

Terrestrial biogeochemical feedbacks in the climate system: from past to future

A. Arneth^{1,2}, S. P. Harrison^{3,4}, K Tsigaridis⁵, S Menon⁶, P.J. Bartlein⁷, H Feichter⁸, A Korhola⁹, M Kulmala¹⁰, D O'Donnell⁸, G Schurgers¹, S Sorvari², T Vesala², S. Zaehle¹⁰

1: Dept. Earth and Ecosystem Science, Lund University, Sölvegatan 12, 22362 Lund, Sweden; +46 46 222 4081; Almut.arneth@nateko.lu.se

2: Department of Physics, POBox 64, FI-00014, University of Helsinki, Finland, +358 40 596 2311; timo.vesala@helsinki.fi; sanna.sorvari@helsinki.fi; kulmala@pcu.helsinki.fi

3: School of Geographical Sciences, University of Bristol, Bristol BS8 1SS, UK; +44 117 331 7223; sandy.harrison@bristol.ac.uk

4: School of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia

5: NASA Goddard Institute for Space Studies, 2880 Broadway, New York, NY 10025, USA; +1 (212) 678-5668; ktsigaridis@giss.nasa.gov

6: LBNL, MS90KR109, 1 Cyclotron Road, Berkeley, CA 94720, Phone: 1 510 486 6752; smenon@lbl.gov

7: Department of Geography, University of Oregon, Eugene, Oregon, USA; +1 541 346 4967; bartlein@uoregon.edu

8: Max Planck Institute for Meteorology, Hamburg, Germany; declan.odonnell@zmaw.de; +49 40 41173388

9: Department of Bio- and Environmental Sciences, University of Helsinki, PO. Box 57, 00014 University of Helsinki, Finland; + 358 50 415 4528; atte.korhola@helsinki.fi

10: Max-Planck-Institute for Biogeochemistry, Dept. Biogeochemical Systems, Hans-Knöll-Str 10, 07745 Jena, Germany; +49 3641 576325; soenke.zaehle@bgc-jena.mpg.de

Thoughts on possible Reviewers:

Peter Cox

Paolo Artaxo

Andi Andreae

David Fowler

The terrestrial biosphere plays a major role in the regulation of atmospheric composition, and hence climate, through multiple interlinked biogeochemical cycles (BGC). Ice-core and other palaeo-environmental records show a fast response of vegetation cover and exchanges with the atmosphere to past climate change, although the phasing of these responses reflects spatial patterning and complex interactions between individual biospheric feedbacks. Modern observations show a similar responsiveness of terrestrial biogeochemical cycles to anthropogenically-forced climate changes and air pollution, with equally complex feedbacks. For future conditions, although carbon cycle-climate interactions have been a major focus, other BGC feedbacks could be as important in modulating climate changes. The additional radiative forcing from terrestrial BGC feedbacks other than those conventionally attributed to the carbon cycle is in the range of 0.6 to 1.6 Wm^{-2} ; all taken together we estimate a possible maximum of around 3 Wm^{-2} towards the end of the 21st century. There are large uncertainties associated with these estimates but, given that the majority of BGC feedbacks result in a positive forcing because of the fundamental link between metabolic stimulation and increasing temperature, improved quantification of these feedbacks and their incorporation in earth system models is necessary in order to develop coherent plans to manage ecosystems for climate mitigation.

Terrestrial processes and feedbacks in the climate system

Recognition of land-atmosphere exchange processes in climate science has traditionally been largely restricted to 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; at their heart lies the stimulation of all biological processes by increasing temperatures that accelerate cellular metabolism with highly non-linear relationships of variable sensitivity². Many processes additionally respond to changes in atmospheric composition and precipitation. Biogeochemical cycles (BGC) therefore are strongly affected by anthropogenically-forced climate change and other human activities. We identify three principle pathways along which BGC-atmosphere-climate feedbacks operate (Box). Firstly, climate change alters the BGC of an atmospherically well-mixed greenhouse gas which acts directly as a radiative forcing agent. Secondly, changes in atmospheric composition affect the biogeochemistry of a radiatively active compound. Thirdly, climate change affects the biogeochemistry of substances that are not radiatively active in themselves, but that affect the atmospheric concentration of other climatically active compounds. We summarise recent progress in understanding terrestrial BGC cycles and their linkages, and provide a first estimate of the potential magnitude of BGC feedbacks associated with human-mediated changes in the biosphere (Figure 1; see Supplementary information for more detail).

Carbon cycling, nitrogen coupling, and atmospheric greenhouse gas concentration

The terrestrial biota acts as a contemporary carbon sink of around 2.8 Gt C annually. This sink helps restrain the growth rate of atmospheric CO₂ from fossil fuel and land-use change emissions³. Land carbon uptake depends on the balance between net primary productivity (NPP) and C losses from soil heterotrophic carbon decomposition (Box, A) and disturbance. The stimulation of photosynthesis by increasing atmospheric CO₂ concentration and lengthening growing seasons is an important influence of the future trajectory of the land C sink, but regional reforestation and the carbon cycle response to nitrogen deposition also play a role^{4,5}. Heterotrophic C loss is strongly accelerated by enhanced temperatures⁶. Although there is as yet no consensus on the relative climate- and CO₂-trajectories that either NPP or decomposition will follow, model simulations project a reduced carbon sink towards the end of the 21st century, or even a sink-source transition, with terrestrial processes dominating the overall global feedback⁵. The averaged model response yields an extra 75 ppm CO₂ in the atmosphere compared to uncoupled simulations, an additional radiative forcing of 0.5 Wm⁻² (Figure 1; recalculated from^{5,7}, see Supplementary information). The most extreme simulation⁵ yielded an extra 225 ppm CO₂, or up to 1.5 W m⁻².

Carbon is fundamentally linked with other elemental cycles as a result of stoichiometrically determined nutrient requirements for tissue building and decomposition⁸. This suggests that treating carbon biogeochemistry in isolation is unlikely to give the complete answer, even to first-order since the availability of nitrogen, which is limited in many ecosystems, plays a critical role in controlling NPP^{8,9} (Box, B). In model simulations, N availability severely constrains the fertilisation response of terrestrial carbon assimilation to increasing CO₂^{7,10,11}. However, models with coupled carbon-nitrogen cycles also indicate enhanced soil nitrogen mineralization in response to warming, making additional N available to sustain enhanced plant growth. Estimates of this effect diverge: some models indicate a slight reduction¹¹ while others completely remove the net C loss induced by climate change alone^{7,10}. Accounting for the synergistic interactions of changing climate, CO₂ concentration and N deposition, however, results consistently in higher atmospheric CO₂ levels in C-N, compared to C-only simulations^{10,11}, due to the effect of N limitation on CO₂ fertilisation (Figure 1). No study has yet included other climate-feedbacks linked to the terrestrial N-cycle, e.g. soil emissions of N₂O, the most potent of terrestrial greenhouse gases.

The depth of peat accumulation, particularly in high northern latitudes attests to the fact that wetlands have been persistent CO₂ sinks over recent millennia¹². At the same time, wetland methane emissions are prominent even in the 20th century atmospheric methane budget which is dominated by anthropogenic sources¹³. Calculations by Gedney et al.¹⁴, in the only study so far to quantify the impact of changes in global wetland methane emissions in response to anthropogenic climate change, indicate an additional radiative forcing between 0.17 and 0.22 W m⁻² at the end of the 21st century (Figure 1). Global wetland ecosystem climate-feedbacks in their dual role as CO₂ sinks and CH₄ sources (Box, C) have not yet been investigated.

In high-latitude ecosystems, with large peat and soil carbon pools¹⁵, the future role for C sequestration and loss in form of CO₂ and CH₄ will depend on the extent of near-surface permafrost thawing over the 21st century¹⁶, the local thermal vs. hydrological regime¹⁷ and interactions with the nitrogen cycle¹⁸. A potential 200 PgC could be released from combined (global) wetland and permafrost pools by the end of the century¹⁹, equivalent to ~0.3 Wm⁻² global forcing in the form of CO₂ only (Figure 1; Supplementary material). A coupled model experiment in northern ecosystems estimated a considerably lower ± 0.1 Wm⁻¹ feedback, including a 7-17 Pg C loss from permafrost thaw²⁰. The additional heat production during microbial decomposition could accelerate the rate of change in active layer depth, with the potential to trigger sudden and rapid loss of C stored in carbon-rich Siberian Pleistocene loess (Yedoma) soils²¹. Whether surface ponding dampens aerobic decomposition sufficiently to provide resistance to fast carbon loss²² is unresolved. In the Yedoma-case simulation²¹, saturation of the upper meter of soil reduced the annual C flux by ca. 30%, but a total of 180 GtC was emitted in the form of methane by 2400.

Rapidly reactive substances: BVOC and NO_x

On top of influencing CO₂ and CH₄ concentrations, ecosystems exchange substances with the atmosphere that are readily reactive and climatically relevant in their own respect. Tropospheric ozone is especially important in this context, in its dual role of both affecting and being strongly affected by ecosystem processes (Figure 1; Box D, E). It is not only a potent greenhouse gas, narrowly ranked third on the list of culprits for anthropogenic climate change¹³, but also a strong oxidant and as such highly toxic to organisms. Ozone enters plants primarily through the stomata. Background and peak levels in industrialised regions, 35-40 and >70 ppb respectively^{23,24}, degrade plant productivity either from direct damage to cellular processes, from the carbon cost of protection and detoxification, or both. A globally reduced land C sink in response to ozone phytotoxicity could contribute an indirect radiative forcing up to 1.09 W m⁻² (depending on plant O₃ sensitivity) by 2100, exceeding the calculated direct radiative forcing from tropospheric ozone increases²⁵. Using the set of experiments in²⁵ and including the partial protection arising from reduced stomata conductance in a high CO₂ environment, we have adopted the more conservative estimate, 0.17 to 0.32 W m⁻² as the additional O₃-toxicity forcing in 2100 from BGC feedbacks, (Figure 1; Supplementary Material).

Although the chief catalyst, nitrogen oxides (NO_x), is emitted from fossil fuel combustion (ca. 25 TgN a⁻¹²⁶) the atmospheric burden of O₃ is also strongly modulated by biogenic emissions (Box, E). Soil NO_x emissions, which recent global inverse modelling studies place at >20% of the fossil fuel source²⁶ affect O₃ chemistry in clean air environments and provide an important natural background even in polluted regions. Like all processes linked to soil heterotrophic activity, NO_x emissions are sensitive to soil temperature and moisture, and are directly connected to carbon-nitrogen interactions via plant litter input and application of fertiliser. O₃ formation requires also the presence of reduced hydrocarbons (Box, E). A large source of the latter are biogenic volatile organic compounds (BVOC) produced from live vegetation in a light- and/or temperature-dependent process, particularly isoprene with an estimated source strength of 400 to 600 Gt C a⁻¹²⁷. Applying variable BVOC and soil and lightning NO_x emissions resulted in lower O₃ PI burden, implying an up to 25% enhanced PI to present anthropogenic forcing (²⁸; Figure 1). Uncertain BVOC

emissions introduce ambiguities of several tenths of $W m^{-2}$ for present and for future levels of O_3 (Figure 1;²⁹⁻³¹). They also introduce uncertainties in methane lifetime³² (Box, E), since reaction with OH is the dominant atmospheric sink for both. The precise reaction mechanisms are currently under debate and depend on whether these take place in polluted or non-polluted environment^{33,34}. Sound biological and chemical process-understanding for reliable present and future source distributions of BVOC and NO_x is therefore required to curb variation in CH_4 and O_3 radiative forcing estimates.

From gases to particles

The role of aerosol particles and how their properties are perturbed by anthropogenic activity is one of the most difficult aspects of climate change assessments³⁵. Black carbon aerosols, being absorbing in the visible, exert a strong positive forcing that is enhanced by snow albedo changes due to soot deposition. The global present-day forcing from black carbon is estimated to $\sim 0.9 W m^{-2}$, larger than the forcing from methane and 55% of that from CO_2 ³⁶. In contrast, mostly scattering aerosols such as sulphate, organic carbon and nitrate produce a negative direct forcing^{35,37}. Increases in black carbon and concomitant reductions in sulphate pollution were estimated to have contributed to $\sim 70\%$ of the observed warming in the Arctic³⁸. Indirect aerosol effects on cloud microphysics, lifetime and precipitation rate are associated with large, as yet un-quantified climate uncertainties³⁹.

Terpenoid BVOC and their oxidation products are the major source of secondary organic aerosol (SOA; Box, F)⁴⁰. The direct contribution of anthropogenic emissions to SOA is quite small but anthropogenic aerosol may serve as nuclei for biogenic SOA formation and growth⁴¹. Recent work has shown monoterpenes to be chief determinant of aerosol mass at boreal forest⁴², and identified sesquiterpene-oxidation products as crucial for the initial stages of particle formation⁴³. The situation with isoprene is more complex: isoprene has been recognised as a SOA source⁴⁴ via photo-oxidation³⁴ but competition for OH has been shown to suppress particle formation from monoterpenes⁴⁵. Of all the biosphere-atmosphere feedbacks highlighted here, links between enhanced BVOC emissions, accelerated SOA production and larger SOA burden in a warmer climate is the sole mechanism to possibly result in a cooling through the direct aerosol effect and changes in cloud-albedo^{46,47}.

For present day conditions, the direct shortwave radiative effect from biogenic SOA ranged from -0.02 to $-0.3 W m^{-2}$ in two recent model experiments (Figure 1, Supplementary material; O'Donnell et al, MS in preparation; Tsigaridis and Menon, unpublished). Both studies used a similar SOA scheme but differed greatly in the amount of global BVOC emissions, especially monoterpenes. Results from one modelling study (ECHAM) indicate that the $-0.3 W m^{-2}$ cooling was nearly cancelled by warming (Figure 1) from a reduction of the cloud albedo effect, arising from increased particle sizes due to the condensation of SOA, particularly in anthropogenically perturbed areas (O'Donnell et al, MS in preparation). Applying different BVOC emission estimates, especially for monoterpenes⁴⁸ (Supplementary material) resulted in greatly reduced direct effect ($-0.08 W m^{-2}$), and an all-sky radiative effect of $+0.17 W m^{-2}$. For present day, the SOA radiative effect is responsible for approximately 9% of the total OA forcing, while for the preindustrial period its contribution is somewhat larger (Tsigaridis and Menon, unpublished).

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 and to what degree direct CO_2 inhibition of isoprene production³² affects production of mono- or sesquiterpenes, and future SOA burden and radiative forcing. Monoterpene metabolic production is located in the chloroplast and near-similar to that of isoprene, recent studies indicate reduced production and needle tissue levels in Douglas fir grown at elevated CO_2 ⁵¹. However, more work is required to determine whether there is a general CO_2 -induced decoupling between monoterpene production or its release from storage pools⁴⁸. Using biogenic emissions calculated by a process-based model that includes the effects of temperature, photosynthetically active radiation, and CO_2 ⁴⁸, global aerosol model simulations indicate a decrease in the

global annual mean biogenic SOA burden from 0.46 Tg under end of 20th century conditions to 0.30 Tg in a warmer atmosphere under end of 21st century conditions calculated for SRES scenario A2 (O'Donnell et al, MS in preparation). These results reflect not only conservative biogenic emissions but also the favouring of gas over particle phase partitioning in a warmer atmosphere.

Does it all go up in smoke?

Fire is a natural, regularly recurring episodic event across all vegetated biomes, most prominent in savannas and Mediterranean or boreal forest ecosystems⁵². 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 CO₂ and CH₄⁵². The main atmospheric impacts of fire are related to emissions of particles, ozone, methane and other volatile hydrocarbons, either directly or as their precursors⁵². Global biomass burning emissions represents around one quarter of the global NO_x and CO emissions^{26,53}. Simulations of radiative forcing have demonstrated a substantial sensitivity in response to variation in overall pyrogenic emissions and relative changes in warming (BC) and cooling (OA) aerosol^{52,54,55} and although net effects may be small (Figure 1) a change in burn conditions could easily shift fire-related forcing in either direction.

Palaeo-evidence for the role of BGC in the regulation of atmospheric composition and climate

Ice core records show that atmospheric composition of greenhouse gases and mineral dust aerosol has tracked both rapid and gradual changes in climate at least over the past 800,000 years⁵⁶⁻⁵⁸, with the phasing of changes in individual greenhouse gases modulated by differences in the temporal and spatial patterning of (ocean and terrestrial) biospheric feedbacks (Figure 2; see e.g.⁵⁹). Past vegetation changes, as documented in pollen and plant-macrofossil records, were substantial on glacial-interglacial timescales⁶⁰ and refs. therein). Vegetation types adapted to low CO₂, drought and cool temperatures were widespread at the last glacial maximum (LGM) while orbitally-induced changes in insolation during the early to mid-Holocene resulted in high-latitude warming that led to northward expansion of boreal and temperate forests, and enhanced monsoons that led to northward expansion of Sahelian vegetation into the Sahara⁶¹. These large-scale changes in turn led to changes in dust emission⁶² and fire regimes⁶³. Pollen and charcoal data have also demonstrated extremely rapid responses to climate variability like Dansgaard-Oeschger events or the onset/termination of the Younger Dryas⁶⁴. The palaeo-record thus supports not only a number of terrestrial biogeophysical feedbacks⁶⁵⁻⁶⁷ but suggests that there may have been a substantial impact of BGC processes on atmospheric composition and climate.

Peatland productivity and decomposition are highly sensitive to temperature and precipitation changes, and hence their C sequestration varies on decadal to millennial timescales. Peatland initiation in the northern high latitudes began ca 15ka during the deglaciation and almost half of the modern peatland initiation took place before 8ka⁶⁸. It has been estimated that peatland growth prior to 8ka sequestered ca. 100 PgC, contributing to the observed drawdown of CO₂ and peak in atmospheric CH₄ in the early Holocene⁶⁹. Increased peat accumulation rates are registered during the warmer conditions of early to mid-Holocene in the northern high latitudes⁷⁰, whereas substantially reduced accumulation occurred during the cold intervals of the Younger Dryas and the Little Ice Age (e.g.⁷¹). The most extensive lateral expansion of high-latitude peatlands occurred only after 5 ka⁷², coinciding with the late Holocene increase in CH₄ shown by ice core records. The climate impact of changes in peat accumulation is uncertain because of the competing influences of CO₂-C sequestration and CH₄ emission and the timescales over which these operate. Frohking et al.⁷³ have suggested that the initial impact on of northern peatland growth is a net

warming that peaks after about 50 years after peatland initiation but remains positive for the next several hundred to thousand years, depending on the rate of C 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, C uptake and CH₄ emissions.

Analyses of interhemispheric gradients of ice core CH₄ concentrations, and carbon isotope composition, have been interpreted as indicating that changes in wetland emissions drove glacial-interglacial CH₄ changes^{74,75}. Simulations using simple formulations of wetland extent and emissions have been unable to reduce wetland sources sufficiently to produce the observed changes in atmospheric CH₄ concentrations^{76,77}. Alternatively, since the hydroxyl radical is the chief atmospheric sink for both CH₄ and BVOC, it has been suggested that strongly reduced LGM BVOC emissions in response to cooler temperatures and less productive vegetation led to increased OH levels, decreasing methane lifetime and concentration⁷⁶. However, BVOC emissions under low atmospheric CO₂ levels may have been more conservative⁷⁸ than assumed in this simulation.

Global compilations of charcoal in continuously-deposited lake or bog sediments show less fire during glacial than during interglacial intervals⁶³, 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 CO₂ on plant productivity. On centennial to millennial timescales, fire activity tracks climate changes closely⁷⁹, including a general decline in biomass burning towards the Little Ice Age – supporting Ferretti et al.'s⁸⁰ interpretation of the ice-core record of changes in atmospheric ¹³CH₄ as a reflection of changes in global biomass burning⁷⁹. Fire regimes show a large response to both rapid warming and rapid cooling^{81,82}; during the last glacial, for example, fire regimes tracked Dansgaard-Oeschger warming events with lags on the order of a few decades (Figure 2), lag-response to the cooling associated with Heinrich Stadials was slightly longer⁸¹.

Present-day biosphere-atmosphere-climate interactions, can we detect the signal from the noise?

Present-day observations are consistent with both the palaeo-record and model-based estimates of the importance of biosphere-atmosphere-climate interactions. Remotely sensed vegetation greening⁸³, and ground-based evidence for vegetation changes in northern latitudes that have experienced amplified warming, demonstrate the responsiveness of the terrestrial biota to trends in climate, with corresponding changes in biogeochemical cycling⁸⁴. The interannual variation of the atmospheric CO₂ growth rate is dominated by terrestrial carbon cycle-climate-fire interactions^{83,85,86}. Inversions of atmospheric concentration measurements indicate wetland and, to a lesser extent, fire emissions to dominate the interannual variability in methane growth rate during the last few decades⁸⁷. Interannual variation in atmospheric CO₂ and its isotopic ratios are related to variability in climate-fire-emissions from boreal or tropical regions, e.g. in response to precipitation patterns (see^{52,88} and references therein) 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 high BVOCs were thought to dampen the atmospheric oxidation capacity³³. Substantial observational evidence thus 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 changes will play a dominant role in future BGC

The focus on the interactions between climate, atmospheric composition, and BGC, should not detract attention from anthropogenic land use and land cover change as major influences on surface-atmosphere

exchange and feedbacks. There are large uncertainties in the estimates of radiative forcing resulting from changes in surface albedo and energy balance associated with historic land cover change^{90,91}. Deforestation, particularly by fire, releases a large amount of carbon and reactive substances into the atmosphere which are not returned into the terrestrial system when forests are replaced by agricultural systems⁵². The BVOC emission spectra of forests and agricultural systems are very different⁹², 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 and NO₂ emissions also differ between forest and crops, with the escape of NO_x into the atmosphere being much larger in low canopies²⁶. Moreover, fertilisation and irrigation of agricultural systems provide an overriding cause for altered carbon-nitrogen cycling and reactive N trace gas emissions⁹. Existing experimental observations and simulations are insufficient to provide a quantitative synthesis of the impacts of land-cover changes, and it is clear that field and model experiments addressing this must be a future research priority.

What's in a global number?

There is growing evidence that it is not acceptable to ignore the impact of BGC feedbacks in climate change studies: assuming additive behaviour for simplicity, the combined forcing from carbon, nitrogen and atmospheric gas-chemistry BGC feedback estimates in response to climate warming ranges from ca. 0.6 to 3 Wm⁻² (Figure 1). SOA formation is the only BGC-related mechanism which could act as a counterforce, but direct and indirect aerosol effects may nearly cancel each other, at least for present-day simulations. Given the limited number of quantitative experiments available, these numbers can only be a very rough guide. It is important though to recognise the multitude of terrestrial BGC-feedback processes that operate in the climate/chemistry system since most provide a positive forcing in response to fundamental biological principles of metabolic stimulation by temperature.

Global metrics such as radiative forcing can provide only a very limited characterisation of BGC feedbacks in the climate system. The path from a change in emission to a change in radiative forcing, and henceforward to a change in climate is convoluted, particularly for the heterogeneously mixed atmospherically reactive substances. Each of the steps produces a geographically varied pattern and when overlain, these patterns do not match⁹³. Reaction pathways of the same trace gas move along very different directions depending on whether they take place in polluted or clean-air, warm or cool, moist or dry environments, and this is further complicated by long-range transport of emission reaction products. A seemingly small change in the global burden of a given substance more often than not hides substantial regional variability that can cause positive as well as negative changes in local radiative forcing^{32,38,47}. Thus while we have summarised the impact of BGC feedbacks in terms of global forcing, by analogy to the global numbers generated by IPCC, we recognise the need for development of a more refined metric⁹⁴.

The modelling of BGC feedbacks is in its infancy: limited process understanding and simplified representations of processes mean that it has been both necessary and wise to focus on individual BGC feedbacks. However, the intricate and multidirectional coupling of terrestrial biogeochemical cycles of inert greenhouse gases with reactive atmospheric chemistry means none of the feedbacks summarised here will act in isolation. By "cutting corners" in our chemistry/climate projections we ignore non-linearities and thus possible thresholds in the system. Improved understanding of BGC interactions should be a priority for the scientific community and will aid development and implementation of atmosphere and ecosystem management, particularly in light of post-Kyoto negotiations⁹⁵ and the development of climate and air pollution control strategies.

Author contributions: This review paper was conceived at a workshop coordinated by MK and SS, and all authors participated in the subsequent discussions and planning. SM, KT, SZ, HF, DD and GS

contributed model simulations, AA, SPH, PJB, SS and SZ were responsible for analyses and figures, AA and SPH were responsible for the first draft of the paper. All authors provided input to the drafting and final version of the manuscript.

Acknowledgements

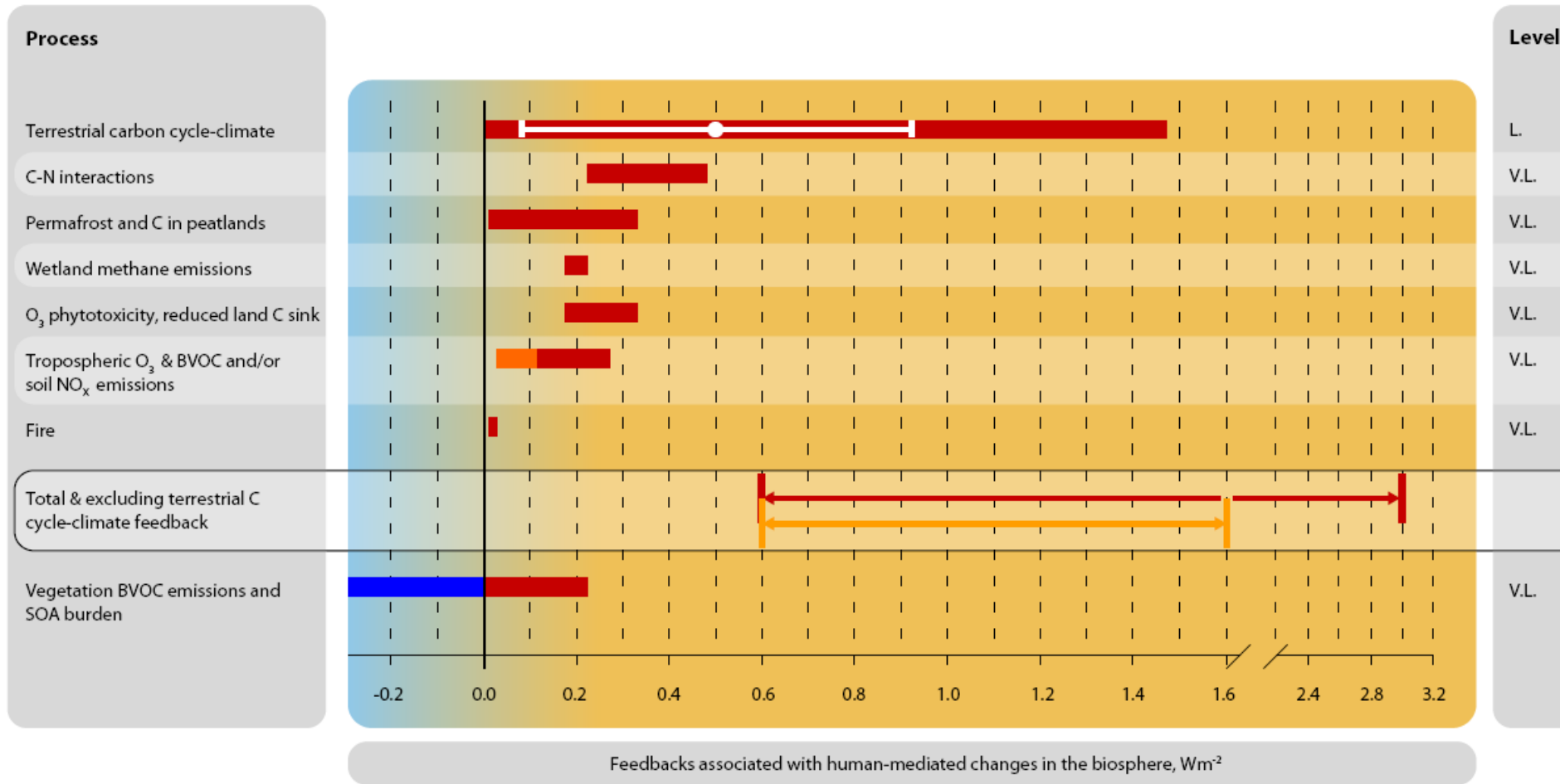
The authors acknowledge discussions at the Science Workshop on Past, Present and Future Climate Change in Helsinki, November 2008, and at the iLEAPS Science conference in Melbourne. The Helsinki workshop and the manuscript preparation was supported by the Finnish Cultural Foundation. AA acknowledges support from the Academy of Finland, iLEAPS, and the Swedish research councils VR and Formas. SPH acknowledges funding from the EU-supported project GREENCYCLES. KT 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. SM acknowledges funding support from the NASA MAP program and the DOE ASR program.

Figure 1: Estimated radiative forcing from terrestrial biogeochemistry feedbacks in response to climate change or changes in atmospheric composition

The bars cover the range between minimum and maximum estimated change in forcing from the pre-industrial period to the end of the 21st century, except for SOA effects which are calculated for present-day only (blue: direct effect; red: indirect effect). The year taken as pre-industrial starting point differed between studies (see Supplementary material). For the methane feedback, baseline year was 1990. For interactions of BVOC and NO_x on tropospheric O₃, the colour shade from left to right indicate pre-industrial-to-present, present-day, and present-to-future experiments. The bar for terrestrial carbon cycle-climate feedback additionally shows the average and standard deviation from a model intercomparison (white); for the other processes shown, data were too limited to calculate averages. The drawn arrows indicate the range of total radiative forcing associated with biogeochemical feedbacks (red bar), and excluding the carbon cycle-climate feedback (orange).

For data sources and further details see Supporting Online Material. The estimates in the Figure are based on a number of assumptions that had to be made and clearly point to the need for more interdisciplinary studies. Confidence in these estimates is at best low (L.), but in most cases very low (V.L).

Figure 1



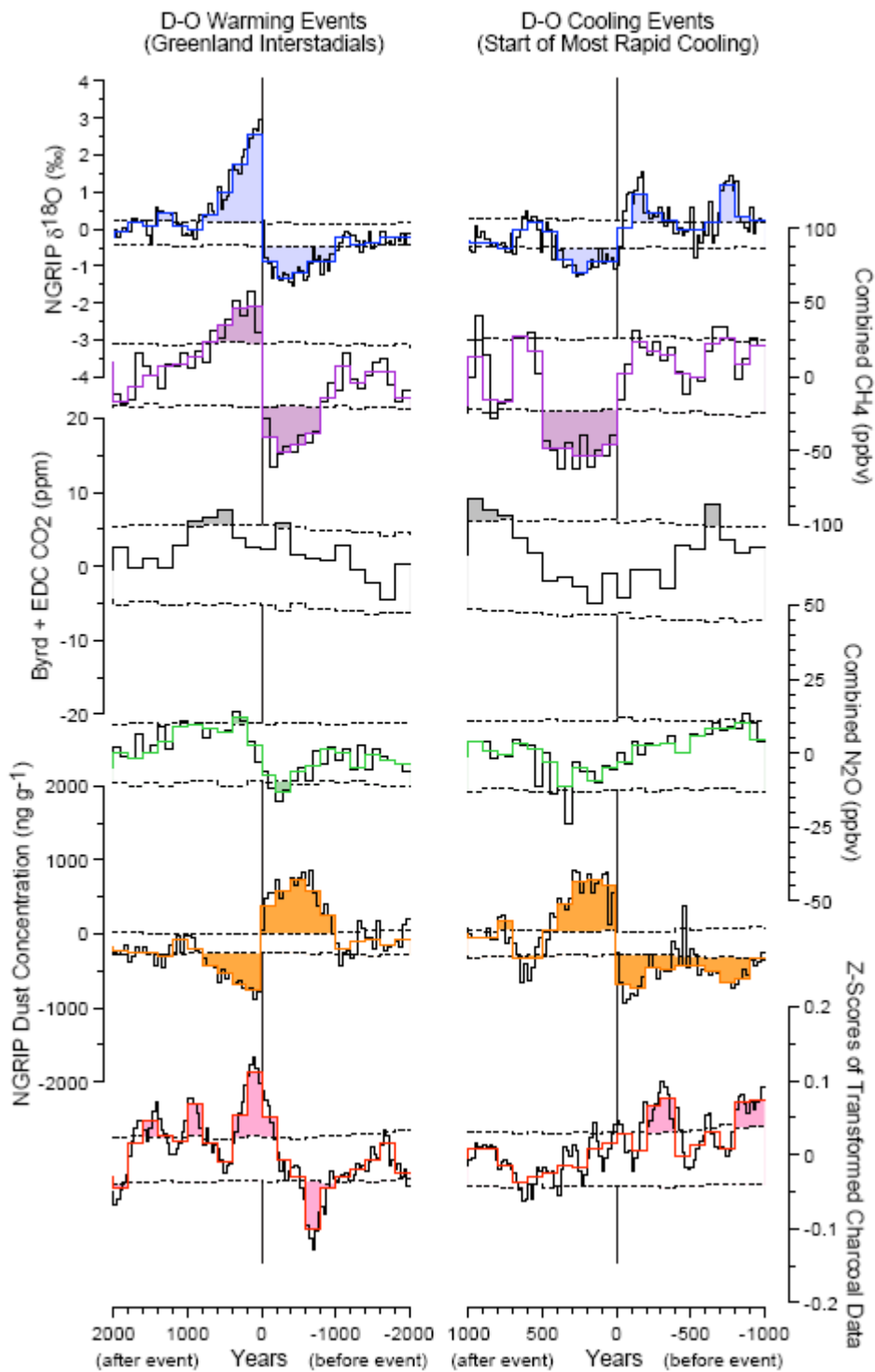
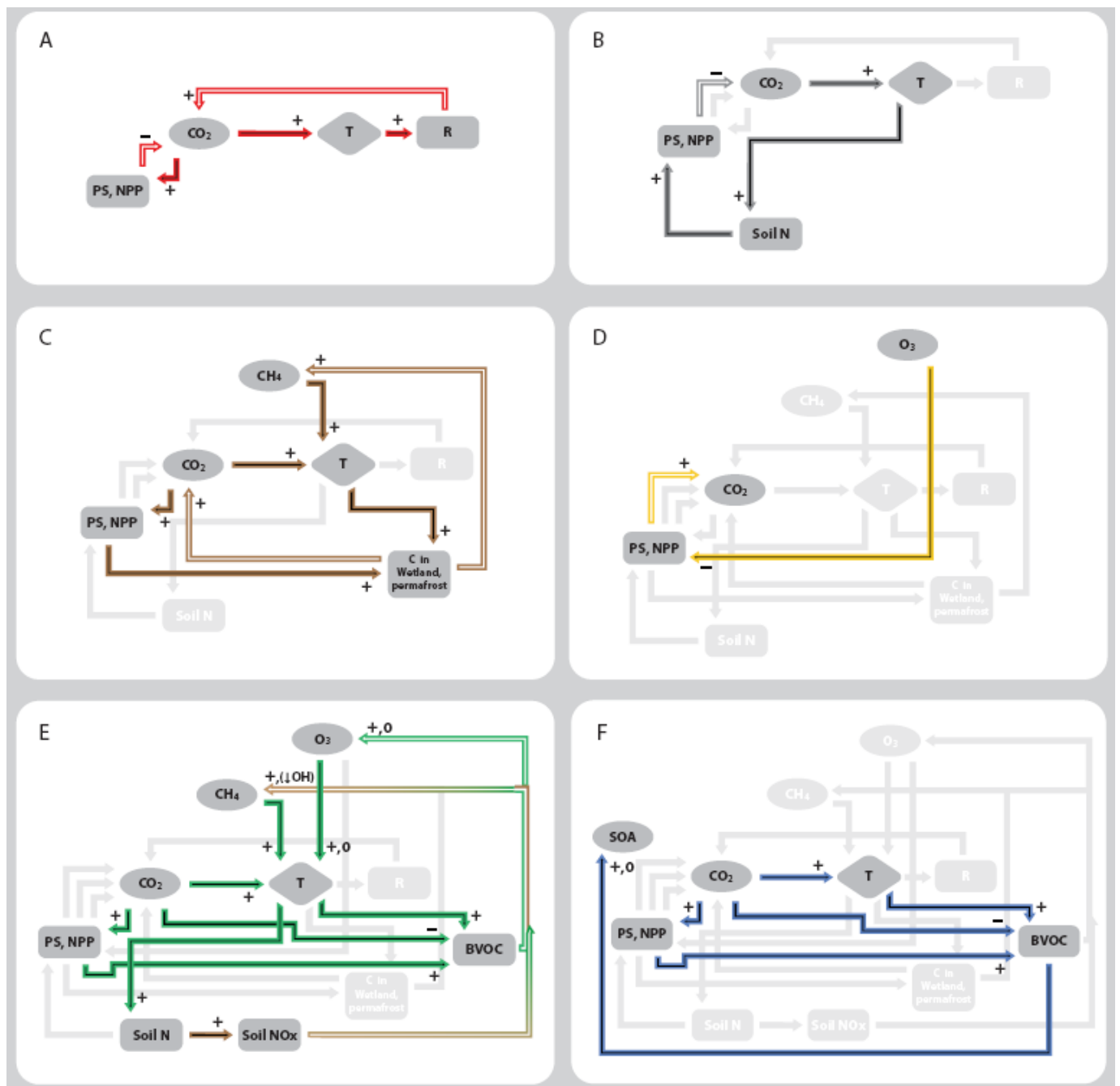


Figure 2 Superposed epoch analysis of ice-core and biomass-burning records over the interval 80 ka to 10 ka. This analysis shows the consistent response of a time series to the repeated occurrence of the abrupt warming and abrupt events that define the Dansgaard-Oeschger (D-O) cycles during the last glacial period. The Greenland oxygen-isotope record (A), an index of regional temperature, shows the characteristic saw-tooth pattern of an individual D-O cycle, and all of the other records show distinctive responses associated with the occurrence of abrupt warming or cooling. The responses of all time series to the events are non-linear (linear responses would appear as inverse mirror images). The individual

responses to abrupt warming can be categorized as abrupt and rapid with no appreciable lag, such as those for methane, dust, and biomass burning, all influenced by the hydrological status of the land surface, the nature of the vegetation cover, and vegetation productivity, and progressive such as those for CO₂ (C) and N₂O (D), with more interconnected biogeochemical cycles. The responses to rapid cooling are similarly mixed, with those for CH₄ and dust again abrupt and rapid with no lag, and those for CO₂ and N₂O more gradual. There is an initial rapid response of biomass burning to cooling, followed by a gradual recovery. For data sources and further details see Supporting Online Material



BOX: Main feedback loops, linking terrestrial biogeochemical cycles, biosphere-atmosphere exchange, atmospheric composition and climate (here: temperature change). The main forcings are illustrated with full, feedbacks by open arrows. Only feedbacks to atmospheric composition are shown here: feedbacks on temperature or precipitation exist but are not shown for clarity. Atmospheric drivers are indicated by ovals, climate (i.e. temperature) responses by diamonds. Biogeochemical processes responding to atmospheric driver that can feed back on atmospheric composition (and thus climate) are shown by squares.

(I) Climate warming in response to anthropogenic emissions (for simplicity only CO₂ is indicated as forcing agent) alters biogeochemical cycling (BGC) of a compound that directly acts as radiative forcing agent (e.g., a well-mixed greenhouse gas).

Panel A: Terrestrial carbon cycle-climate feedback. Increasing atmospheric CO₂ concentration warms climate. Increased temperatures stimulate ecosystem respiration which further enhances CO₂ concentration (and temperature.) Enhanced CO₂ can also stimulate carbon assimilation; CO₂ uptake by higher net primary productivity (NPP) reduces atmospheric CO₂ growth rate. The net between stimulated NPP and heterotrophic respiration determines whether the net land carbon sink declines⁵.

Panel B: In nitrogen limited ecosystems, the CO₂ fertilisation response of NPP may be small. However, warmer temperatures could stimulate soil mineralization making nitrogen available to plants^{7,10,11}. Simulations to-date indicate that the effect of additionally available N may be small compared with the overall reduced CO₂-fertilisation response in models that include C-N interactions^{10,11}.

Panel C: Elevated temperature and enhanced NPP stimulate CO₂ and methane emissions from global wetlands and northern permafrost soils. Both lead to a positive climate feedback either by enhanced atmospheric methane or enhanced CO₂ concentration^{14,21,22,96}.

(II) Feedbacks due to anthropogenic changes in atmospheric composition that affects BGC of a radiatively active compound.

Panel D: Increased tropospheric O₃ burden from anthropogenic pollution reduces plant photosynthesis due to its phytotoxic effects. This reduces the global terrestrial net carbon sink, resulting in accelerating CO₂ concentration in the atmosphere, and positive warming feedback²⁵.

(III) Feedbacks due to climate change altering BGC of substances that in turn affect atmospheric composition of other, climatically active compounds.

Panel E: Emissions of biogenic volatile organic compounds (BVOC) from vegetation are stimulated by warmer temperature and enhanced NPP. In anthropogenically polluted, high NO_x environment this fosters tropospheric ozone production^{28-31,97}. Stimulation of natural NO_x emissions from soil by warmer temperatures will also need to be taken into account for O₃ formation. Enhanced O₃ levels have positive feedback on climate because of its greenhouse gas characteristics, and also via the indirect feedback plotted in (D). A further positive climate feedback of enhanced BVOC emissions is via increased methane lifetime and hence concentration, since BVOC and methane have the same atmospheric sink in their reaction with the hydroxyl radical, OH^{31,98}.

At least in case of isoprene, the most abundant BVOC, increasing atmospheric CO₂ concentration leads to a decline in leaf production. The competing effects of temperature and NPP stimulation vs. CO₂ inhibition on BVOC-O₃ interactions are not yet resolved; one study indicated on global scale little effect on overall burden (indicated as "0" along the arrows in panel (E), but with large geographic variation³².

Panel F: BVOC emissions are the chief precursors for biogenic secondary aerosol (SOA) growth, and determine the SOA background even in the anthropogenic atmosphere^{49,50,99}. SOA affect climate mainly via scattering and absorption of light (direct aerosol effect, a negative temperature feedback)⁴⁶, and by enhancing cloud albedo⁴⁷. SOA are also efficient cloud condensation nuclei, with larger number concentration possibly leading to less precipitative clouds³⁹. Possible offsets between stimulation of BVOC emissions by warming and inhibition by increasing CO₂ represents a chief source of uncertainty for the magnitude of the proposed feedback loops. Faster chemistry due to elevated O₃ levels also increases SOA (not shown).

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