through complex and poorly understood pathways. For example,
there is evidence to show that, under future global warming, fire disturbances will increase in several regions such as those with a Mediterranean climate, leading to reduced soil C residence times and thereby reduced sink capacity of the land biosphere.

Future higher atmospheric CO₂ can reduce residence times by accelerating competition and mortality in forest stands, and by priming soil C decomposition through fresh organic matter input. Elevated CO₂ increases turnover rates of new soil C, thus limiting the potential for additional soil C sequestration. The CO₂ fertilization effect produces soil organic matter of lower nutritional quality (higher C:N and C:P ratios), hindering decomposition but further increasing nutrient limitation on plant C uptake. In addition to enhanced above-ground growth, several free-air carbon dioxide enrichment (FACE) experiments observed an increase in below-ground C allocation—therefore not storage in a long-lived C compartment despite fine-root litter being in part converted to soil organic matter, which also includes long-lived components. These experiments are, however, of short duration, so long-term storage changes could not really be quantified.

In addition to atmospheric and climatic changes, most land use changes, fires and harvests, which are expected to increase in the future, reduce C residence times, thereby reducing the sink capacity of the land biosphere.

**Modelling**

The potential saturation or slower increase of the sink capacity of terrestrial ecosystems, or even its transition into a source of CO₂, beyond what is reflected in several ESMs, shows the exceptional
relevance of climate policy that is now focused on achieving the temperature targets agreed at the 2015 UN Climate Change Conference in Paris, France, the 21st Conference of the Parties (COP21). For example, ESMs and the climate projections of the Intergovernmental Panel on Climate Change (IPCC) could be improved by a better quantification of land C sinks with more realistic constraints from nutrient limitation. Models and projections could also be improved by a better quantification of the natural ecosystem responses to the different aspects of warming (for example, the contrast between nocturnal and diurnal warming) and drought/climate extremes or the interaction between environmental pollution (for example, ozone, heavy metals or organic pollutants) and increasing atmospheric CO₂ concentrations. In addition to the role of terrestrial ecosystems in CO₂ uptake, other influences on climate of biogeochemical and biophysical processes of terrestrial ecosystems must be quantified, such as exchanges of biogenic volatile organic compounds, CH₄ and N₂O, latent and sensitive heat, albedo and roughness. Biochemical, optical and gaseous signals of the energetic status and structure and functioning of plants and ecosystems could be useful in this regard. Such improved models could then help with understanding the responses to different levels of global warming (especially in the 1.5–3 °C range according to the Paris Agreement and current intended policies).

Arguably, some ESMs already incorporate several of these processes (such as chilling, or different effects of Tₘₐₓ and Tₘᵦᵯ). There is currently also a lot of modelling work on the dynamics of terrestrial sinks into the future, including experiments with and without nutrient limitations, with and without land use change, with and without permafrost thawing, with different sensitivities to changes in rainfall and temperature, and so on. These are not the big ensembles reported in the IPCC, but there are plenty of advancements at the individual model level, and several of these processes will be considered in the upcoming Coupled Model Intercomparison Project Phase 6 (CMIP6) experiments. However, there are other mechanisms still missing in ESMs, such as the legacy effects of land use changes, disturbance and extreme climate events on C sink activity, and the factors that control stand structure, density, management and disturbance in the Northern Hemisphere. Similarly, the effect of increased competition in tropical forests—in which CO₂ fertilization could increase individual growth but in turn cause more self-thinning and increase biomass C turnover and sink capacity—is missing. Current climate models do not necessarily well represent extreme events due to coarse resolution (for example, extreme precipitation, wind storms and tropical cyclones) or insufficiently constrained soil–atmosphere interactions. Likewise, many models show an effective slowdown in the growth of sinks, with some showing saturated sinks and a few even having declining terrestrial sinks. Adding more processes to models will only serve to make complex, poorly understood models even more complex and poorly understood, so we call for modellers to increase their focus on process-oriented model evaluation, based on hypotheses that can be discriminated by data. For example, rather than benchmarking process-based models for stocks and fluxes, estimating sensitivities of fluxes and stocks to variable drivers such as elevated CO₂ and climate can be achieved to enable a comparison with both local manipulative experiments (for example, FACE experiments, warming, altered rainfall and nutrient fertilization experiments) and global observation-based estimates of C variables.

**Final remarks**

We thus hypothesize that a long-term weakening of the natural land sink relative to fossil fuel CO₂ emissions may be driving the beginning of a transition between a vegetation-fertilization-dominated period to one dominated by nutrient and climate constraints on plant growth, and larger climate change impacts. The CO₂ and N fertilization effects are two main drivers of the increase in the natural land sink. However, the future strength of these fertilization drivers in the coming decades is uncertain, in the presence of emerging nutrient limitations that progressively limit the effect of elevated CO₂ on increased C storage, as observed in some long-term FACE experiments. In contrast, the continuous warming and the associated reduction in water availability in several regions are gaining significance, resulting in growing negative impacts on the biosphere. Compared to the historical period, future warming and drought and their impacts are thus likely to be larger than the benefits gained from the effects of CO₂ and N fertilization because of nutrient and climatic constraints, intensified land management and shifts in disturbance regimes that reduce C stocks and thus the sequestration capacity of terrestrial ecosystems. There are many unknowns in the timing of this transition, so in light of the recent COP21 Paris Agreement, a better understanding of the impacts of climate change on C stocks remains paramount to understand the level of climate mitigation required to achieve the agreed temperature goals.

In addition, it must be noted that the effect of CO₂ on photosynthesis is one of diminishing returns, and that CO₂ fertilization only leads to enhanced plant growth and storage as long as atmospheric CO₂ increases. Even if the CO₂ effect would not be reduced until well into the second half of this century because plants would be able to use excess CO₂ to meet the C costs of getting access to extra N and P (for example, through increased below-ground root allocation and mycorrhizae association, or increased biological N fixation), our hypothesis will hold as the climate continues to warm and extremes become even more extreme. This dynamic underscores the importance of investigating climate change impacts on C sinks more than to hope for the benefits of CO₂ fertilization, which will become smaller particularly in the low temperature scenarios set under the Paris Agreement.

Although the climate has not yet changed dramatically in the Anthropocene, the coming decades will undoubtedly be different: atmospheric CO₂ levels will remain high, but the climate will have no analogue in recent human history, even for so-called safe scenarios. The lower panels of Fig. 3 show that a warming of 2 °C would slightly increase the frequency of 2003-like heatwaves in northern France. A warming of 3 °C would produce very different conditions, with one summer like that of 2003 occurring every two or three years, which would therefore affect the forest C sink in Europe much more than in the past.

In addition to the trends described in this Perspective, there is also the possibility of the occurrence of low-probability but high-impact phenomena that would lead to rapid positive feedbacks in the climate system. These include, among others: the potential for rapid regional transitions in the climate system; massive dieback of Amazon rainforest because of reduced rainfall; and dramatic temperature drop in the North Atlantic because of the collapse of the ocean current that carries warm surface water north, ice sheet collapse, or and permafrost C decomposition. The occurrence of these phenomena is highly uncertain, particularly for low-temperature scenarios. However, it is much more certain that we are currently entering a new warming period where ecosystems are put under increasing stresses. The extreme and record temperatures of 2015 and 2016 are illustrative of such a transition, with unprecedented levels of fires in Southeast Asia, coral bleaching in Australia, drought in Africa and floods in South America, all associated with one of the largest El Niño events in history. Consistent with the high temperatures, 2015 and 2016 also recorded the largest annual atmospheric CO₂ growth rate since atmospheric observations began in Mauna Loa in 1959 (NOAA/ESRL and Scripps Institution of Oceanography).

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**Author contributions**
J.P. designed the study. J.P., P.C., M.F.-M., R.V. and J.S. conducted the analyses with support from J.C., I.A.J., J.C., M.O. and S.P. The paper was drafted by J.P. and P.C. M.F.-M., R.V., J.S., J.C., I.A.J., J.C., M.O. and S.P. contributed to the interpretation of the results and to the text.

**Competing interests**
The authors declare no competing financial interests.

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