Review

CrossMark
click for updates

Carbon cycle feedbacks and future climate change

Pierre Friedlingstein

College of Engineering, Mathematics and Physical Sciences, University of Exeter, Exeter EX4 4QE, UK

Climate and carbon cycle are tightly coupled on many timescales, from interannual to multi-millennial timescales. Observations always evidence a positive feedback, warming leading to release of carbon to the atmosphere; however, the processes at play differ depending on the timescales. State-of-the-art Earth System Models now represent these climate–carbon cycle feedbacks, always simulating a positive feedback over the twentieth and twenty-first centuries, although with substantial uncertainty. Recent studies now help to reduce this uncertainty. First, on short timescales, El Niño years record larger than average atmospheric CO_2 growth rate, with tropical land ecosystems being the main drivers. These climate–carbon cycle anomalies can be used as emerging constraint on the tropical land carbon response to future climate change. Second, centennial variability found in last millennium records can be used to constrain the overall global carbon cycle response to climatic excursions. These independent methods point to climate–carbon cycle feedback at the low-end of the Earth System Models range, indicating that these models overestimate the carbon cycle sensitivity to climate change. These new findings also help to attribute the historical land and ocean carbon sinks to increase in atmospheric CO_2 and climate change.

1. Introduction

The physical mechanisms describing the link between change in atmospheric CO_2 concentration and global temperature were first described more than a century ago [1,2]. Over the second part of the twentieth century, much evidence has confirmed the human perturbation of the global carbon cycle and its potentially large implication on the climate system.

THE ROYAL SOCIETY
PUBLISHING

Probably the most striking evidence was the atmospheric measurements of carbon dioxide initiated by R. Revelle and C.D. Keeling in the late 1950s [3]. The CO_2 record at the Mauna Loa Observatory, now known as the Keeling Curve, showed two prominent features of the global carbon cycle. First, the seasonal pulse of the terrestrial biosphere faithfully captured by atmospheric CO_2, with lower than average atmospheric CO_2 during the Northern Hemisphere summer and conversely during the winter. The second unambiguous signal from the Keeling Curve is the gradual increase in atmospheric CO_2 concentration from year to year. When Keeling started the measurements at Mauna Loa, atmospheric CO_2 concentration was around 315 ppm, it passed the symbolic 400 ppm level in 2014, with a current rate of CO_2 increase of about 2 ppm per year [4].

Additional, as powerful, evidence came from ice cores measurements in the early 1980s; spectrometric measurements of air bubbles captured in ice cores allowed to reconstruct the atmospheric CO_2 concentration [5,6]. Parallel measurements of isotopic composition of the ice allowed the Antarctic temperature to be inferred. The ice-core measurements were essential (i) to demonstrate how unusual are the current level of atmospheric CO_2 and (ii) to illustrate how closely CO_2 and temperature varied in the past. Ice-core records are now going back 800 000 years, spanning eight glacial–interglacial cycles and clearly indicate that 'The atmospheric concentrations of carbon dioxide, methane, and nitrous oxide have increased to levels unprecedented in at least the last 800 000 years' [7].

Climate models are the third essential elements of the climate story, their development started in the 1960s [8] being continuously improved since, and used to primarily address two key questions. (i) Can we attribute the climate change observed over the instrumental period to human activities or could it be due to natural variations of the Earth system. The answer to that question is now unambiguous: 'human influence on the climate system is clear', and more precisely, 'It is *extremely likely*[1] that more than half of the observed increase in global average surface temperature from 1951 to 2010 was caused by the anthropogenic increase in greenhouse gas concentrations and other anthropogenic forcings together' [7]. (ii) What is the response of the climate system to an increase in greenhouse gases concentrations and other forcing agents? In the early days, this was investigated looking at the response of atmospheric general circulation models (GCMs) to a doubling of the atmospheric CO_2 concentration [9,10]. Nowadays, the climate community uses Earth System Models (ESMs), which couple the atmosphere–ocean–land physical system to the global carbon cycle and atmospheric chemistry (including aerosols). These models simulate the transient response of the climate system over the twentieth and twenty-first centuries, assuming different scenarios of greenhouse gases and aerosols emissions for the future [11].

Despite the tremendous effort from the climate community to address that second question of central policy relevance, the uncertainty on climate projection remains high. There is obviously a large uncertainty in the future of greenhouse gases emissions, depending on future socio-economic development, climate mitigation policies, etc. However, there is a large uncertainty coming from the climate response itself, for a given change in the radiative forcing. That uncertainty, primarily due to physical feedbacks, has been a major concern for several decades. In 1979, the US National Academy of Science report led by J. Charney entitled 'Carbon dioxide and Climate, a scientific assessment' estimated 'the most probable global warming for a doubling of atmospheric CO_2 to be near 3 K with a probable error of ± 1.5 K' [12]. The latest estimate reported in the Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC AR5) happens to be identical with an equilibrium climate sensitivity[2] *likely* range of 1.5–4.5 K [7]. A large fraction of this uncertainty comes from the unknown fate of clouds in a warming world and their net radiative forcing [13,14].

---

[1]In the IPCC terminology, extremely likely indicates a likelihood above 95%.

[2]The equilibrium climate sensitivity is defined as the change in global mean surface temperature at equilibrium that is caused by a doubling of atmospheric CO_2 concentration.

The 'other side of the coin', i.e. the effect of climate change on atmospheric CO_2 only emerged as a scientific concern in the late 1980s–early 1990s. Probably, the first paper that described and attempted to quantify the climate-carbon cycle feedback was written by Lashof in 1989 [15]. Lashof identified several biogeochemical feedbacks defined as 'those that involve the response of the biosphere and components of the geosphere not considered in typical climate models'. He listed 10 potential biogeochemical feedbacks involving ocean and terrestrial systems (see table 1 in [15]). With great intuition, he wrote, 'ideally these feedbacks should be analysed by incorporating their effects . . . into a dynamic model that includes the general circulation of the atmosphere and oceans, marine chemistry and biology, atmospheric chemistry, and terrestrial ecosystems. Such an approach would allow explicit consideration of the time dependence of each feedback process, but is not feasible at this time'. Nevertheless, he provided an original, back of the envelope calculation of these biogeochemical feedbacks.

2. Modelling 'evidences'

Global simulations of biogeochemical processes embedded in climate models only appeared at the turn of the century [16,17]. These new models coupled standard GCMs with land and ocean carbon cycle models in order to interactively simulate the evolution of atmospheric CO_2 (as opposed to prescribe it in a standard GCMs). These developments occurred almost simultaneously at the Hadley Centre, UK and at the Institut Pierre-Simon Laplace (IPSL), France. Although these new models and their main result, *there is a positive feedback between climate change and the global carbon cycle*, had a profound impact on the climate modelling community; in retrospect, they were only the natural outcome of growing evidences that pointed to the sensitivity of the global carbon cycle to climate change.

Both on the ocean and on the land side, global models have been developed, starting from simple box models in the early days [18,19], to full three-dimensional models for the ocean biogeochemistry [20,21] and spatially explicit models of terrestrial ecosystems [22,23]. The first objective of these models was to quantify the contribution of ocean and land ecosystems to the current or historical global carbon budget. Indeed, C. D. Keeling was the first to quantify the *airborne fraction*, the fraction of the anthropogenic CO_2 emissions that remains in the atmosphere, to be about 60% of the fossil fuel emissions [3,24]. That implied that the ocean and the terrestrial ecosystems sequestered a significant fraction of the perturbed atmospheric CO_2. It was initially believed that the ocean was the main sink of carbon until it became clear that a land sink was needed to close the carbon budget [25]. It is now admitted that both the land and the ocean play a comparable role, each removing from the atmosphere about 25% of the anthropogenic CO_2 emissions [4,26,27].

However, the obvious question is whether the ocean and the land ecosystems will continue to provide such a service to humanity, removing about half of the CO_2 emitted by human activities. Without these land and ocean sinks, the atmospheric CO_2 increase would be about twice as fast; current atmospheric CO_2 concentration would be already above 500 ppm, inducing a warming of more than 2 K above pre-industrial level (assuming a median estimate of 3 K for the climate sensitivity). There was, and there still is, an urgent need to better understand the process governing these carbon sinks and whether they would continue to operate in the future. Global land and ocean models were used to investigate the fate of ocean or land carbon storage under future change in environmental conditions, mainly elevated atmospheric CO_2 and climate change. Global ocean models forced with a scenario of atmospheric CO_2 over the twenty-first century would simulate a continuous increase in ocean CO_2 uptake, driven by the growing imbalance of CO_2 partial pressure between the atmosphere and the ocean surface. When the same models would additionally account for climate change (changes in ocean temperature, salinity, ocean circulation, etc.), they would show a significant reduction of carbon uptake, primarily driven by the ocean stratification, and reduced ocean thermohaline circulation [28–30]. Terrestrial models also investigated the effect of CO_2 and climate, always agreeing on the positive response of land carbon storage to atmospheric CO_2 increase (the so-called *fertilization effect*), but not

reaching consensus on the terrestrial ecosystem response to the associated climate change. Some earlier studies found an enhanced terrestrial productivity [31] while later studies found the opposite [32,33]. The third assessment report of IPCC concluded that, by mid-twenty-first century, climate change would reduce the land carbon uptake by 21% to 43% and the ocean carbon uptake by 6% to 25%, relative to CO_2 only driven uptakes [34]. This IPCC range was very conservative, as further discussed below.

Nevertheless, all these studies gave a clear signal to the climate modelling community: one cannot simulate future climate change assuming atmospheric CO_2 can be known, *a priori*, from the CO_2 emissions trajectory. The evolution of atmospheric CO_2 results from the balance between the CO_2 emissions and the land and ocean carbon sinks, these last ones being a complex function of atmospheric CO_2 and climate. Hence the CO_2-climate system is coupled, future climate change depends on atmospheric CO_2 increase (and other forcing agents); but in return, atmospheric CO_2 increase depends on climate change.

The two above-mentioned coupled climate-carbon cycle models from the Hadley Centre and the IPSL modelling groups just did this. Both modelling groups performed similar simulations; first a fully coupled twentieth and twenty-first centuries run with twenty-first century CO_2 emissions following either the IPCC IS92a (Hadley) or the SRESA2 (IPSL) scenario; second, an uncoupled run with the same emission scenario, but holding the radiative forcing from CO_2 at pre-industrial level. In both runs, the models compute atmospheric CO_2 as the difference between the prescribed emissions and the simulated land and ocean carbon sinks. However, in the coupled runs the land and ocean carbon cycle are 'seeing' both CO_2 increase and climate change (as the climate evolves as the simulated atmospheric CO_2 increases); while in the uncoupled runs the land and ocean carbon cycle are only 'seeing' the atmospheric CO_2 increase (as the climate is held at its pre-industrial level). From the coupled and uncoupled simulation, one can compare the simulated atmospheric CO_2; any difference will be due to the effect of climate change on the carbon sinks. Indeed, the difference in simulated atmospheric CO_2 is a measure of the gain of the climate-carbon cycle feedback:

$$g = \frac{\Delta C_a^{cou} - \Delta C_a^{unc}}{\Delta C_a^{cou}}, \qquad (2.1)$$

where ΔC_a^{cou} and ΔC_a^{unc} are the increase in atmospheric CO_2 relative to pre-industrial in the coupled and uncoupled simulations, respectively, and g is the gain of the climate-carbon cycle system. The gain of the Hadley centre model was about 0.4 while the gain of the IPSL model amounted to 0.17. In units of atmospheric CO_2, the Hadley model simulated a CO_2 concentration about 250 ppm higher in the coupled simulation than in the uncoupled simulation, while the IPSL model 'only' simulated an 75 ppm higher concentration in the coupled simulation [16,35,36].

This wide range, although only based on two models, generated a worldwide interest in climate-carbon cycle modelling. Quite rapidly the Climate Carbon Cycle Model Intercomparison Project (C^4MIP) was set up [37,38] and within less than 5 years, 11 models had performed similar experiments [39]. The bad news is that the uncertainty increased, with some models simulating near zero climate-carbon cycle gain (although still positive). Most of the uncertainty originated from the land biosphere and its response to atmospheric CO_2 increase and climate change. The fertilization effect, that largely contributes to the current land carbon sinks showed a factor of 10 uncertainty in the future, with a sensitivity (called β_l) ranging by 2100 between 0.2 and 2.8 GtC per ppm. Likewise, the climate effect on the carbon cycle (called γ_l) showed a similar uncertainty, ranging between −20 and −177 GtC per K. Mathematically, these two terms can be estimated from the coupled and uncoupled simulations, assuming that the carbon cycle responds linearly to atmospheric CO_2 and climate change:

$$\Delta C_l = \beta_l \Delta C_a + \gamma_l \Delta T, \qquad (2.2)$$

where ΔC_l is the change in the land carbon store, ΔC_a the change in atmospheric CO_2 and ΔT the change in global temperature; a similar equation applying for the change in the ocean carbon

storage ΔC_o:

$$\Delta C_o = \beta_o \Delta C_a + \gamma_o \Delta T. \qquad (2.3)$$

The sensitivity terms β and γ for the land and ocean can be diagnosed successively, solving for β from the uncoupled simulation (above equations where ΔT equals zero), and then solving for γ from the coupled simulation (above equations).

Despite the large uncertainty, all models agreed that climate change would reduce carbon storage (i.e. γ is negative), primarily due to an enhancement of soil organic decomposition under a warming world [39]. Almost 10 years later, within the Coupled Model Intercomparison Project Phase 5 (CMIP5), a similar analysis was performed with CMIP5 ESMs, giving essentially the same conclusion, the land carbon cycle response to atmospheric CO_2 and climate change is still poorly constrained [40]. New ESMs now include a representation of the nitrogen cycle. This has two opposite effects on land carbon storage. First, accounting for nitrogen leads to a lower response to atmospheric CO_2; as nitrogen limitations reduce the photosynthesis enhancement under increasing atmospheric CO_2. Second, nitrogen also reduces the carbon loss due to climate change; as soil warming leads to increased nitrogen mineralization, hence increasing nitrogen availability to the plant [41,42].

The Summary for Policy Makers of the Working Group I of the IPCC AR5 headlined that 'Climate change will affect carbon cycle processes in a way that will exacerbate the increase of CO_2 in the atmosphere (*high confidence*)'. More specifically, it stated 'Based on Earth System Models, there is *high confidence* that the feedback between climate and the carbon cycle is positive in the 21st century; that is, climate change will partially offset increases in land and ocean carbon sinks caused by rising atmospheric CO_2. As a result more of the emitted anthropogenic CO_2 will remain in the atmosphere. A positive feedback between climate and the carbon cycle on century to millennial timescales is supported by palaeoclimate observations and modelling.'

3. Observational constraints

Clearly, models alone are not helping to constrain the carbon cycle feedbacks; observations are needed to reduce uncertainties. However, there is a fundamental issue when trying to constrain feedbacks from observations. As by definition, a feedback is estimated from the difference between a coupled system and the theoretical system where this feedback does not operate, one cannot directly observe and measure a feedback. Observations are made in the real world where all feedbacks operate. Nevertheless, there are at least two methods that have been used to help constraining the carbon cycle feedbacks.

The first method makes use of concurrent records of atmospheric CO_2 and temperature over given timescales (figure 1). The analysis of the covariance of the two records informs on relationship between the climate system and the carbon cycle. The first who explored that route was G. Woodwell [43,44], who used past records of atmospheric CO_2 and temperature to try to infer the strength of the climate-carbon cycle feedback. Using the ice-core data of atmospheric CO_2 and Antarctic temperature from the Vostok record over the last 150 000 years, he quantified the strength of climate-carbon cycle feedback [6]. Ice-core data clearly show the natural swing between glacial stages characterized cold temperature associated with low atmospheric CO_2 concentration and interglacial stages characterized with warmer temperature and higher CO_2 levels. Woodwell wrote 'the record for the Vostok core suggests that a change of 1 K in this period was equivalent to a change of 10–15 ppmv of carbon dioxide or about 25 GtC in the atmosphere'. Such analysis has been reproduced since by several authors, giving essentially the same estimate [45,46].

The sensitivity estimate from ice-core records, i.e. a change in atmospheric CO_2 due to a change in global temperature is not directly comparable to γ, the climate-carbon cycle sensitivity as estimated by ESMs.

The ice-core sensitivity describes an atmospheric CO_2 change while γ describes a change in land (or ocean) carbon stores. These two quantities are different as not all of carbon loss by the
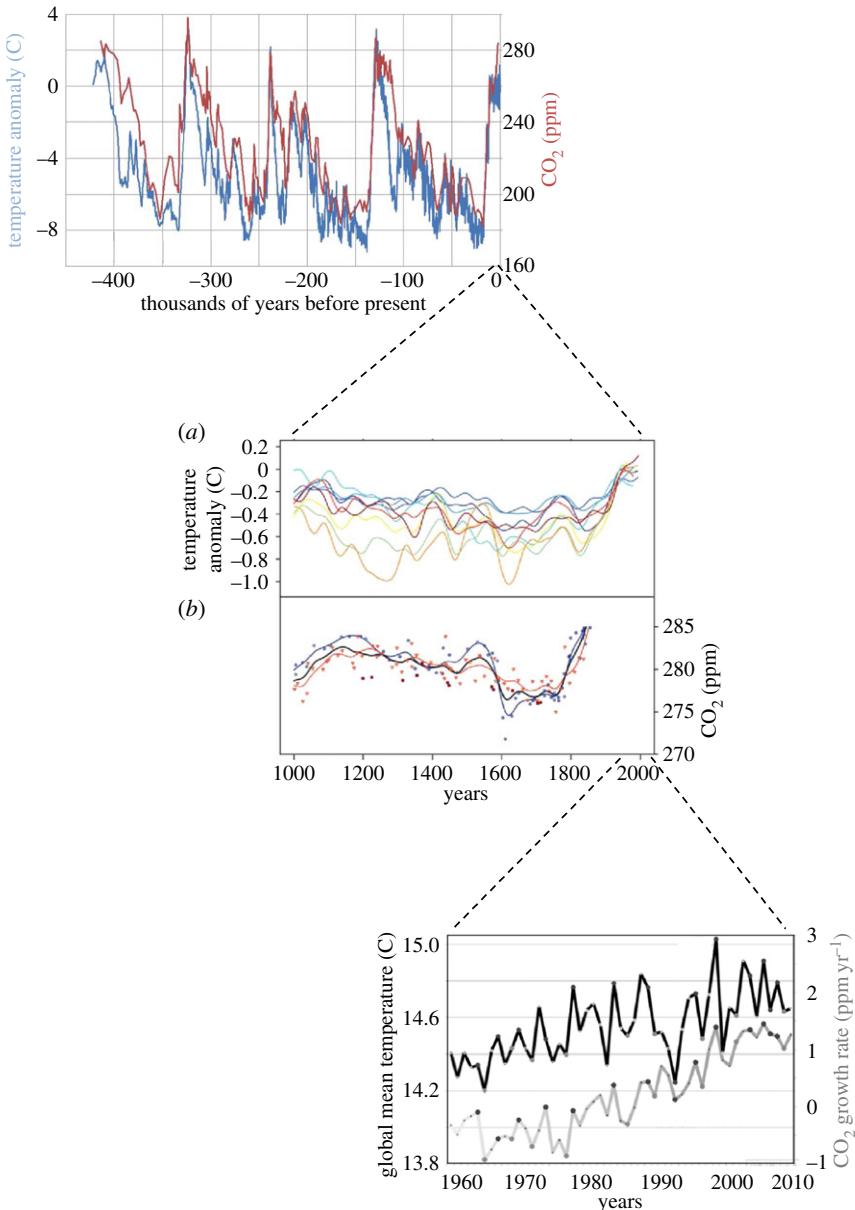
Figure 1. Relationship between global temperature and atmospheric CO_2 across multiple timescales. Top panel shows the Vostok ice core with atmospheric CO_2 (red) and global temperature (blue); middle panel shows last millennium temperature reconstruction (top) and atmospheric CO_2 from several ice cores (bottom); bottom panel shows atmospheric CO_2 annual growth rate from the Mauna Loa record, and global average surface temperature.

land and ocean reservoirs stays in the atmosphere forever; a large fraction is reabsorbed by these two reservoirs in response to the atmospheric concentration perturbation induced by this initial carbon release. For example, if the glacial–interglacial warming induces a release of carbon from the ocean, atmospheric CO_2 will increase, inducing a land and ocean uptake of carbon. What remains in the atmosphere, and hence measured from the ice-core record, is the final outcome of these concurrent processes. Mathematically this can be written as

$$\frac{\Delta C_a}{\Delta T} = \frac{(\Delta C_{o+1}/\Delta T)}{(1 + \beta_o + \beta_l)},$$

(3.1)

with ΔC_a being the change in atmospheric CO_2, ΔC_{o+l} the change in the ocean and land carbon stores for a given ΔT, while β_o and β_l are the CO_2-carbon cycle sensitivity terms described above. The implication is that one need to know the β factors to translate the change in atmospheric CO_2 per unit of warming into a change in carbon store per unit of warming (γ). β is not directly observed, one needs a carbon cycle model to estimate it, and to make it more complicate, β changes with the timescale considered as it represents the uptake of carbon by land and ocean following an increase in atmospheric CO_2. CO_2 is a complex gas in the sense that it does not have one single residence time in the atmosphere. Several processes occurring on dramatically different timescales are responsible for the removal of CO_2 from the atmosphere. Assume a step increase in atmospheric CO_2, about 50% of this increase is still in the atmosphere after 100 years, about 20% is still in the atmosphere after 1000 years, and about 5–10% remains after 10 000 years [47,48].

The implication is that the estimate of 'about 25 GtC in the atmosphere per 1K' does not directly translate in an unequivocal change in the land and ocean reservoir. In addition, the glacial–interglacial changes in the carbon cycle involve processes, predominantly occurring in the ocean, not directly relevant for the anthropogenic perturbation of the twentieth and twenty-first century. The Vostok ice-core is an unambiguous indication that the carbon cycle does respond to climate change, it also confirms that there is a positive feedback on these long timescales, warming release carbon to the atmosphere, but it does not directly help constraining the carbon cycle feedback of the twenty-first century.

Much more encouraging is the analysis of the last millennium. The principle is the same as for glacial–interglacial cycles; ice-core records of the last millennium show variability of atmospheric CO_2, of the order of a couple of ppm, associated with variability of the climate system [49]. The last millennium record offers the advantage that climate and CO_2 fluctuations are relatively small, and operate on centennial timescales, i.e. more relevant for the current anthropogenic perturbation. However, as opposed to the glacial–interglacial cycles that are entirely natural, over the last millennium there is a possibility that the anthropogenic perturbation is already at play and contributes to the fluctuations in atmospheric CO_2. In particular, it had been argued that early land-use change (mainly agriculture in Eurasia) had a significant impact on atmospheric CO_2 with large release of carbon (approx. 300 GtC) from early agriculture [50]. However, it has since been shown that pre-industrial CO_2 emissions from land use were much lower (approx. 50 GtC at most) (e.g. [51]) and were not a major concern in an analysis that focuses on variability rather than long-term trends. The study by Frank *et al.* [49] combined three ice-core data with multiple reconstruction of temperature from tree ring data. They found a clear positive correlation emerging from the CO_2 and temperature datasets, allowing a quantification of the global carbon sensitivity to climate. They reported a $\Delta C_a / \Delta T$ (misleadingly named γ in their paper) of 7.7 ppm CO_2 per K warming, with a likely range of 1.7–21.4 ppm CO_2 per K. When compared with the $\Delta C_a / \Delta T$ simulated by the C^4MIP models over the twentieth century, they concluded that their observation-based estimate was compatible with the lower end of the range simulated by the C^4MIP models, i.e. large values of the climate-carbon cycle feedback were unlikely compatible with their finding.

A complete different approach, but still based on observations, uses the concept of emerging constraints. The approach relies on the finding that there is an emerging quasi-linear relationship between the response of tropical land carbon storage to twenty-first century warming (γ) and the sensitivity of the year-to-year growth rate of atmospheric CO_2 to tropical temperature anomalies (called γ_{IAV}). As the latter is observed, this relationship allows to constraint γ over the twenty-first century [52]. The rise of atmospheric CO_2 vary from year to year, and is due to climate variability such as the El Niño Southern Oscillation. This has been known for several decades, and attributed to the tropical land biosphere [53,54]. ESMs do simulate interannual variability of atmospheric CO_2 in response to the simulated natural climate variability. The emerging relationship emerges as models that tend to simulate a weak tropical land carbon cycle response to ENSO anomalies (low γ_{IAV}) tend to simulate a weak tropical land carbon response to climate change over the twenty-first century (low γ). Conversely, models with a large γ_{IAV} simulate a large twenty-first century γ. This was first demonstrated for the earlier C^4MIP models [52], and subsequently

reproduced with the more recent CMIP5 ESMs [55]. The observed sensitivity of the carbon cycle on interannual timescale, derived from the Mauna Loa atmospheric CO_2 records allows to constraint the tropical land γ to $53 \pm 17\,$GtC per K warming. Again, this estimate is consistent with the lower end of the C^4MIP and CMIP5 ESMs estimates.

These two, completely independent, approaches, one based on millennium variability, and one based on interannual variability agree on two important findings. First, the climate-carbon cycle feedback is positive; and second, the feedback is not as large as simulated by most of the comprehensive models, it is more likely to be in the lower end of the models range.

4. What are we missing?

The emerging constraint presented above only applies for the tropical land carbon, as the interannual variability of atmospheric CO_2 is essentially dominated by tropical land ecosystems. One cannot rule out additional carbon cycle feedbacks arising from non-tropical ecosystems. In particular, permafrost ecosystems are 'the elephant in the room' of the global carbon cycle. Permafrost contains the largest amount of carbon on land, about $1700\,$GtC of organic soils are estimated for the northern permafrost regions [56]. Global warming, exacerbated in high latitudes, is anticipated to induce a thawing of permafrost soils, potentially leading to decomposition of soil carbon currently isolated from the atmosphere. None of the C^4MIP or CMIP5 models included permafrost carbon. Hence the estimations of the climate-carbon feedback for lands are probably conservative for high latitude ecosystems. The same applies for the observation-based estimates; the last millennium climate probably explores a too narrow range of climate variations to trigger large release of carbon from permafrost, and, as mentioned above, the emerging constraint is limited to tropical ecosystems.

Although not included in ESMs yet, permafrost ecosystems are now being represented in land surface models, and estimate of the potential release of carbon from these systems have been made recently [57–60]. Estimates vary widely due to uncertainty in the processes at play (rate of soil thawing, fine-scale processes, fraction of carbon released, potential mitigating role of nutrient, etc.). The IPCC AR5 concluded, 'There is *high confidence* that reductions in permafrost extent due to warming will cause thawing of some currently frozen carbon. However, there is *low confidence* on the magnitude of carbon losses through CO_2 and CH_4 emissions to the atmosphere, with a range from 50 to $250\,$GtC between 2000 and 2100 under the RCP8.5 scenario' [4]. The climate-permafrost carbon gain is hence very uncertain; as the RCP8.5 emissions are about $2000\,$GtC for the twenty-first century, the permafrost carbon release, 50–250 GtC, translates into a gain ranging between 2.5% and 12.5%.

CO_2 fertilization, i.e. the increase of terrestrial plants productivity as a response to atmospheric CO_2 increase, remains one of the major source of uncertainty in the CMIP5 ESMs carbon cycle projections [40]. Although the basic process is relatively well understood: elevated CO_2 stimulates plant photosynthesis, increasing biomass production and hence carbon uptake, the quantification at the global scale remains poorly constrained. There are no long-term global observations of photosynthesis yet that could be used to evaluate models responses. In addition, the induced carbon sink does not only depends on the rate of increase of photosynthesis, it also depends on the residence time of carbon in biomass and soils, delaying the increase in heterotrophic decomposition. Surprisingly, CMIP5 ESMs showed a very wide range of residence time and hence global vegetation and soil carbon estimates [61,62]. For example, simulated global soil carbon ranged between about 500 and 3000 GtC while the observation-based estimate is around 1300 GtC. This is clearly an area where models improvement and evaluation is essential and does not seem out of reach.

On a related topic, nitrogen control on terrestrial plant productivity and hence on carbon sink was not represented in any of the earlier C^4MIP models. For CMIP5, it was introduced in only one land surface model, CLM, which was common to two CMIP5 ESMs (CESM and NorESM). These two models simulated a much lower CO_2-carbon cycle sensitivity (β) and a much lower climate-carbon cycle sensitivity (γ) than the carbon-only ESMs. Although such results were

expected, see discussion before, it is too premature to conclude on the actual strength of the nitrogen limitation.

As mentioned earlier, direct observations of biogeochemical feedbacks or sensitivities (β, γ) are by definition inexistent, one has to rely either on indirect evidences (correlations or emerging constraints) or on direct evidences of other quantities that potentially include other processes. For example, we have a reasonably good understanding of the global ocean and land carbon sinks, but the attribution of these sinks to CO_2, increase, change in climate, atmospheric deposition of nutrients, or changes in land management cannot be directly measured. Nevertheless, there is hope that remote sensing of atmospheric CO_2 could provide better spatial and temporal coverage of atmospheric CO_2 and hence carbon sinks, allowing the attribution of their spatial–temporal patterns to their drivers, in a similar way that attribution of climate change.

Benchmarking of carbon cycle models is now possible, several datasets can be used to constrain global carbon cycle models, both for the land and the ocean [61,63]. Although they cannot directly constrain the carbon cycle sensitivities, they can help evaluate to ability of models to simulate the mean state of the system, such as gross fluxes and reservoirs.

Finally, there are numerous other biological processes that can be affected by climate change, and potentially induce a feedback on the human induced warming, such as N_2O emissions, isoprene and ozone chemistry, fires and aerosols emissions. A recent review of these candidates showed a very low confidence in their estimate as often based on very few studies, but fail to find large potential feedbacks others than the ones already discussed here [64].

5. Putting the pieces together

Combining the model-based estimates of the carbon cycle feedbacks with the recent observation-based studies allows drawing several important conclusions from which one can tentatively revisit the historical global carbon budget (figure 2).

The CO_2-carbon cycle feedback is negative, both for land and ocean systems; an increase in CO_2 concentration induces an increase in land and ocean carbon uptake, mitigating the atmospheric growth rate of CO_2.

The climate-carbon cycle feedback is positive, both for land and ocean systems; global warming induces a reduction of land and ocean carbon uptake, enhancing the atmospheric growth rate of CO_2.

Over the historical period, the CO_2-induced feedbacks are by far dominant; land and ocean act as strong carbon sinks.

Oceanic inventories confirm the large uptake of the global ocean, about 155 ± 30 GtC between 1750 and 2011 [65,66]. This estimate of ocean carbon sink allows putting some new constraint on the ocean CO_2-carbon cycle sensitivity term (β_o). As the atmospheric CO_2 concentration increased by about 100 ppm since 1750, β_o is estimated to amount 1.55 ± 0.3 GtC ppm^{-1} (or 0.7 ± 0.15 ppm ppm^{-1}). This estimate should be seen as conservative as it does not include any climate effect on ocean carbon uptake. However, the climate effect is probably of second order for the ocean and within the uncertainty on the ocean uptake estimate. Assuming a climate-ocean carbon sensitivity (γ_o) of -8 ± 3 GtC K^{-1} (CMIP5 multi-model mean and s.d.), the historical warming (0.85 ± 0.2 K) leads to an ocean carbon loss of only about 7 ± 4 GtC, having virtually no effect on the above estimate of β_o.

The quantification of the land carbon cycle sensitivity of CO_2, β_l, is less trivial as the contribution from historical climate change on the land carbon cannot be neglected anymore. Both the estimate based on the last millennium CO_2 and climate variability, and the emerging constraint estimate based on the interannual variability of atmospheric CO_2 point to a γ_l towards the low-end of the ESM range. The last millennium estimate, $\Delta C_a/\Delta T$ of 7.7 ppm K^{-1} implies a combined ($\gamma_o + \gamma_l$) of about -36 GtC K^{-1} for the twentieth century, broadly consistent with the emerging constraint estimate of a γ_l for the tropics of about -50 ± 20 GtC K^{-1} by 2100, when considering that γ_l does increase with global temperature [40]. Assuming the same γ_o of -8 GtC K^{-1} for the ocean, this gives a climate-land carbon sensitivity (γ_l) of about -28 GtC K^{-1}
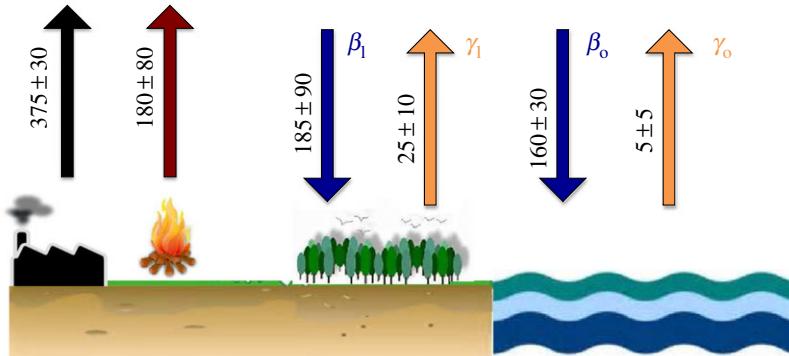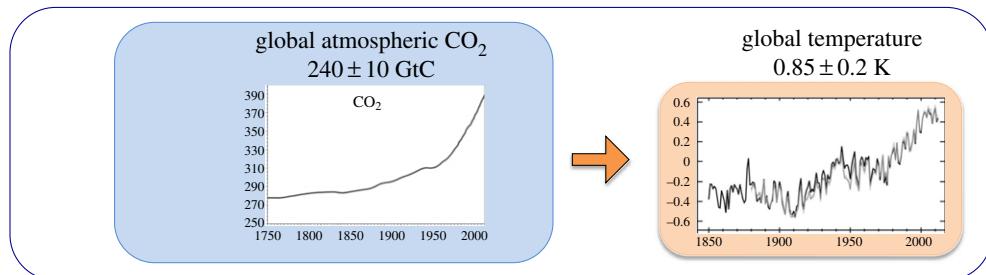
Figure 2. Global carbon budget over the historical period (1750–2011) adapted from IPCC AR5. Fossil fuel (black arrow) and land-use changes emissions (brown arrow) as in IPCC and attribution of land and ocean carbon sinks to atmospheric CO_2 increase (blue arrows) and climate change (orange arrows) as done in this study. All fluxes are in GtC and rounded to the nearest 5. Top panels show atmospheric CO_2 increase since 1750 and global average surface temperature since 1880 for illustration.

Table 1. Global carbon budget over the historical period (1750–2011) as in IPCC and attribution of land and ocean carbon sinks to atmospheric CO_2 increase and climate change as done in this study. All fluxes are in GtC and rounded to the nearest 5, sign convention is positive when to the atmosphere.

sources	
fossil fuel emissions	375 ± 30
net land-use change	180 ± 80
sinks	
atmospheric increase	240 ± 10
oceanic uptake	-155 ± 30
CO_2 driven	-160 ± 30
climate driven	$+5 \pm 5$
land uptake	-160 ± 90
CO_2 driven	-185 ± 90
climate driven	$+25 \pm 10$

for the twentieth century, implying that the terrestrial biosphere already lost about 25 ± 10 GtC in response to the historical warming.

Finally, combining this estimate with the historical global carbon budget reported in the IPCC AR5 allows a quantification of β_1 over the historical period. The difference between the CO_2

emissions from fossil fuel burning and the land-use change (375 ± 30 GtC and 180 ± 80 GtC for the 1750–2011 period, respectively) and the accumulation in the atmosphere and the oceans (240 ± 10 GtC and 155 ± 30 GtC for the same period, respectively) leaves a residual of 160 ± 90 GtC, attributed to the land carbon sink. This sink results from the combined effect of land response to atmospheric CO_2 and to climate change (assuming here that other factors, such as nitrogen deposition are of second order for driving the land carbon sink [67]). Taking a climate-induced land loss of 25 ± 10 GtC as derived above implies a CO_2-induced land sink of 185 ± 90 GtC. Given the atmospheric CO_2 increase of about 100 ppm since 1750, β_1 is estimated to amount 2 ± 0.9 GtC ppm^{-1} (or 0.9 ± 0.4 ppm ppm^{-1}).

These estimate of land and ocean sensitivities allow revisiting the historical global carbon budget, and attributing land and ocean net carbon fluxes to their two primarily drivers, atmospheric CO_2 and climate change (figure 2; table 1).

6. Concluding remarks

The anthropogenic perturbation, through the increase of greenhouse gases, primarily carbon dioxide, is very likely to be responsible for the observed climate change. Further CO_2 emissions will inevitably lead to additional warming over the twenty-first century. The anthropogenic perturbation has a profound impact on the natural global carbon cycle with all reservoirs, the atmosphere, the land ecosystems and the global ocean, being pushed away from their pre-industrial quasi-steady state. Increase in atmospheric CO_2 leads to land and ocean uptake of CO_2, a strong negative feedback on the anthropogenic perturbation. Only about half of CO_2 emissions currently remain in the atmosphere. Without the service provided by the land and ocean systems, atmospheric CO_2 would already be above 500 ppm today. However, climate change also has an impact on the land and ocean carbon cycle, which operates in the opposite direction, warming leads to carbon release from both land and ocean, a positive feedback on the anthropogenic perturbation. The quantification of these four terms, the ocean and land carbon cycle sensitivity to atmospheric CO_2 (β_o, β_1), and the ocean and land carbon cycle sensitivity to climate change (γ_o, γ_1) has been impeding progress in Earth System science for the last decade. Recent use of observations gives some hope on constraining the most uncertain term, γ_1.

For the historical period, the land and ocean sinks are primarily due to the response to atmospheric CO_2 increase, with the historical warming inducing a non-negligible release of carbon from the land.

References

1. Arrhenius S. 1896 On the influence of carbonic acid in the air upon the temperature of the ground. *Philos. Mag.* **41**, 237–276. (doi:10.1080/14786449608620846)
2. Callendar GS. 1938 The artificial production of carbon dioxide and its influence on temperature. *Q. J. R. Meteorol. Soc.* **64**, 223–240. (doi:10.1002/qj.49706427503)
3. Keeling CD, Bacastow RB, Bainbridge AE, Ekdhal CA, Guenther PR, Waterman LS. 1976 Atmospheric carbon dioxide variations at Mauna Loa Observatory, Hawaii. *Tellus* **28**, 538–551. (doi:10.1111/j.2153-3490.1976.tb00701.x)
4. Ciais P *et al.* 2013 Carbon and other biogeochemical cycles. In *Climate Change 2013: The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds TF Stocker *et al.*), pp. 465–570. Cambridge, UK: Cambridge University Press.
5. Delmas RJ, Ascencio J-M, Legrand M. 1980 Polar ice evidence that atmospheric CO_2 20,000yr BP was 50% of present. *Nature* **284**, 155–157. (doi:10.1038/284155a0)
6. Barnola JM, Raynaud D, Korotkevich YS, Lorius C. 1987 Vostok ice core provides 160,000-year record of atmospheric CO_2. *Nature* **329**, 408–414. (doi:10.1038/329408a0)

7. IPCC. 2013 Summary for Policymakers. In *Climate Change 2013: The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds TF Stocker *et al.*), pp. 1–29. Cambridge, UK: Cambridge University Press.

8. Manabe S, Strickler RF. 1964 Thermal equilibrium of the atmosphere with a convective adjustment. *J. Atmos. Sci.* **21**, 361–385. (doi:10.1175/1520-0469(1964)021<0361:TEOTAW>2.0. CO;2)

9. Manabe S, Stouffer R. 1980 Sensitivity of a global climate model to an increase of CO_2 concentration in the atmosphere. *J. Geophys. Res.* **85**, 5529–5554. (doi:10.1029/JC085iC10 p05529)

10. Hansen J *et al.* 1984 Climate sensitivity: analysis of feedback mechanisms. In *Climate processes and climate sensitivity* (eds J Hansen, T Takahashi), pp. 130–163. AGU Geophysical Monograph. 29. Washington, DC: American Geophysical Union.

11. Collins M *et al.* 2013 Long-term climate change: projections, commitments and irreversibility. In *Climate Change 2013: The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. TF Stocker), pp. 1029–1136. Cambridge, UK: Cambridge University Press.

12. Charney JG. 1979 *Carbon dioxide and climate: a scientific assessment*, p. 22. Washington, DC: National Academy of Science.

13. Bony S *et al.* 2006 How well do we understand and evaluate climate change feedback processes? *J. Clim.* **19**, 3445–3482. (doi:10.1175/JCLI3819.1)

14. Flato G *et al.* 2013 Evaluation of Climate Models. 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), pp. 741–866. Cambridge, UK: Cambridge University Press.

15. Lashof DA. 1989 The dynamic greenhouse: feedback processes that may influence future concentrations of atmospheric trace gases and climatic change. *Clim. Change* **14**, 213–242. (doi:10.1007/BF00134964)

16. Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ. 2000 Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184–187. (doi:10.1038/35041539)

17. Friedlingstein P, Bopp L, Ciais P, Dufresne J-L, Fairhead L, LeTreut H, Monfray P, Orr J. 2001 Positive feedback between future climate change and the carbon cycle. *Geophys. Res. Lett.* **28**, 1543–1546. (doi:10.1029/2000GL012015)

18. Bolin B. 1975 Requirements for a satisfactory model of the global carbon cycle and current status of modeling efforts. In *The changing carbon cycle* (eds JR Trabalka, DE Reichle). New York, NY: Springer, 403–424.

19. Oeschger H, Siegenthaler U, Schotterer U, Gugelmann A. 1975 Box diffusion-model to study carbon-dioxide exchange in nature. *Tellus* **27**, 168–192. (doi:10.1111/j.2153-3490.1975. tb01671.x)

20. Maier-Reimer E, Hasselmann K. 1987 Transport and storage of CO_2 in the ocean - an inorganic ocean-circulation carbon cycle model. *Clim. Dyn.* **2**, 63–90. (doi:10.1007/BF01054491)

21. Sarmiento JL. 1986 Three-dimensional ocean models for predicting the distribution of carbon dioxide between the ocean and atmosphere. In *The changing carbon cycle* (eds JR Trabalka, DE Reichle). New York, NY: Springer, 279–294.

22. Rastetter EB, Ryan MG, Shaver GR, Melillo JM, Nadelhoffer KJ, Hobbie JE, Aber JD. 1991 A general biogeochemical model describing the responses of the c-cycle and n-cycle in terrestrial ecosystems to changes in CO_2, climate, and n-deposition. *Tree Physiology* **9**, 101–126. (doi:10.1093/treephys/9.1-2.101)

23. Potter CS, Randerson JT, Field CB, Matson PA, Vitousek PM, Mooney HA, Klooster SA. 1993 Terrestrial ecosystem production—a process model-based on global satellite and surface data. *Glob. Biogeochem. Cycles* **7**, 811–841. (doi:10.1029/93GB02725)

24. Keeling CD. 1973 The carbon dioxide cycle: reservoir models to depict the exchange of atmospheric carbon dioxide with the oceans and land plants. In *Chemistry of the lower atmosphere* (ed. SI Rasool). New York, NY: Springer, 251–329.

25. Tans PP, Fung IY, Takahashi T. 1990 Observational constraints on the global atmospheric CO_2 budget. *Science* **247**, 1431–1438. (doi:10.1126/science.247.4949.1431)

26. Le Quere C *et al.* 2009 Trends in the sources and sinks of carbon dioxide. *Nat. Geosci.* **2**, 831–836. (doi:10.1038/ngeo689)

27. Le Quéré C *et al.* 2013 The global carbon budget 1959–2011. *Earth System Science Data* **5**, 165–186. (doi:10.5194/essd-5-165-2013)

28. Sarmiento JL, LeQuere C. 1996 Oceanic carbon dioxide uptake in a model of century-scale global warming. *Science* **274**, 1346–1350. (doi:10.1126/science.274.5291.1346)

29. Sarmiento JL, Hughes TMC, Stouffer RJ, Manabe S. 1998 Simulated response of the ocean carbon cycle to anthropogenic climate warming. *Nature* **393**, 245–249. (doi:10.1038/30455)

30. Maier-Reimer E, Mikolajewicz U, Winguth A. 1996 Future ocean uptake of CO_2: interaction between ocean circulation and biology. *Clim. Dyn.* **12**, 711–722. (doi:10.1007/s003820050138)

31. Melillo JM, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ, Schloss AL. 1993 Global climate-change and terrestrial net primary production. *Nature* **363**, 234–240. (doi:10.1038/363234a0)

32. Cao MK, Woodward FI. 1998 Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. *Glob. Change Biol.* **4**, 185–198. (doi:10.1046/j.1365-2486.1998.00125.x)

33. Cao MK, Woodward FI. 1998 Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature* **393**, 249–252. (doi:10.1038/30460)

34. Prentice IC *et al.* 2001 The carbon cycle and atmospheric carbon dioxide. In *Climate Change 2001: The Scientific Basis Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (eds JT Houghton, Y Ding, DJ Griggs, M Noguer, PJ van der Linden, X Dai). Cambridge, UK: Cambridge University Press, 183–237.

35. Dufresne J, Friedlingstein P, Berthelot M, Bopp L, Ciais P, Fairhead L, Monfray P. 2002 On the magnitude of positive feedback between future climate change and the carbon cycle. *Geophys. Res. Lett.* **29**, 43. (doi:10.1029/2001GL013777)

36. Friedlingstein P, Dufresne J, Cox P, Rayner P. 2003 How positive is the feedback between climate change and the carbon cycle? *Tellus* **55**, 692–700. (doi:10.1034/j.1600-0889.2003.01461.x)

37. Cox P, Friedlingstein P, Rayner P. 2002 Modelling climate-carbon cycle feedbacks: a cross disciplinary collaboration priority. *IGBP Glob. Change Newslett.* **49**, 12–14.

38. Fung I, Rayner P, Friedlingstein P, Sahagian D. 2000 Full-form earth system models: coupled carbon-climate interaction experiment (the flying leap). *IGBP Glob. Change Newslett.* **41**, 7–8.

39. Friedlingstein P *et al.* 2006 Climate-carbon cycle feedback analysis: results from the C^4MIP model intercomparison. *J. Clim.* **19**, 3337–3353. (doi:10.1175/JCLI3800.1)

40. Arora VK *et al.* 2013 Carbon-concentration and carbon-climate feedbacks in CMIP5 Earth System Models. *J. Clim.* **26**, 5289– 5314. (doi:10.1175/JCLI-D-12-00494.1)

41. Zaehle S, Friedlingstein P, Friend AD. 2010 Terrestrial nitrogen feedbacks may accelerate future climate change. *Geophys. Res. Lett.* **37**, L01401. (doi:10.1029/2009GL041345)

42. Zaehle S, Friend AD, Friedlingstein P, Dentener F, Peylin P, Schulz M. 2010 Carbon and nitrogen cycle dynamics in the O-CN land surface model: 2. Role of the nitrogen cycle in the historical terrestrial carbon balance. *Glob. Biogeochem. Cycles* **24**, GB1006. (doi:10.1029/2009GB003522)

43. Woodwell GM, Mackenzie FT. 1995 Biotic feedbacks in the global climatic system: will the warming feed the warming? Oxford, UK: Oxford University Press.

44. Woodwell GM, Mackenzie FT, Houghton R, Apps M, Gorham E, Davidson E. 1998 Biotic feedbacks in the warming of the earth. *Clim. Change* **40**, 495–518. (doi:10.1023/A:1005345429236)

45. Scheffer M, Brovkin V, Cox PM. 2006 Positive feedback between global warming and atmospheric CO_2 concentration inferred from past climate change. *Geophys. Res. Lett.* **33**, L10702. (doi:10.1029/2005GL025044)

46. Torn MS, Harte J. 2006 Missing feedbacks, asymmetric uncertainties, and the underestimation of future warming. *Geophys. Res. Lett.* **33**, L10703. (doi:10.1029/2005GL025540)

47. Archer D, Buffett B. 2005 Time-dependent response of the global ocean clathrate reservoir to climatic and anthropogenic forcing. *Geochem. Geophys. Geosyst.* **6**, Q03002. (doi:10.1029/2004GC000854)

48. Joos F *et al.* 2013 Carbon dioxide and climate impulse response functions for the computation of greenhouse gas metrics: a multi-model analysis. *Atmos. Chem. Phys.* **13**, 2793–2825. (doi:10.5194/acp-13-2793-2013)

49. Frank DC, Esper J, Raible CC, Büntgen U, Trouet V, Stocker B, Joos F. 2010 Ensemble reconstruction constraints on the global carbon cycle sensitivity to climate. *Nature* **463**, 527–530. (doi:10.1038/nature08769)

50. Ruddiman WF. 2003 The anthropogenic greenhouse era began thousands of years ago. *Clim. Change* **61**, 261–293. (doi:10.1023/B:CLIM.0000004577.17928.fa)

51. Pongratz J, Reick CH, Raddatz T, Claussen M. 2009 Effects of anthropogenic land cover change on the carbon cycle of the last millennium. *Glob. Biogeochem.Cycles* **23**, GB4001. (doi:10. 1029/2009GB003488)

52. Cox PM, Pearson D, Booth BB, Friedlingstein P, Huntingford C, Jones CD, Luke CM. 2013 Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* **494**, 341–344. (doi:10.1038/nature11882)

53. Bacastow R. 1976 Modulation of atmospheric carbon dioxide by the Southern Oscillation.

54. Keeling CD, Whorf TP, Wahlen M, Vanderplicht J. 1995 Interannual extremes in the rate of rise of atmospheric carbon-dioxide since 1980. *Nature* **375**, 666–670. (doi:10.1038/375666a0)

55. Wenzel S, Cox PM, Eyring V, Friedlingstein P. 2014 Emergent constraints on climate-carbon cycle feedbacks in the CMIP5 Earth system models. *J. Geophys. Res.* **119**, 794–807. (doi:10.1002/2013JG002591)

56. Tarnocai C, Canadell J, Schuur E, Kuhry P, Mazhitova G, Zimov S. 2009 Soil organic carbon pools in the northern circumpolar permafrost region. *Glob. Biogeochem. Cycles* **23**, GB2023. (doi:10.1029/2008GB003327)

57. MacDougall AH, Avis CA, Weaver AJ. 2012 Significant contribution to climate warming from the permafrost carbon feedback. *Nat. Geosci.* **5**, 719–721. (doi:10.1038/ngeo1573)

58. Koven CD, Ringeval B, Friedlingstein P, Ciais P, Cadule P, Khvorostyanov D, Krinner G, Tarnocai C. 2011 Permafrost carbon-climate feedbacks accelerate global warming. *Proc. Natl Acad. Sci. USA* **108**, 14 769–14 774. (doi:10.1073/pnas.1103910108)

59. Burke EJ, Jones CD, Koven CD. 2012 Estimating the permafrost-carbon-climate response in the CMIP5 climate models using a simplified approach. *J. Clim* **26**, 4897–4909. (doi:10.1175/JCLI-D-12-00550.1)

60. Schneider von Deimling T, Meinshausen M, Levermann A, Huber V, Frieler K, Lawrence D, Brovkin V. 2012 Estimating the near-surface permafrost-carbon feedback on global warming. *Biogeosciences* **9**, 649–665. (doi:10.5194/bg-9-649-2012)

61. Anav A *et al.* 2013 Evaluating the land and ocean components of the global carbon cycle in the CMIP5 Earth System Models. *J. Clim.* **26**, 6801–6843. (doi:10.1175/JCLI-D-12-00417.1)

62. Carvalhais N *et al.* 2014 Global covariation of carbon turnover times with climate in terrestrial ecosystems. *Nature* **514**, 213–217. (doi:10.1038/nature13731)

63. Randerson JT *et al.* 2009 Systematic assessment of terrestrial biogeochemistry in coupled climate-carbon models. *Glob. Change Biol.* **15**, 2462–2484. (doi:10.1111/j.1365-2486.2009. 01912.x)

64. Arneth A *et al.* 2010 Terrestrial biogeochemical feedbacks in the climate system. *Nat. Geosci.* **3**, 525–532. (doi:10.1038/ngeo905)

65. Sabine CL *et al.* 2004 The oceanic sink for anthropogenic CO_2. *Science* **305**, 367–371. (doi:10.1126/science.1097403)

66. Khatiwala S *et al.* 2013 Global ocean storage of anthropogenic carbon. *Biogeosciences* **10**, 2169–2191. (doi:10.5194/bg-10-2169-2013)

67. Zaehle S, Ciais P, Friend AD, Prieur V. 2011 Carbon benefits of anthropogenic reactive nitrogen offset by nitrous oxide emissions. *Nat. Geosci.* **4**, 601–605. (doi:10.1038/ngeo1207)