

Terrestrial biogeochemical feedbacks in the climate system

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The terrestrial biosphere is a key regulator of atmospheric chemistry and climate. During past periods of climate change, vegetation cover and interactions between the terrestrial biosphere and atmosphere changed within decades. Modern observations show a similar responsiveness of terrestrial biogeochemistry to anthropogenically forced climate change and air pollution. Although interactions between the carbon cycle and climate have been a central focus, other biogeochemical feedbacks could be as important in modulating future climate change. Total positive radiative forcings resulting from feedbacks between the terrestrial biosphere and the atmosphere are estimated to reach up to 0.9 or 1.5 W m⁻² K⁻¹ towards the end of the twenty-first century, depending on the extent to which interactions with the nitrogen cycle stimulate or limit carbon sequestration. This substantially reduces and potentially even eliminates the cooling effect owing to carbon dioxide fertilization of the terrestrial biota. The overall magnitude of the biogeochemical feedbacks could potentially be similar to that of feedbacks in the physical climate system, but there are large uncertainties in the magnitude of individual estimates and in accounting for synergies between these effects.

Research into land–atmosphere exchange processes in climate science has traditionally focused on the surface radiation budget and its effects on sensible and latent heat fluxes, and more recently on carbon-cycle–climate interactions¹. But many more bidirectional land–atmosphere fluxes modulate atmospheric composition and climate. Biogeochemical feedbacks are intrinsic to the climate system, owing to the nonlinear stimulation of all biological processes by increasing temperatures. Many biogeochemical processes also respond to changes in atmospheric composition and precipitation. Biogeochemical cycles are therefore strongly affected by anthropogenically forced climate change and other human activities².

In this Review we highlight three principal pathways along which biogeochemical cycles interact with the atmosphere and climate. First, climate change alters the biogeochemical cycling of atmospherically well-mixed greenhouse gases, which act directly as radiative forcing agents (Box 1a–c; Supplementary Information). Second, changes in atmospheric composition influence the biogeochemistry of radiatively active compounds (Box 1d). Third, climate change alters the biogeochemistry of substances that are not radiatively active in themselves, but that affect the atmospheric concentration of other climatically active compounds (Box 1e,f). We summarize recent progress in understanding terrestrial biogeochemical feedbacks and their linkages, and provide a first estimate of the potential magnitude of biogeochemical feedbacks associated with human-mediated changes in the biosphere (Fig. 1; Supplementary Information).

Carbon cycling, nitrogen dynamics and greenhouse gases

Terrestrial biota acts as a contemporary carbon sink of around 2.8 petagrams (Pg) of carbon annually, thereby restraining the

growth rate of atmospheric CO₂ from fossil-fuel and land-use-change emissions³. The net land-carbon uptake depends on the balance between net primary productivity (NPP) and losses from soil heterotrophic carbon decomposition (Box 1a) and disturbance. The stimulation of photosynthesis by increasing atmospheric CO₂ concentrations and lengthening growing seasons exerts a key influence on the future trajectory of the land-carbon sink, but regional reforestation and ecosystem responses to nitrogen deposition also play a role^{1,4}. Furthermore, heterotrophic carbon loss is strongly accelerated by enhanced temperatures⁵. As yet, there is no consensus on the relative climate and CO₂ trajectories that either NPP or decomposition will follow. But model simulations project a notably reduced carbon sink towards the end of the twenty-first century, with terrestrial processes dominating the global climate feedback⁴. Applying a unifying framework for feedback analyses following Gregory *et al.*⁶, the average model response yields a further radiative forcing of 0.4 W m⁻² K⁻¹ — and up to 0.9 W m⁻² K⁻¹ in the most extreme simulation — owing to the reduced carbon-sink strength that results from the climate sensitivity of terrestrial processes^{4,6} (Fig. 1; Supplementary Information). These processes substantially reduce the cooling that would be expected from CO₂-induced increases in land-carbon uptake in a terrestrial carbon cycle that is insensitive to climatic change.

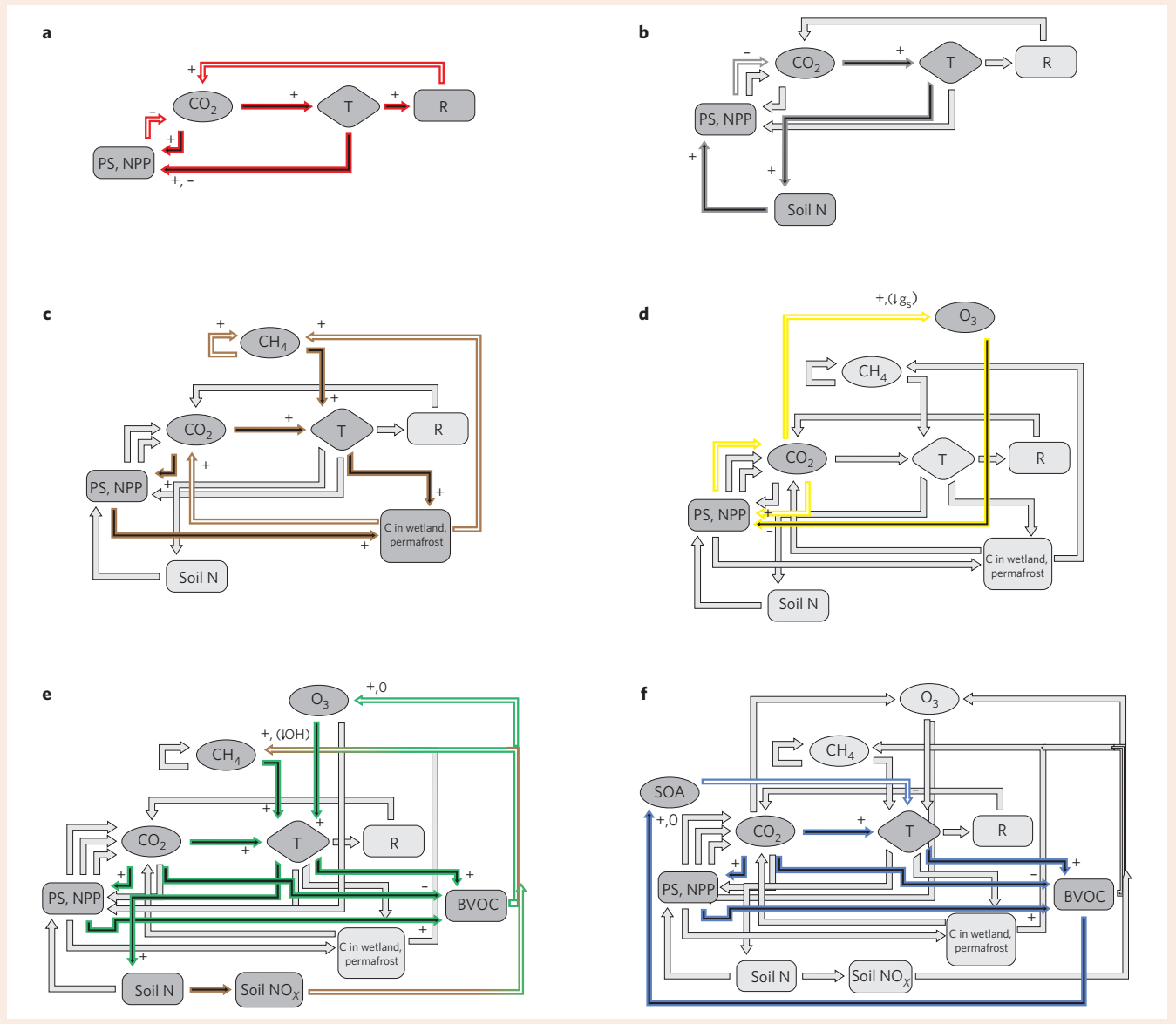
Carbon is fundamentally linked with other elemental cycles as a result of stoichiometrically determined nutrient requirements for tissue building and decomposition⁷. The availability of nitrogen, which is limited in many ecosystems, plays a critical role in controlling NPP^{7,8} (Box 1b). In model simulations, nitrogen availability severely constrains the fertilization response of terrestrial carbon assimilation to increasing CO₂ concentrations^{9–11}

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Box 1 | Important feedback loops linking terrestrial biogeochemical cycles, biosphere–atmosphere exchange, atmospheric composition and climate (here taken as temperature change).

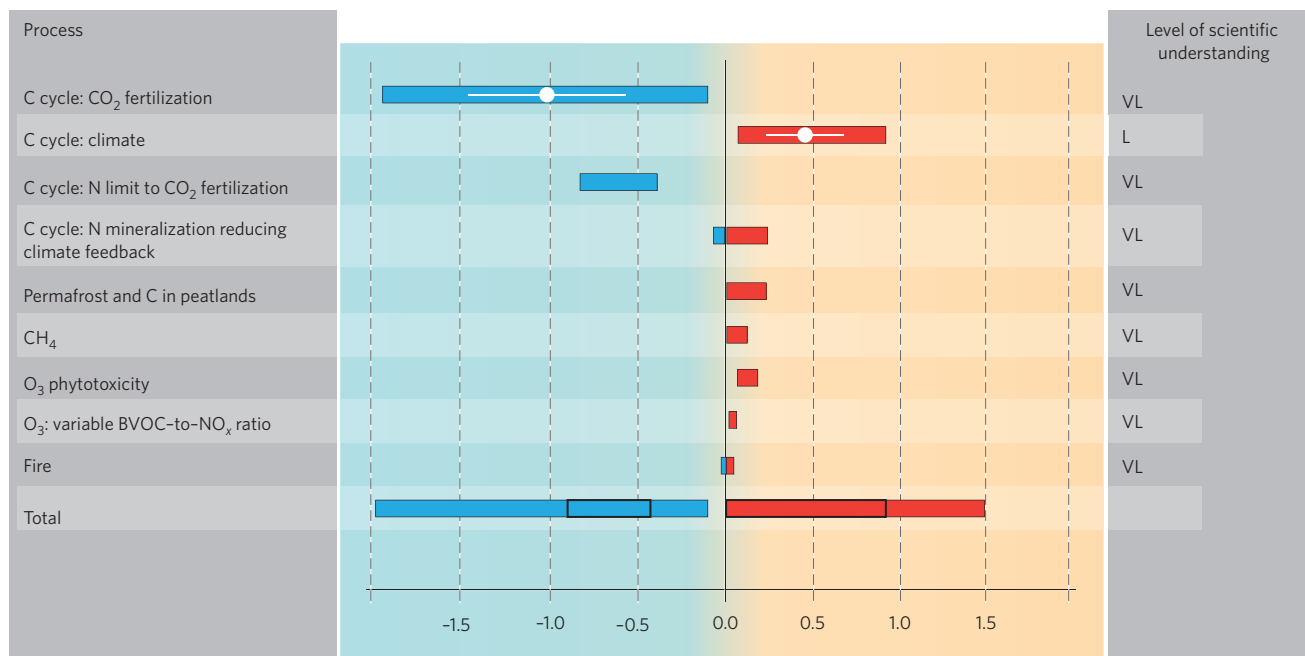
The main forcings and their effects on biogenic emissions are connected by closed arrows; feedbacks are shown by open arrows. Colours highlight a number of different processes and feedbacks. Only feedbacks to atmospheric composition are shown; further feedbacks from atmospheric composition to temperature are omitted for visual clarity. For the same reason, feedbacks occurring through changes in precipitation or radiation are not plotted. We also omit further interactions that might arise from changes in vegetation type (for example, drying of wetlands, migration of forests, leaf-area index change). **a**, Increased CO₂ concentration fosters terrestrial carbon uptake by enhancing photosynthesis (PS) and NPP. Increased temperature (T) also affects PS and NPP, but

also stimulates ecosystem respiration (R), which has a positive feedback on atmospheric CO₂ levels and thus T. **b**, Warmer T could stimulate soil mineralization, making nitrogen available to sustain terrestrial carbon uptake. **c**, Elevated T stimulates CO₂ and CH₄ emissions from global wetlands and northern permafrost soils. **d**, Increased tropospheric O₃ burden from anthropogenic pollution reduces plant photosynthesis owing to its phytotoxic effects. (g_s is stomatal conductance.) **e**, Changed BVOC and soil NO_x emissions in a warmer, high CO₂ environment affect tropospheric O₃ formation as well as methane lifetime. **f**, BVOC emissions are the chief precursors for the growth of biogenic secondary aerosols. For further details see Supplementary Information.



(Fig. 1; -0.4 to -0.8 versus -0.17 to -1.9 W m⁻² K⁻¹). However, models with coupled carbon–nitrogen cycles also indicate that warming will enhance soil-nitrogen mineralization, making more nitrogen available to sustain enhanced plant growth (-0.1 to 0.25 W m⁻² K⁻¹). As a result, some coupled models indicate

a slight reduction in net carbon loss¹¹, whereas others completely remove it^{9,10}. Accounting for the synergistic interactions of changing climate, CO₂ concentrations and nitrogen deposition, however, consistently results in higher atmospheric CO₂ levels in coupled carbon–nitrogen compared with carbon-only simulations, owing



Feedbacks associated with human-mediated changes in the biosphere ($\text{W m}^{-2} \text{K}^{-1}$)

Figure 1 | Radiative forcing from terrestrial biogeochemistry feedbacks in response to anthropogenic atmospheric and climate changes. Bars indicate the approximated minimum-to-maximum feedback range over the twenty-first century. The carbon cycle CO₂ and climate feedbacks include average and standard deviations (white). For calculations, adopted from ref. 6, and data sources see Supplementary Information. Totals include top-end estimates, without and with (black rectangle) C-N interactions. Estimates are based on a number of assumptions that had to be made and clearly point to the need for more interdisciplinary studies. Confidence in scientific understanding is at best low (L), in most cases very low (VL).

to the stronger effect of nitrogen limitation on CO₂ fertilization^{10,11}. This suggests that the rate of climate change is greater than that predicted by carbon-cycle-only models. No study has yet included other nitrogen-cycle climate feedbacks, for example changes in soil emissions of nitrous oxide, the most potent terrestrial greenhouse gas in view of its global warming potential on a time horizon of 20 to 500 years¹².

The depth of peat attests to the fact that wetlands have been persistent carbon sinks over recent millennia¹³. At the same time, wetland methane (CH₄) emissions were prominent even in the twentieth-century atmospheric CH₄ budget, which was dominated by anthropogenic sources¹². Anthropogenic climate change is expected to enhance CH₄ emissions from wetlands^{14–16}, resulting in an estimated further radiative forcing of up to $0.1 \text{ W m}^{-2} \text{K}^{-1}$ at the end of the twenty-first century (Fig. 1). In high-latitude ecosystems with large peat- and soil-carbon pools¹⁷ the future net CO₂ and CH₄ exchange (Box 1c) will depend on the extent of near-surface permafrost thawing¹⁸, the local thermal versus hydrological regimes¹⁹ and interactions with the nitrogen cycle²⁰. A potential 200 Pg of carbon could be released from combined (global) wetland and permafrost pools by the end of the twenty-first century²¹, equivalent to $\sim 0.24 \text{ W m}^{-2} \text{K}^{-1}$ global forcing if in the form of CO₂ (Fig. 1; Supplementary Information). A coupled-model experiment in northern ecosystems estimated a considerably lower feedback, and a loss of only 7 to 17 Pg of carbon owing to permafrost thaw²². The extra heat produced during microbial decomposition could accelerate the rate of change in active-layer depth, potentially triggering a sudden and rapid loss of carbon stored in carbon-rich Siberian Pleistocene loess (yedoma) soils²³. Whether surface ponding will dampen aerobic decomposition sufficiently to provide resistance to fast carbon loss²⁴ is unresolved. In the yedoma-case simulation²³, saturation of the upper metre of soil reduced the annual carbon flux by around 30%, but a total of 180 Pg of carbon was emitted in the form of CH₄ by the year 2400.

Rapidly reactive substances

As well as influencing atmospheric CO₂ and CH₄ concentrations, ecosystems exchange substances with the atmosphere that are readily reactive and climatically relevant. Tropospheric ozone (O₃) is especially important in this context, because of its dual role in affecting, and being strongly affected by, ecosystem processes (Fig. 1; Box 1d,e). Ozone is not only a potent greenhouse gas, narrowly ranked third on the list of forcings for anthropogenic climate change²⁵, but is also a strong oxidant, and as such highly toxic to organisms. It enters plants primarily through the stomata. Background and peak levels in industrialized regions — 35 to 40 and >70 ppb respectively²⁶ — reduce plant productivity through direct cellular damage and/or the carbon cost of protection and detoxification. Indeed, O₃ phytotoxicity could reduce the global land-carbon sink by 120 to 240 Pg (depending on plant O₃ sensitivity) by 2100; the resultant increase in atmospheric CO₂ concentrations would exceed the direct radiative forcing associated with increased levels of tropospheric O₃ (ref. 27). Using the set of experiments carried out by Sitch *et al.*²⁷, and including the partial protection arising from reduced stomatal conductance in a world rich in CO₂, we estimate that the detrimental effects of O₃ on carbon uptake could increase radiative forcing by 0.08 to $0.17 \text{ W m}^{-2} \text{K}^{-1}$ by the end of the twenty-first century, in the framework of Gregory *et al.*⁶ (Fig. 1; Supplementary Information).

Nitrogen oxides (NO_x) are the chief precursors of tropospheric O₃, mainly released during fossil-fuel combustion (around 25 Tg N yr^{-1}) but also with a notable biogenic source²⁸ (Box 1e). Global soil NO_x emissions — which recent global inverse-modelling studies place at >20% of the total source²⁸ — affect O₃ chemistry in clean-air environments and provide an important natural source of O₃, even in polluted regions. Like all processes linked to soil microbial activity, NO_x emissions are

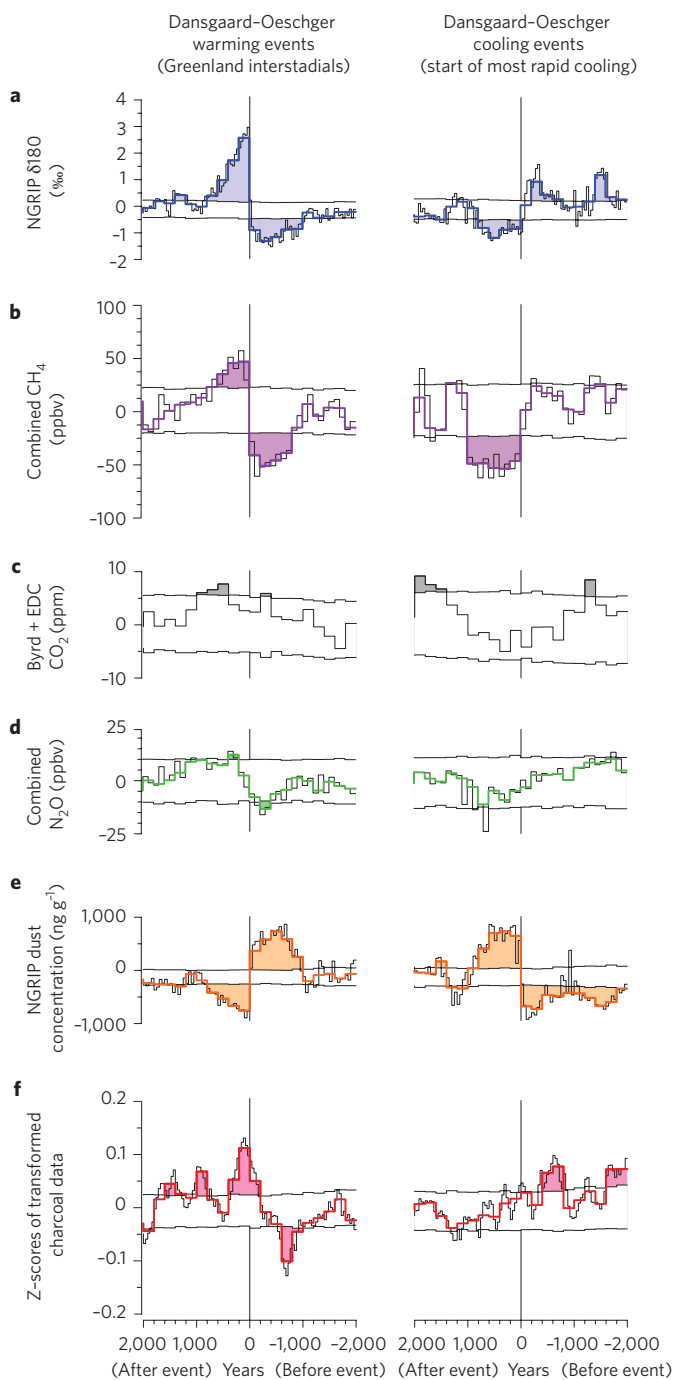


Figure 2 | Superposed epoch analysis of ice-core and biomass-burning records over the interval 80 ka to 10 ka. This analysis shows the consistent response of a time series to the repeated occurrence of the abrupt warming and cooling events that define the Dansgaard-Oeschger cycles during the last glacial period. Shading indicates significant patterns in the response of the time series to the events of abrupt warming and rapid cooling. **a**, The Greenland oxygen-isotope record, an index of regional temperature, shows the characteristic saw-tooth pattern of an individual Dansgaard-Oeschger cycle. **b–f**, Distinctive responses associated with the occurrence of abrupt warming or cooling. BYRD: Byrd station, Antarctica; EDC: EPICA Dome C; NGRIP: North Greenland Ice Core Project. For data sources and further discussion see Supplementary Information.

sensitive to temperature and moisture, and are directly connected to carbon–nitrogen interactions through plant-litter input and application of fertilizer.

O₃ formation also requires the presence of reduced hydrocarbons (Box 1e). Biogenic volatile organic compounds (BVOCs) — which are emitted from live vegetation in a light- and/or temperature-dependent process — constitute a key source of reduced atmospheric hydrocarbons. Isoprene is one of the most important BVOCs. Between 400 and 600 Tg of isoprene are thought to be emitted annually²⁹. Model simulations incorporating variable BVOCs, soil and lightning NO_x emissions yield lower pre-industrial O₃ levels than previously thought, implying a larger present-day anthropogenic O₃ burden of up to 25% (ref. 30). Estimates in Fig. 1 are for 2100, based on enhanced BVOC emissions in response to warmer temperatures³¹ (Supplementary Information), and disregarding extra effects from CO₂ inhibition of BVOC emissions^{32,33}. So far, no study has systematically investigated the impact of future global soil NO_x emissions on the O₃ burden and associated radiative forcing. Enhanced BVOC emissions also raise uncertainties regarding the lifetime of atmospheric CH₄ (ref. 33; Box 1e), because reaction with the hydroxyl radical (OH) is the dominant atmospheric sink for both BVOCs and CH₄. The precise OH-reaction mechanisms are under debate at present, and depend on whether these take place in high-NO_x (polluted) or low-NO_x (non-polluted) environments^{34,35}. A process-based understanding of present-day and future source distributions of BVOCs and NO_x is therefore needed to constrain estimates of CH₄ and O₃ radiative forcing.

From gases to particles

The influence of aerosol particles on climate, and how their properties are perturbed by anthropogenic activity, is one of the key uncertainties in climate change assessments¹². Black-carbon aerosols, which absorb in the visible spectrum, exert a strong positive forcing that is enhanced by snow-albedo changes owing to soot deposition. Black carbon has been proposed to increase radiative forcing by a maximum of ~0.9 W m⁻² globally, which is larger than the forcing associated with CH₄, and is 55% of that associated with CO₂ (ref. 36). However, other studies suggest a lower average black-carbon forcing¹². In contrast, mostly scattering aerosols such as sulphate, organic carbon and nitrate produce a negative direct forcing^{12,37}. Increases in black carbon and concomitant reductions in sulphate pollution were estimated to have contributed ~70% of the observed warming in the Arctic³⁸. Indirect aerosol effects on cloud microphysics, lifetime and precipitation rate are associated with large, poorly constrained climate uncertainties^{39,40}.

Terpenoid BVOC emissions and their oxidation products are the largest global source of secondary organic aerosols (SOA) (Box 1f)⁴¹. The direct contribution of anthropogenic emissions to SOA is small, but anthropogenic aerosols may serve as nuclei for biogenic SOA formation and growth⁴². Recent work has shown that monoterpenes are the chief determinant of aerosol mass over boreal forests⁴³, and that sesquiterpene oxidation products are crucial for the initial stages of particle formation⁴⁴. The situation with isoprene is more complex: it has been recognized as an SOA precursor^{45,35}, but isoprene has also been shown to suppress particle formation from monoterpenes, probably through competing reactions with OH (ref. 46). Links between enhanced BVOC emissions, accelerated SOA production and larger SOA burden in a warmer climate are one of only a few biosphere–atmosphere feedbacks that could result in a cooling, through the direct aerosol effect or changes in cloud albedo^{40,47}.

No study so far has investigated the effects of changes in global biogenic emissions on radiative forcing in future-warming experiments. For present-day conditions, O'Donnell *et al.*⁴⁸ estimated the shortwave radiative effect of SOA, which originate mostly from biogenic precursors, in terms of differences with and without them. The annual mean direct effect was modelled as –0.3 W m⁻². This effect was mitigated by a positive cloud-albedo effect in polluted areas,

amounting to more than $+0.2 \text{ W m}^{-2}$ in the global mean, a result that is so far unique to this model (Supplementary Information). K. Tsigaridis and S. Menon (unpublished data) determined direct radiative forcing of SOA based on differences between present-day and pre-industrial aerosol loadings; applying notably lower BVOC emissions in their study, they estimate a direct SOA-induced forcing of -0.02 W m^{-2} , compared with a total aerosol direct forcing of -0.21 W m^{-2} .

Allowing for the sensitive response of BVOC leaf emissions to warmer temperatures, SOA production is estimated to increase substantially in a future warmer climate^{49,50}. It is as yet unknown whether processes leading to direct CO_2 inhibition of isoprene production³³ also affect production of monoterpenes or sesquiterpenes, their release from storage pools, and hence future SOA burden and radiative forcing. Monoterpene metabolic production, located in the chloroplast, is rather similar to that of isoprene. Recent studies indicate reduced production and needle-tissue levels of monoterpenes in Douglas firs grown at elevated CO_2 levels⁵¹. Whether or not the interactive effects of temperature, photosynthetically active radiation and CO_2 (ref. 52) will indeed lead to a strong increase in terpenoid emissions is so far unresolved.

Up in smoke

Fire is a natural, regularly recurring episodic event across all vegetated biomes, most prominent in savannas and Mediterranean or boreal forest ecosystems⁵³. In the absence of transient changes in fire regimes caused by climate or land-use change, fires have little effect on the average annual net carbon balance because the carbon released is rapidly recaptured by regrowing vegetation. However, fires act on the carbon cycle by accelerating both primary production and respiration, and fire patterns have a strong influence on the interannual variation in the atmospheric growth rates of CO_2 and CH_4 (ref. 53). Large atmospheric impacts of fire are related to emissions of particles, O_3 , CH_4 and other volatile hydrocarbons, either directly or as their precursors⁵³. Global biomass burning represents between around 15 to 40% of the global NO_x and CO emissions, respectively^{28,54}. Model simulations suggest that radiative forcing is highly sensitive to variations in overall pyrogenic emissions^{54–56}. Although net effects may be small (Fig. 1), a change in burn conditions could easily shift fire-related forcing in either direction.

Past links between biogeochemical cycles and climate

Ice-core records reveal that the atmospheric composition of greenhouse gases and mineral-dust aerosol has covaried with rapid and gradual changes in climate, over at least the past 800,000 years^{57–59}, with the phasing of changes in individual greenhouse gases modulated by differences in the temporal and spatial patterning of (ocean and terrestrial) biospheric feedbacks (Fig. 2; also see ref. 60 for example). Substantial glacial–interglacial vegetation changes are documented in pollen and plant-macrofossil records⁶¹. Vegetation types adapted to low CO_2 levels, drought and cool temperatures were wide-spread at the Last Glacial Maximum, whereas orbitally induced insolation changes during the first part of the Holocene resulted in high-latitude warming that led to northward expansion of boreal and temperate forests, and enhanced monsoons that caused northward expansion of Sahelian vegetation⁶². These large-scale changes in turn led to changes in dust emission⁶³ and fire regimes⁶⁴. Pollen and charcoal data have also demonstrated extremely rapid responses to climate variability such as Dansgaard–Oeschger events (rapid climate events that occurred during the last glacial period) or the onset/termination of the Younger Dryas⁶⁵. The palaeorecord thus points not only to a number of terrestrial biogeophysical feedbacks^{66–68}, but also to substantial impacts of biogeochemical cycling on atmospheric composition and climate.

For example, peatland productivity and decomposition are highly sensitive to temperature and precipitation changes, hence their carbon sequestration varies on decadal to millennial timescales. These changes in sequestration in turn feed back to atmospheric composition. Peatland initiation in the northern high latitudes began around 15,000 years ago, during the deglaciation. Almost half of the modern peatland began to form before 8,000 years ago⁶⁹; around 100 Pg of carbon were sequestered in the process, contributing to the observed drawdown of atmospheric CO_2 and the peak in atmospheric CH_4 in the early Holocene⁷⁰. Increased peat-accumulation rates are registered during the warmer conditions of the early to mid-Holocene in the northern high latitudes⁷¹, whereas substantially reduced accumulation occurred during the cold intervals of the Younger Dryas and the Little Ice Age⁷². The most extensive lateral expansion of high-latitude peatlands occurred only after 5,000 years ago⁷³, coinciding with the late-Holocene increase in CH_4 shown by ice-core records. The overall climate impact of changes in peat accumulation is uncertain because of the competing influences of CO_2 carbon sequestration and CH_4 emissions. Frolking *et al.*⁷⁴ have suggested that the initial impact of northern peatland growth is a net warming that peaks about 50 years after peatland initiation, but remains positive for the next several hundred to thousand years, depending on the rate of carbon sequestration, although after this peatlands would have an ever-increasing net cooling impact. However, these calculations were made without taking into account the impact of climate variability on peatland growth, carbon uptake and CH_4 emissions.

Analyses of interhemispheric gradients of ice-core CH_4 concentrations and carbon isotope composition have been interpreted as indicating that changes in wetland emissions drove glacial–interglacial CH_4 changes^{75,76}. However, simulations using simple formulations of wetland extent and emissions have been unable to reduce wetland sources sufficiently to produce the low levels of glacial atmospheric CH_4 concentrations^{77,78}. Alternatively, as OH is the chief atmospheric sink for both CH_4 and BVOCs, it has been suggested that strongly reduced BVOC emissions during the Last Glacial Maximum, in response to cooler temperatures and less-productive vegetation, led to increased OH levels, decreasing the lifetime and concentration of CH_4 (ref. 77). Yet, these model experiments disregard the suggestion that BVOC emissions under low atmospheric CO_2 levels may have been more conservative³² than assumed in this simulation.

The palaeorecord of changes in fire regime provides a second example of biogeochemistry–atmosphere–climate feedbacks. Global compilations of charcoal in continuously deposited lake or bog sediments show less fire during glacial than interglacial intervals⁶⁴, as a consequence of the reduction in biosphere productivity and hence fuel availability that occurs as a result both of cold, dry glacial climates, and the direct impact of low levels of CO_2 on plant productivity. On centennial to millennial timescales, fire activity covaries with climate change⁷⁹ — indeed, biomass burning declined towards the Little Ice Age — supporting the interpretation by Ferretti *et al.*⁸⁰ of the ice-core record of changes in $^{13}\text{CH}_4$ as a reflection of changes in biomass burning. Fire regimes show a large response to both rapid warming and rapid cooling^{81,82}; during the last glacial period, for example, fire regimes tracked Dansgaard–Oeschger warming events with lag times on the order of a few decades (Fig. 2); the lag in response to the cooling associated with Heinrich stadials was slightly longer⁸¹.

Detecting the signal from the noise

Remotely sensed vegetation greening⁸³, and ground-based evidence for vegetation changes in northern latitudes that have experienced amplified warming, demonstrate the responsiveness of terrestrial biota to trends in climate, with corresponding changes in biogeochemical cycling⁸⁴. The interannual variation in the atmospheric CO_2 growth rate is dominated by interactions between the terrestrial carbon cycle, climate and fire^{83,85,86}. Inversions of atmospheric

concentration measurements suggest that wetland and, to a lesser extent, fire emissions have dominated the interannual variability in CH₄ growth rate during the past few decades⁸⁷. Interannual variation in atmospheric CO, CO₂ and its isotopic ratios are related to variability in climate–fire emissions from boreal or tropical regions, for example in response to precipitation patterns^{53,88}, and further feedbacks exist between increased post-burn surface temperature and substantially reduced vegetation productivity⁸⁹. In unpolluted tropical forests, atmospheric OH levels are remarkably stable even when BVOC emissions are high, although such emissions were thought to dampen the atmospheric oxidation capacity³⁴. The multitude of processes that need to be considered makes it close to impossible to detect actual system feedback responses with present observations. But the observational evidence supports the view of tight connections between climate, vegetation and biogeochemical cycling both in terms of greenhouse gas exchange and of atmospheric–reactivity–climate interactions.

Land cover and biogeochemical cycling

Our focus on the interactions between climate, atmospheric composition and biogeochemical cycles should not detract attention from changes in natural vegetation cover, and those in anthropogenic land use and land cover, as the main influences on surface–atmosphere exchange and feedbacks^{90,91}. There are large uncertainties in the estimates of radiative forcing resulting from changes in surface albedo, and the energy balance associated with historic land-cover change^{92,93}. Deforestation, particularly by fire, releases a large amount of carbon into the atmosphere that is not returned into the terrestrial system when forests are replaced by agricultural systems⁵³. The BVOC emission spectra of forests and agricultural systems are very different⁹⁴; the former dominated by terpenoids — which are prime precursors of SOA and O₃ — the latter dominated by oxygenated BVOCs, with different but poorly understood atmospheric chemistry. In-canopy reactions of soil NO_x emissions also differ between forests and crops, with escape into the atmosphere being much larger in short canopies²⁸. Moreover, fertilization and irrigation of agricultural systems provide an overriding cause for altered carbon–nitrogen cycling and reactive emissions of nitrogen-containing trace gases⁸. Existing experimental observations and simulations are insufficient to provide a quantitative synthesis of the impacts of land-cover changes; field and model experiments addressing this must be a future research priority⁹⁵.

What's in a global number?

There is growing evidence that the impact of biogeochemical feedbacks must not be ignored in climate change studies. For simplicity, in this Review we assume that individual effects add up, with maxima depending on the extent to which nitrogen limits or stimulates carbon sequestration. According to our analysis, the combined estimated positive forcing from feedbacks associated with carbon, nitrogen and atmospheric chemistry in response to anthropogenic warming could further increase warming. Indeed, biogeochemical positive forcing could potentially cancel out cooling associated with CO₂ fertilization of the biosphere, an effect that has been proposed to mitigate warming (Fig. 1). SOA formation could also act to cool the climate, but at least for present-day simulations, the relative magnitude of the direct and indirect effects depends strongly on assumptions in SOA models. Given the limited number of quantitative experiments available, our estimates of the total radiative forcing from biogeochemical feedbacks that operate in the climate–chemistry system can only serve as a very rough guide. Nonetheless, we conclude that the climate effect of changes in element cycles and atmospheric chemistry is comparable in magnitude to that of physical feedbacks such as water vapour or clouds⁹⁶.

The path from a change in emissions to a change in radiative forcing, and henceforward to a change in climate, is convoluted,

particularly for heterogeneously mixed reactive substances in the atmosphere. Each of these changes has its own geographically varied pattern, and, when overlain, these patterns generally do not match⁹⁷. Chemical reactions of a trace gas depend on the degree of pollution, temperature and humidity; chemistry–climate interactions are also affected by long-range transport of emission reaction products. A small change in the global burden of a given substance can hide substantial regional variability, thus averaging over positive or negative changes in local radiative forcing^{33,38}. Here, we have summarized the interactions of biogeochemical cycles with the climate system in terms of global forcing feedbacks, by analogy to the global radiative forcing estimates generated by the IPCC. But we stress the need for the development of a more refined metric⁹⁸, and for the consideration not only of radiative effects, but also of other important ecosystem functions⁹⁹.

Because our understanding of the processes is limited, it has been necessary to focus on individual biogeochemical feedbacks. However, the intricate coupling of terrestrial biogeochemical cycles of inert greenhouse gases with reactive atmospheric chemistry means that none of the feedbacks summarized here will act in isolation. At present we have to ignore nonlinearities, and thus possible thresholds in the system, to make simulations with ecosystem–chemistry–climate models feasible. But improved understanding of biogeochemical cycle interactions should be a priority for the scientific community. This will aid development and implementation of atmosphere and ecosystem management, particularly in light of post-Kyoto negotiations¹⁰⁰, and the development of climate and air-pollution control strategies.

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Acknowledgements

The authors acknowledge the Integrated Land Ecosystem–Atmosphere Processes Study (iLEAPS), core project of the International Geosphere–Biosphere Programme (IGBP), and the discussions at the Science Workshop on Past, Present and Future Climate Change in Helsinki, November 2008. The Helsinki workshop and the manuscript preparation were supported by the Finnish Cultural Foundation. A.A. acknowledges support from the Academy of Finland, and the Swedish research councils VR and Formas. S.P.H. and S.Z. acknowledge funding from the EC-supported project GREENCYCLES (MRTN-CT-2004-512464). K.T. was supported by an appointment to the NASA Postdoctoral Program at the Goddard Institute for Space Studies, administered by Oak Ridge Associated Universities through a contract with NASA. The work at Lawrence Berkeley National Laboratory was performed under Contract No. DE-AC02-05CH11231. S.M. acknowledges funding support from the NASA MAP program and the DOE ASR program. P.J.B. acknowledges support from the US NSF Paleoclimate program. Suggestions made by Chris Jones helped to improve our analysis substantially.

Author contributions

This Review was conceived at a workshop coordinated by M.K., A.K. and S.S., and all authors participated in the subsequent discussions and planning. S.M., K.T., S.Z., H.F., D.D. and G.S. contributed model simulations; A.A., S.P.H., P.J.B., S.S. and S.Z. were responsible for analyses and figures; and A.A. and S.P.H. were responsible for the first draft of the paper. All authors provided input to the drafting and final version of the manuscript.

Additional information

The authors declare no competing financial interests.