Quantifying the Influence of the Terrestrial Biosphere on Glacial-interglacial Climate Dynamics

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Abstract. The terrestrial biosphere is thought to be a key component in the climatic variability seen in the paleo record. It has a direct impact on surface temperature through changes in surface albedo and evapotranspiration (so called biogeophysical effects) and in addition, has an important indirect effect through changes in vegetation and soil carbon storage (biogeochemical effects) and hence modulates the concentrations of greenhouse gases in the atmosphere. The biogeochemical and biogeophysi-

5   cal effects generally have opposite signs meaning that the terrestrial biosphere could potentially have played only a very minor role in the dynamics of the glacial-interglacial cycles of the late Quaternary. Here we use a fully-coupled dynamic atmosphere-ocean-vegetation General Circulation Model (GCM) to generate a set of 62 simulations spanning the last 120 ka. The analysis of these simulations elucidates the relative importance of the biogeophysical versus biogeochemical terrestrial biosphere interactions with climate. We find that the biogeophysical effects of vegetation account for up to an additional -0.84°C global

10   mean cooling, with regional cooling as large as -5°C, but with considerable variability across the glacial-interglacial cycle. By comparison, while opposite in sign, our model estimates of the biogeochemical impacts are substantially smaller in magnitude. Offline simulations show a maximum of +0.33°C warming due an increase of 25 ppm above our (pre-industrial) baseline atmospheric CO_2 mixing ratio. In contrast to shorter (century) time-scale projections of future terrestrial biosphere response where direct and indirect responses may at times, cancel out, we find that the biogeophysical effects consistently and strongly

15   dominate the biogeochemical effect over the inter-glacial cycle. In addition, depending on the assumptions about soil carbon under ice-sheets and sea level rise, we find a range in terrestrial carbon storage change from a reduction in LGM carbon storage of -440 PgC, to a gain of +37 PgC. We suggest that prevailing uncertainties allow for only a small net transfer of carbon between terrestrial biosphere and ocean atmosphere implying that explaining the observed CO_2 ice core record could be rather simpler than previously thought.

20   # 1   Introduction

Terrestrial vegetation interacts with the climate in complex ways, both responding to and impacting climate conditions and hence creating an important feedback in the Earth system (e.g., Claussen, 2009; Davies-Barnard et al., 2014b; Harrison and Prentice, 2003; Jahn et al., 2005; Matthews et al., 2003; Pongratz et al., 2010). The influence of the terrestrial biosphere on

climate occurs in two distinct ways. Firstly, there are a number of biogeophysical mechanisms such as changes in albedo or evapotranspiration that provide a direct physical influence on surface climate via changes in net solar radiation transfer, infrared loss, roughness length, latent heat loss, and less directly, via changes in moisture exchange and hence transport. Climate feedbacks driven by these changes in terrestrial vegetation have been hypothesised to be partially responsible for some

5   of the major past climate states (e.g., Bradshaw et al., 2015; Claussen et al., 2006; Crucifix and Loutre, 2002; de Noblet et al., 1996; Zhou et al., 2012), with many studies particularly focussing on the biogeophysical effects at the last glacial maximum (LGM) (e.g., Hopcroft and Valdes, 2014; Jahn et al., 2005; Kageyama et al., 2012; O'ishi and Abe-Ouchi, 2013). The second way in which the terrestrial biosphere can influence climate is via variations in the carbon stored in vegetation and soil. This is a crucial component for understanding changes in the carbon cycle through the last glacial-interglacial cycle (Montenegro

10   et al., 2006) and numerous attempts have been made to estimate the total carbon storage using a range of methods, such as inferences from marine and terrestrial carbon isotopes (e.g., Shackleton et al., 1977; Bird et al., 1994), databases of pollen (e.g., Adams and Faure, 1998; Crowley, 1995), and simple and complex modelling (e.g., Prentice et al., 1993; Kaplan et al., 2002; Köhler and Fischer, 2004; Brovkin et al., 2012; O'ishi and Abe-Ouchi, 2013). The resulting range of carbon storage change estimates is from a few hundred to about 1000 PgC (Ciais et al., 2012). One could add to this changes in the weathering of

15   soil minerals and hence CO_2 uptake from the atmosphere, and nutrient, particularly phosphate, supply to the ocean and hence changes in in the ocean productivity. For simplicity, we will not address these further here (except to include a basic silicate weathering feedback in our model analysis of the impacts of terrestrial carbon storage change).

Simulations of future vegetation changes show that the biogeochemical aspect can globally be around the same magnitude as the biogeophysical effects (e.g., Davies-Barnard et al., 2014b) meaning that there is uncertainty even in the sign of the

20   net feedback with climate change. Both biogeophysical and biogeochemical effects likely also play an important role in past climate change and potentially the same fundamental uncertainty in the sign of the climate feedback might arise. However, model simulations have generally focussed on either the biogeophysical impacts of vegetation changes (e.g., Bradshaw et al., 2015; Claussen et al., 2006; Jahn et al., 2005; O'ishi and Abe-Ouchi, 2013; Shellito and Sloan, 2006) or biogeochemical impacts (e.g., Kaplan et al., 2002; Ciais et al., 2012) and the question of the overall feedback on climate rarely addressed,

25   although Claussen (2009) argues that the net effect at the LGM is dominated by the biogeophysical effects.

One of the few examples where both have been combined and the net effects of vegetation on past climate estimated over long time periods, is Brovkin et al. (2012). They used an earth system model of intermediate complexity (EMIC) to suggest that the net effect of vegetation is to decrease global temperatures during the last glacial-interglacial cycle. But the model used is relatively coarse in resolution (10° in latitude and 51° in longitude) and reduced in physical process complexity. This may be

30   important because of the local and spatially heterogeneous nature of biogeophysical effects and depending on the location of the forest, the biogeophysical and biogeochemical effects of forest change can be very different (Bonan, 2008). For this reason, fully coupled General Circulation Models (GCM) are commonly used in quantifying future climate changes to vegetated land surface (Brovkin et al., 2013a, b; Davies-Barnard et al., 2015; Davin and de Noblet-Ducoudré, 2010). The importance of considering both biogeophysical and carbon cycle impacts together at finer scale when assessing the climate impacts of

35   vegetation is illustrated by work quantifying the climate impacts of forest changes. Studies have found that deforestation

would cause local high latitude cooling (Betts, 2000), global warming (Davin and de Noblet-Ducoudré, 2010), or even slight global cooling (Davies-Barnard et al., 2014b, a). These outcomes are not predictable from looking at the biogeophysics or terrestrial biogeochemistry alone at coarse resolutions.

Here we present the first model analysis using a fully-coupled dynamic atmosphere-ocean-vegetation GCM over the last

5 120 ka that quantifies the net effect of vegetation on climate. (A prior study – Singarayer and Valdes (2010) – did not have dynamic vegetation and hence could not directly evaluate the biogeophysical effects.) We separate the biogeophysical and biogeochemical effects of vegetation to understand the overall climate effect of vegetation over the last glacial cycle. We show that over the whole period the biogeophysical is the dominant effect, and that the biogeochemical impacts may have a lower possible range than typically estimated. We also highlight how the temporal scale affects the net impact of terrestrial biosphere

10 changes.

2 Methods

We use the GCM HadCM3 to run a series of simulations with and without dynamic vegetation to provide the biogeophysical changes and the terrestrial vegetation carbon changes. To look at the climate impact of those vegetation carbon changes, we then use the GCM terrestrial carbon changes as an input to the EMIC cGENIE to calculate the resulting change in atmospheric

15 CO_2 and global temperature.

2.1 Climate Model Description

The GCM used in the simulations in this study is the UK Met Office Hadley Centre's HadCM3-M2.1 and HadCM3-M2.1D (Valdes et al., 2017). Though not from the latest generation of climate models, HadCM3 remains an extensively used model for many research applications around the world due to its computational efficiency, which means that long integrations and

20 many ensemble members can be run.

HadCM3 is a three dimensional, fully coupled, fully dynamic ocean, non-flux adjusted global climate model (Collins et al., 2001). The atmosphere component, HadAM3, has a cartesian grid with a horizontal resolution of 2.5° x 3.75°, 19 vertical levels and a time step of 30 minutes (Pope et al., 2000). The ocean and sea-ice component has the same horizontal resolution as the atmosphere, with 20 vertical ocean levels.

25 The land surface scheme used for the atmosphere component of HadCM3 is the Met Office Surface Exchange Scheme, MOSES2.1 (Gregory et al., 1994; Cox et al., 1999). MOSES can also use an additional vegetation and terrestrial carbon model, TRIFFID (Top-down Representation of Interactive Foliage and Flora Including Dynamics) (Cox, 2001; Cox et al., 1998). TRIFFID predicts the vegetation based on plant functional types using a competitive, hierarchical model. TRIFFID has two modes, equilibrium mode, which quickly brings the vegetation cover into equilibrium by running fifty years of TRIFFID for

30 each five years of the climate model run, and dynamic, which runs TRIFFID every ten days. TRIFFID and MOSES have nine land surface types, five of which are vegetation: broadleaf trees, needle leaf trees, shrubs, C_3 grasses and C_4 grasses. These are known as plant functional types (PFTs) and have different leaf area index limits and other phenological differences in the

model. Soil moisture in the model is represented on 4 layers of thicknesses (measured from the top) of 0.1, 0.25, 0.65 and 2.5 m (Essery et al., 2001).

2.1.1 GCM Simulations and Experimental Methodology

The simulations used here are revised versions of those described in Singarayer and Valdes (2010), who used HadCM3 version HadCM3-M1, which has an older surface scheme (MOSES1) than the MOSES2.1 used here, and no dynamic vegetation. Two sets of 62 simulations were performed, covering the time period 0 - 120 ka BP:

- The first set of 62 simulations used TRIFFID to predict vegetation changes. Each individual simulation was initialised from the previous MOSES1 simulations (which were run for 600 years) and were then run for a further 300 years with 'equilibrium' TRIFFID and a final 300 years with fully dynamic vegetation. This set will be referred to as the Dynamic set.

- A second set of simulations uses static vegetation based on the pre-industrial simulation of the dynamic set (extrapolated to new land areas using a simple nearest neighbour algorithm) but is otherwise identical to the Dynamic set. These will be referred to as the Static set.

(The differences between Dynamic and Static allows us to evaluate the biogeophysical and biogeochemical responses of terrestrial carbon cycle change.)

Both sets of simulations are forced with changes in orbit, greenhouse gases (CO_2, CH_4, and N_2O) and ice sheets, as in Singarayer and Valdes (2010) except that we use a revised ice sheets extent and elevation, as discussed in Singarayer et al. (2011). Note that this model does not have a closed carbon cycle. There is no representation of carbon in the ocean and terrestrial carbon changes do not feedback to the atmosphere (since the greenhouse gas forcings are prescribed). However, the carbon that would have returned to the atmosphere can be inferred from the change in the carbon stores in the soil and vegetation, allowing the biogeochemical impact of vegetation to be understood, as well as the biogeophysical. From the pre-industrial to 22 ka, simulations are run for every 1000 years. From 22 ka to 80 ka, simulations are run for every 2000 years. For 80 ka to 120 ka, simulations are run for every 4000 years. (See grey points in Figure 2 for a representation of the temporal distribution of the 62 simulations.) Reported final climatologies are based on the last 30 years of each simulation.

2.2 cGENIE/EMIC Carbon Cycle Simulations

For future climate changes studies, the response of atmospheric CO_2 concentrations (and hence climate) to changes in terrestrial carbon storage can be calculated using the Transient Response to Cumulative Emissions (TRCE) approach (Gillett et al., 2013), which demonstrated proportionality between carbon emissions and temperature rise (Goodwin et al., 2015). However, this is only valid for relatively rapid changes. On the longer timer scales of glacial-interglacial change, we need to take into account the full changes in ocean carbon chemistry and including the interactions of ocean and atmosphere with the solid Earth (e.g. weathering). To do this, we employ the 'cGENIE' Earth system Model of Intermediate Complexity (EMIC). This model

can calculate the impacts on atmospheric CO_2 over the glacial cycle and hence the contribution of biogeochemical changes to glacial-interglacial climate change. cGENIE is based around a fast energy-balance based atmosphere model coupled to a 3D ocean circulation component and dynamic-thermodynamic sea-ice (Edwards and Marsh, 2005), plus representations of ocean-atmosphere (Ridgwell and Hargreaves, 2007), ocean-sediment (Ridgwell et al., 2007), and atmosphere-land (terrestrial

5 weathering) (Colbourn et al., 2013) carbon cycling. The non-seasonally forced ocean has 8-levels and the configuration and selection of model parameterizations and parameter values is identical to that described in Lord et al. (2016).

 The evolution of terrestrial carbon storage simulated by HadCM3 from 120 ka to pre-industrial was used to derive a forcing for cGENIE. In this, we created a continuous time-series of the carbon flux from the terrestrial biosphere by calculating the difference in carbon storage calculated at the end of each HadCM3 time-slice and then assuming a linear interpolation

10 between these points. For the 'Full' simulations, cGENIE was then run for 120 ka using this forcing and starting from a fully spun-up state of global carbon cycling including an initial balance between the rate of silicate rock weathering and volcanic CO_2 outgassing (see Lord et al. (2016) for details). For the 'Carbonate' simulations, the model was run with just carbonate compensation only, as per Ridgwell and Hargreaves (2007); For the 'Closed' simulations, there was no weathering or sediment response, and hence is just ocean-atmosphere repartitioning. For the 'AirOcean' simulations, the carbon remains

15 in the atmosphere. Both the resulting history of atmospheric CO_2 as well as annual mean global surface air temperature were extracted and calculated as anomalies relative to the late Holocene (pre-industrial).

3 Results

3.1 Results: Vegetation Dynamics

The changes in climate over time affects the vegetation cover in the Dynamic simulations (shown in Figure 1). In general,

20 cooling leads to an equator-ward shift in vegetation, as the high latitudes become covered in ice or otherwise inhospitable for significant quantities of vegetation. There is also exposure of continental shelves, providing potential for vegetation increases. At the last glacial maximum (LGM) at 21 ka, we can see needleleaf trees and shrubs giving way to very low productivity grasses in the high latitudes. However, because of the small number of PFTs (five) in this model, the shifts may be underestimated, as each PFT represents a wide range of vegetation types. The shrubs and trees do not have a significant presence in northern

25 Europe after 100 ka until the climate ameliorates into the Holocene. It is the vegetation changes shown in Figure 1, and their associated soil changes, that drive the climate feedbacks and other changes described hereafter.

 Hoogakker et al. (2016) have shown that HadCM3 broadly reproduces the known changes in vegetation across the glacial-interglacial cycle. They did this by running an offline vegetation model, BIOME4, driven by the climate anomalies from HadCM3. Our results from TRIFFID are consistent with the relative changes although, since TRIFFID uses the actual climate

30 from the models, the vegetation can have biases (e.g. Australia has a tendency to be too wet in HadCM3 in the present day and hence the coupled model has too much vegetation in this region). However, during glacial times there is a decrease in biomass, consistent with Hoogakker et al. (2016).
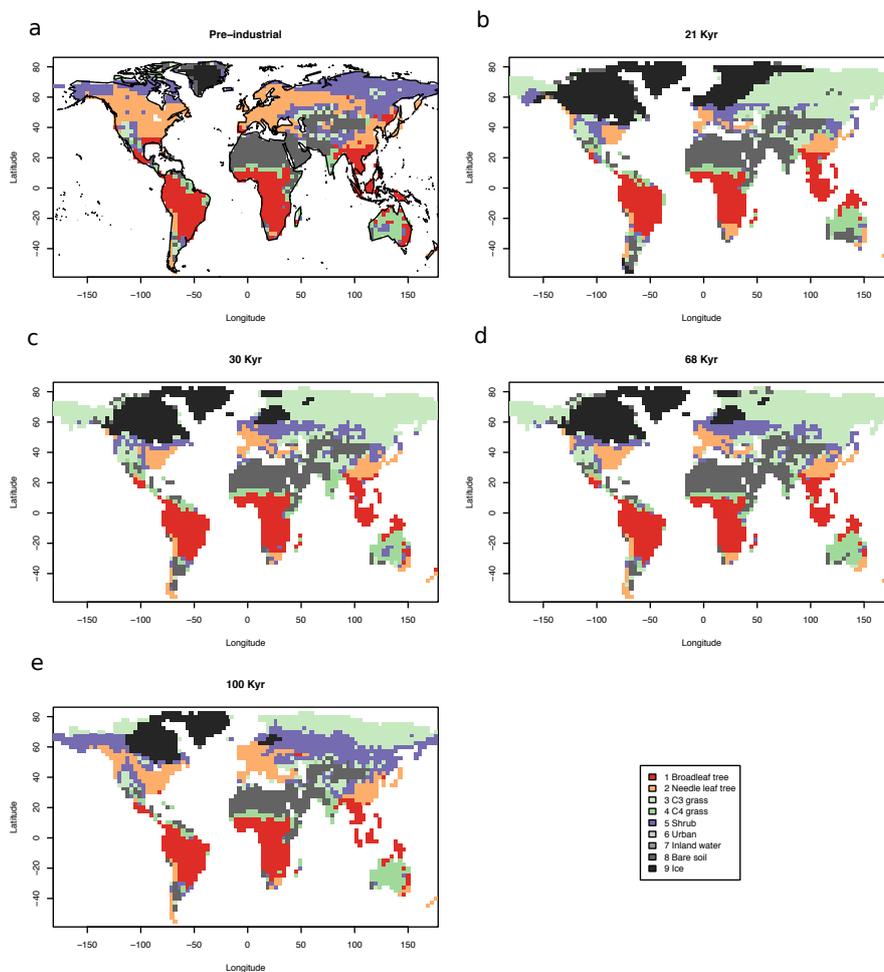
Figure 1. Dominant plant functional type (PFT) for some time periods of interest in the 120 ka covered by the simulations. a) Pre-Industrial, b) 21 ka, c) 30 ka d) 68 ka, e) 100 ka. Note that the dominant PFT is calculated as the land cover with the highest proportion of cover, compared to the other land surface types, and does not necessarily indicate the highest or a significant amount of net primary productivity (NPP).

3.2 Results: Biogeophysical Feedbacks

The biogeophysical impacts of vegetation are calculated by subtracting the Dynamic simulations from the corresponding Static simulations. We find that vegetation is acting as a positive feedback to the climate, enhancing the cooling (Figure 2a). Broadly, the Static and Dynamic simulations both agree with an approximation of global temperature over the whole period (the EPICA dataset halved). The Static set generally do better in 10 ka to 70 ka, whereas the Dynamic set are closer to the EPICA data in the period 70 to 110 ka. The biogeophysical differences between the Static and Dynamic sets alter global, annual mean surface temperature by as much as -0.91°C (see Figure 2b). Regionally this temperature cooling is up to 5°C (Figure 3).
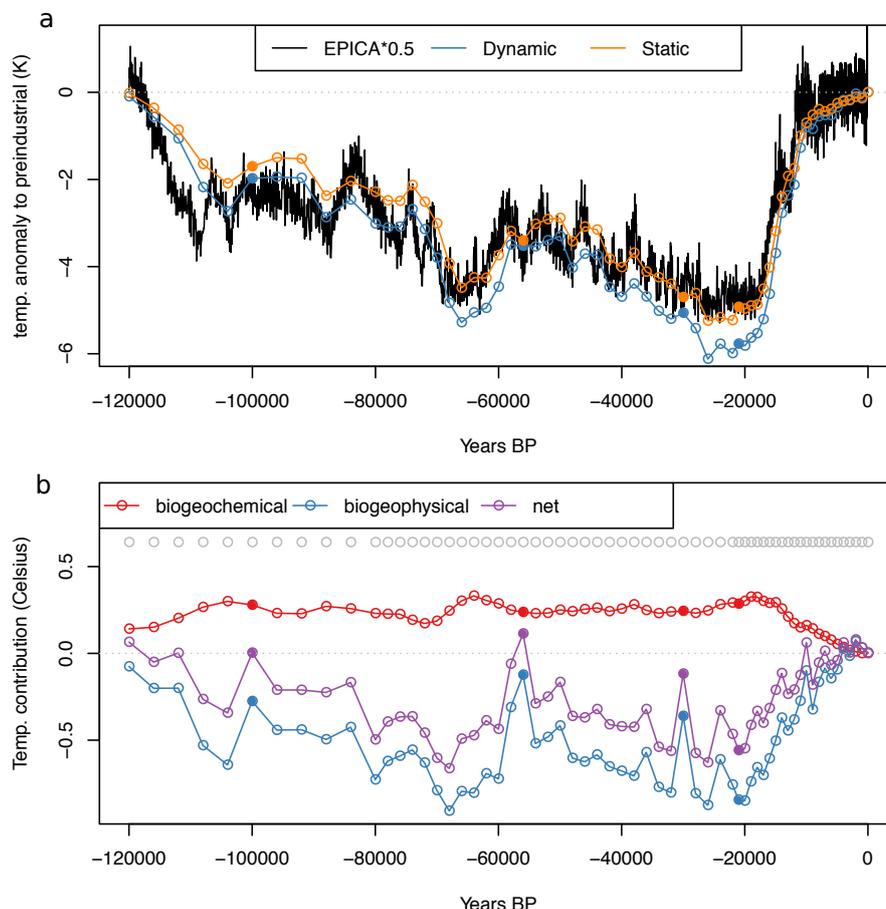
Figure 2. a) Global mean annual temperature (Celsius at 1.5m) for: Static vegetation simulation (orange); Dynamic vegetation (blue); and the EPICA core inferred temperature data (black), halved. Time periods of particular interest are highlighted as filled points: 21, 30, 56, 68 and 100 ka. b) Temperature anomaly over time of Dynamic - Static simulations for: biogeochemical temperature effects of the vegetation change, calculated with GENIE, averaged to the same temporal resolution as the HadCM3 simulations (red); biogeophysical temperature effects of vegetation change (blue); the net (biogeophysical and biogeochemical) effect of vegetation on temperature (purple). Grey points show the time points of the HadCM3 simulations.

These temperature differences are mainly driven by reductions of tree cover and its replacement with bare soil or grasses, which is a result of the vegetation dynamics in the model (see Figure 1 and Figure 4). Trees have a lower albedo, and when they are replaced by higher albedo grasses, there is a cooling effect. The change in tree fraction between the Static and Dynamic sets is a good predictor of the temperature changes ($r^2 = 0.79$ using a linear model of the global temperature and tree anomalies).

5   This is exacerbated by the presence of snow cover as the snow covered visible and near infrared albedo of grasses, shrubs and bare soil is higher than that of trees (Essery et al., 2001). Therefore when trees are replaced by grasses where there is snow cover for part of the year, there is a larger change in albedo than where there is no snow cover. Thus the albedo changes can
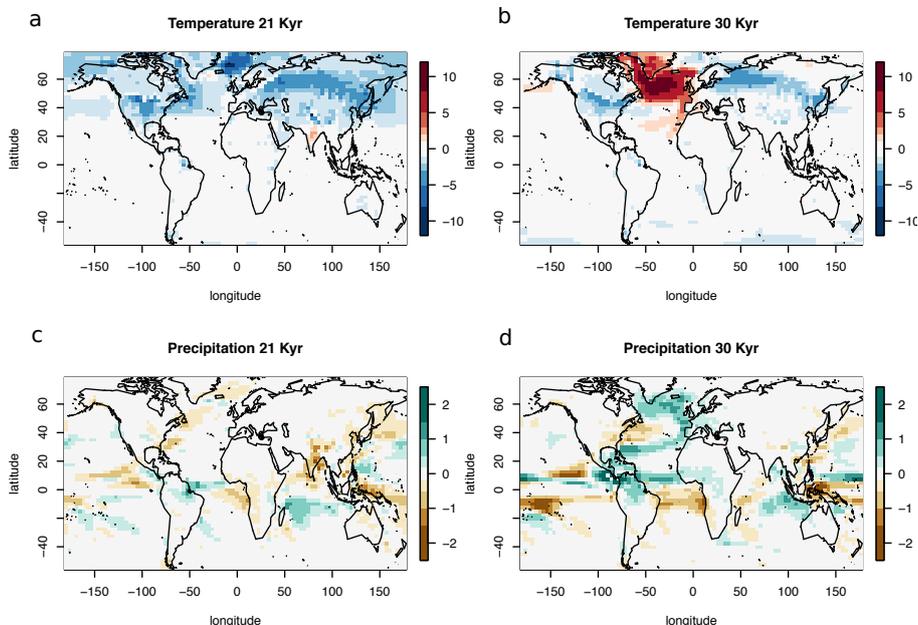
Figure 3. Anomaly of (a and b) temperature at 1.5m (Celsius); and (c and d) precipitation (mm day^{-1}); between the Dynamic Vegetation simulation and the equivalent Static Vegetation simulation. For (a and c) 21 ka and (b and d) 30 ka. The pattern of reduced surface albedo at 30 ka is similar to the pattern at 56 ka and 100 ka.

be seen mainly where a change between trees and grasses occurs in an area with snow cover (see Figure 1 and Figure 5). The exact contribution of the snow as opposed to the no-snow albedo is difficult to disentangle, but the influence of this effect is well established (Betts, 2000).

The land surface albedo changes caused by the vegetation have an even stronger correlation with these biogeophysical
5 temperature changes ($r^2 = 0.86$). However, we can see that although the forcing is land based (the dynamic vegetation), significant changes occur in the ocean (see Figure 4 and Figure 3) that drive the resulting temperature changes. Ocean only surface albedo anomaly as a determinant of global temperature anomaly has an r^2 of 0.95 - lower only than the r^2 of the global (land and ocean) surface albedo of 0.96. By comparison, the r^2 of the latent heat anomaly as a predictor of temperature anomaly is lower for land, ocean, and global than surface albedo (0.70, 0.93 and 0.91 respectively).

10 Although the biogeophysical changes cause cooling, there are some minima of biogeophysical temperature change seen at 30 ka, 56 ka and 100 ka (Figure 2, filled symbols). These minima have an oceanic source and are caused by vegetation interacting with thermohaline circulation changes. For instance, in some of the Static Vegetation simulations there is a temporary weakening of the Atlantic Meridional Overturning Circulation (AMOC). In the Dynamic Vegetation simulations, the weakening of the AMOC only occurs for 32 ka. This results in the 30 ka simulation being relatively warmer in the dynamic simulation and
15 hence the cooling effect of vegetation is temporarily reduced (see Figure 2a). This 'threshold' type behaviour of the AMOC
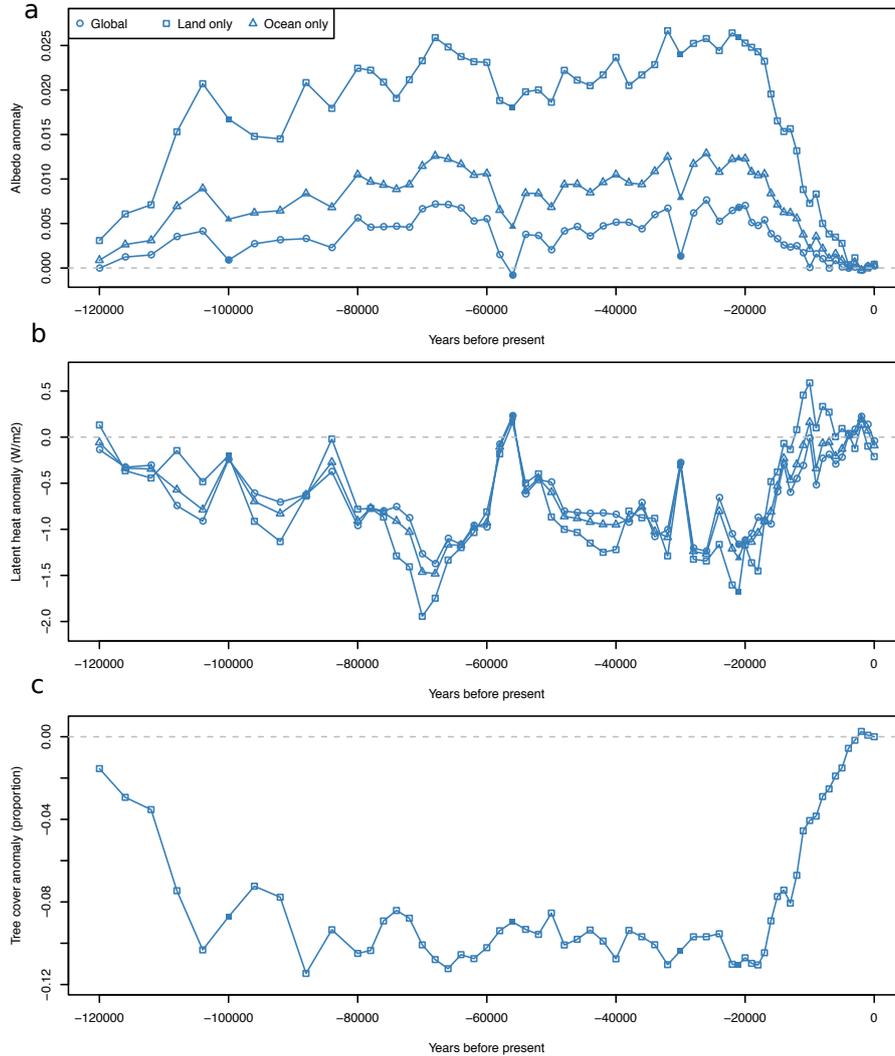
Figure 4. Anomaly over time of Dynamic - Static simulations for: a) surface albedo b) latent heat (W/m^2) and c) tree cover (proportion of land area).

is unlikely to be robust because AMOC changes can be highly non-linear and variable across models, and the biogeophysical effects are also spatially heterogeneous and hence these minima in biogeophysical effects should be treated with some caution.

The regional patterns of cooling also temporarily affect the precipitation regime (see Figure 3). This appears to be related to the AMOC weakening. There are some suggestions of similar relationships between the increases in precipitation and the terrestrial changes to previous studies (Gedney and Valdes, 2000; Singarayer et al., 2009). Similar to the temperature changes, it unclear how model-specific these changes are.
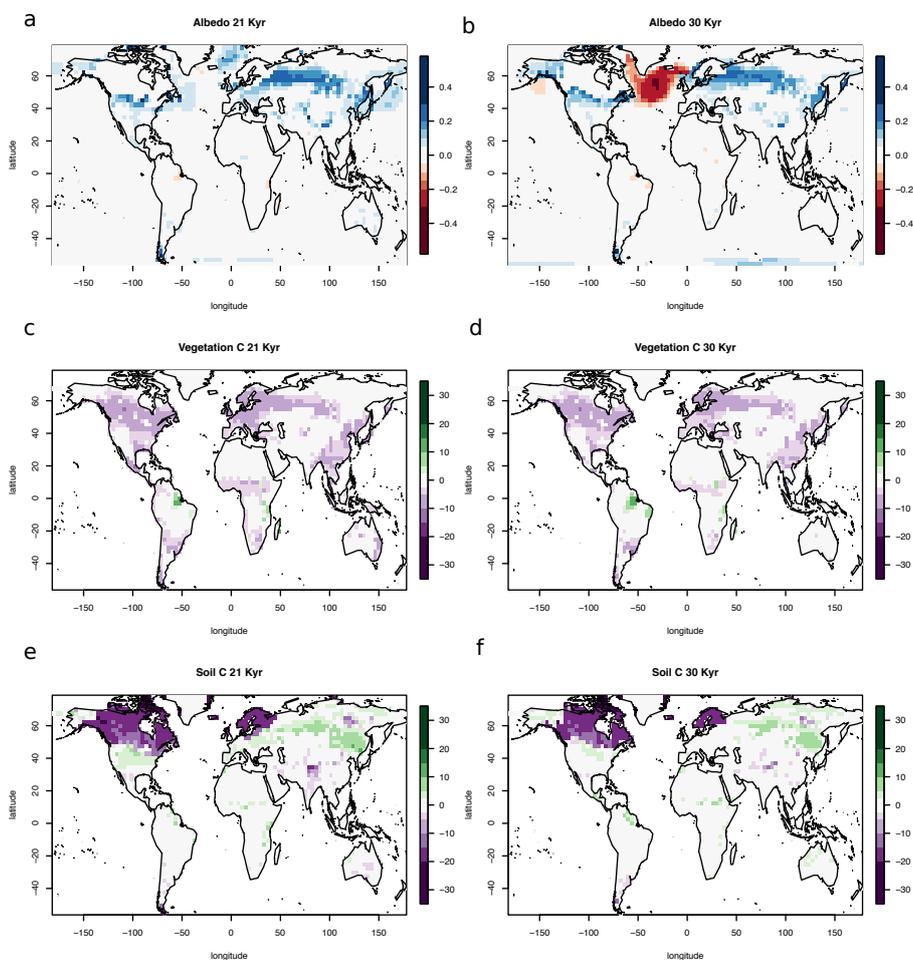
Figure 5. Anomaly of: a) and b), surface albedo (unitless); c) and d), vegetation carbon (kg C m^{-2}); and e) and f), soil carbon (kg C m^{-2}), between the Dynamic Vegetation simulation and the equivalent Static Vegetation simulation. For 21 ka (a, c, and e) and 30 ka (b, d, and f). The pattern of reduced surface albedo at 30 ka is similar to the pattern at 56 ka and 100 ka.

3.3 Results: Biogeochemistry

We now calculate the total change in terrestrial carbon stores changes in the HadCM3 simulations. We consider scenarios of terrestrial carbon change with combinations of including or excluding uncertain aspects of the carbon cycle, specifically depending on the fate of soil carbon under ice and the changes related to the expansion of land. Zeng (2003) suggested that the

5 soil and vegetation carbon formed during the warm last interglacial could simply get covered by ice and is stored there, rather than being released into the rest of the system as is typically assumed in past estimates. Similarly, the amount of carbon stored on newly emerged land is also uncertain as it depends on both the area of emergent land and the surface properties. Therefore

Table 1. Terrestrial carbon changes from pre-industrial to LGM. For storage values at the LGM, see Appendix Table 1.

Name	Carbon storage Scenarios	Soil C change (PgC)	Vegetation C change (PgC)	Total C change (PgC)
GCI_ELE	Carbon under ice sheets released to atmosphere. No carbon on expanded land area.	-145	-295	-440
GCE_ELE	Carbon under ice sheets stored under the ice. No carbon on expanded land area.	+77	-222	-146
GCE_ELI	Carbon under ice sheets stored under the ice. Modelled carbon storage on new land included.	+211	-173	+37
GCI_ELI	Carbon under ice sheets released to atmosphere. Modelled carbon storage on new land included.	-11	-246	-257

we calculate the changes in soil and vegetation carbon from these various sources. In Table 1 we focus on the changes between pre-industrial and LGM, which corresponds to the largest overall change through the glacial-interglacial cycle.

In the model, approximately 220 PgC of soil carbon and 70 PgC of vegetation carbon is associated with areas covered with ice at the LGM (see Figure 8). Similarly, about 130PgC of soil carbon and 50PgC of vegetation carbon is associated with new land. The resulting range of total carbon storage is large, from a loss of 440 PgC at the LGM (no carbon stored under new ice sheets with all being released to ocean-atmosphere, and no build-up of carbon on new land surface) to a possible small increase of carbon (if carbon is stored under the new ice sheets and there is no carbon storage on new land).

In reality, glacial systems are known to export carbon in a highly labile form (Lawson et al., 2014), erode soil and bedrock creating major landscape changes, and release large amounts of methane when they retreat (Wadham et al., 2012). Although the conversion of this terrestrial carbon to atmospheric carbon may be through riverine or oceanic systems, it seems likely it would return to the atmosphere within the time periods we consider. We therefore use this largest scenario as a conservative option for our main analysis.

The other major change to soil carbon in the model is newly exposed land, which is revealed when the water in the ice-sheets causes lower sea levels (see Figures 1 and 5). For the new land we use a nearest-neighbour interpolation of basic soil properties (e.g. water holding capacity etc.) and the model is run for sufficient length of time for the soil and vegetation carbon to reach equilibrium.

This estimate of carbon on expanded lands also has uncertainties. We have reasonable confidence in the sea level estimates and consequent change in land area, but it is much more uncertain the state of the land and whether carbon could accumulate
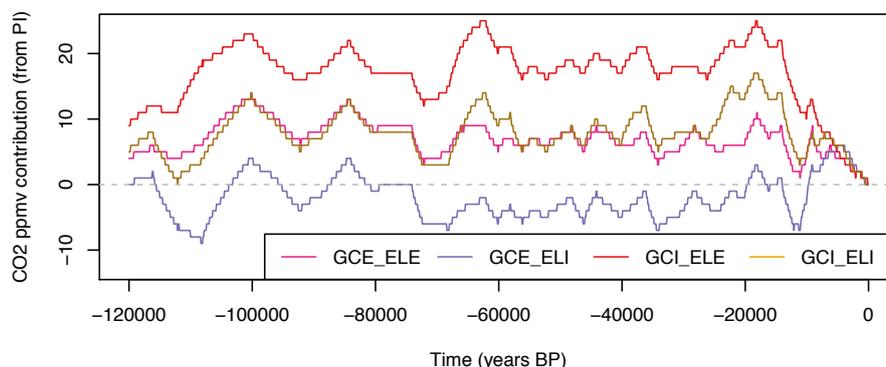
Figure 6. Contribution of terrestrial biosphere carbon emissions to atmospheric CO_2. Run with the cGENIE 'Full' configuration and normalised to pre-industrial CO_2 levels. The four scenarios are as detailed in Table 1.

on it. For instance, in our simulations the East Siberia ice-sheet is absent (see Figure 1), whereas many other ice-sheet reconstructions include it (e.g., Niessen et al., 2013). The area of the ice sheet alone accounts for an average of 56 PgC soil carbon in these simulations when it is absent. But soil carbon takes a long time to accumulate, especially with low NPP and vegetation carbon storage averages just 0.5 PgC over all the expanded lands.

5   If exposed land carbon was included and glacial land soil carbon excluded, the terrestrial carbon is a gain from PI to LGM of +37 PgC (see Table 1). However, as discussed above, we would argue that excluding glacial land soil carbon change is probably unreasonable. Most previous studies have also assumed that all carbon under ice is removed. If we include the loss of carbon, then the range in total amount of terrestrial carbon lost in this model between pre-industrial (PI) and the LGM at 21 ka is -440 to -257 PgC.

10   The change in terrestrial carbon found in our simulations contributes to atmospheric carbon dioxide change. Using the cGENIE model to approximate the carbon uptake by the ocean we therefore calculate the atmospheric carbon dioxide change (see methods and Figure 6).

Selecting the largest change in carbon storage (-440 PgC at the LGM, including glacial soil carbon changes and excluding expanded lands) the results suggest a peak contribution compared to pre-industrial CO_2 of 25 ppm CO_2 (Figure 6). In all

15   scenarios except GCE_ELI, the terrestrial carbon contribution to atmospheric CO_2 acts as a negative feedback to the climate, dampening the effect of other climate forcings, including the net contribution of the terrestrial biosphere (Figure 2b).

Within cGENIE, the change in atmospheric CO_2 produces a warming at the LGM of 0.29°C (equivalent to a climate sensitivity of around 2 Wm^{-2} °C^{-1}, see Figure 2b). This is much smaller than the biogeophysical contribution of -0.84°C. It is also much less variable. For most of the glacial period, from 100 ka to 20 ka, the implied biogeochemical warming is around 0.26

20   °C (Figure 2b). This results in the dominance of the biogeophysical impacts over biogeochemical feedbacks.

However, with different earth system processes included, the biogeochemical effects vary substantially (see Figure 7). In the simulations discussed above, silicate and carbonate weathering are both included and this results in the lowest temperature
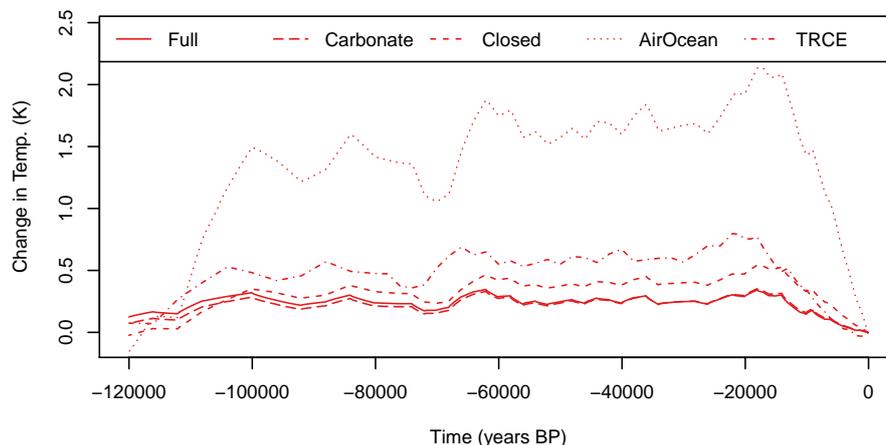
Figure 7. Temperature changes resulting from the same terrestrial carbon emissions scenario (GLI_ELE) with different model set-up for cGENIE and for the TRCE of HadCM3. cGENIE simulations were: 'Full' with silicate weathering feedback and just carbonate compensation, as Lord et al. (2016); 'Carbonate' with just carbonate compensation only, as Ridgwell and Hargreaves (2007); 'Closed' with no weathering or sediment response, and hence is just ocean-atmosphere repartitioning; 'AirOcean' where the carbon remains in the atmosphere. 'TRCE' is the simple calculation of the TRCE of HadCM3 (taken from Matthews et al. (2009)) for the same carbon inputs into the atmosphere as used for the cGENIE simulations.

change from the same carbon emissions. The temperature contribution at the LGM increases (from Full, 0.29°C); as the silicate weathering is excluded (Carbonate, 0.30°C); all weathering is excluded (Closed, 0.47°C); a decadal to millennial scale carbon uptake is used (TRCE, 0.86°C); and if all carbon remains in the atmosphere (AirOcean, 1.92°C). Note that the TRCE as shown above includes the terrestrial biosphere as a sink, so will slightly overestimate how much carbon will be removed from the

5 atmosphere when the source is the natural vegetation. Comparing these values to the biogeophysical terrestrial effect in Figure 2b, we can see that the shorter the timescale, the more likely biogeochemical terrestrial processes will dominate as it weakens over time. On longer timescales the biogeophysics dominates because the scale of the effect doesn't diminish over time relative to the control.

4   Discussion

10 The biogeophysical results found here broadly concur with comparable model studies of past vegetation biogeophysics. Claussen et al. (2006) found the biogeophysical contribution of vegetation to LGM cooling of around 1°C in the northern hemisphere, whereas Jahn et al. (2005) found around -0.6°C, and up to 2°C locally. Our result of -0.84°C is in the middle of the other LGM studies.

The dominance of the biogeophysical effects found here is contrary to the results found for short time scale problems, which
15 find that biogeochemistry tends to be comparable in magnitude to biogeophysical effects (e.g., Davies-Barnard et al., 2014b; Pongratz et al., 2010). This is because the centennial simulations have a stronger biogeochemical effect since the transient

response to cumulative emissions is stronger than the equilibrium response. In climate simulations up to around a century long, more carbon tends to remain in the atmosphere. This makes a strong warming effect that is approximately linearly related to the amount of greenhouse gas emissions (Matthews et al., 2009; Gillett et al., 2013). The transient response to cumulative emissions (TRCE) accounts for the uptake of atmospheric carbon by the ocean and terrestrial biosphere, but only on short

5   timescales. The uptake of atmospheric carbon by the ocean requires hundreds or thousands of years, and is slower when the increase of carbon into the system is small and staggered (Lord et al., 2016). However, the simulations we use are on a millennial timescale, allowing much of the carbon to be taken up by the ocean (Lord et al., 2016).

For the biogeochemical effects of the terrestrial biosphere, previous estimates of carbon stocks on exposed continental shelves based on models are between -112 to -323 PgC at the LGM (Montenegro et al., 2006). The comparable number in this

10   simulation is -183 PgC, which is on the lower end of the wide range of other models. However, it has good agreement with the vegetation reconstruction (not model) values by Montenegro et al. (2006) of -182 to -220 PgC. The LGM terrestrial carbon change here is -440 to +37 PgC, including a zero contribution of terrestrial carbon. This is smaller than the values of -900 to -400 PgC range reviewed by Kohfeld and Ridgwell (2009). More recent studies also conclude an inventory change are also somewhat larger than our estimate range, such as -500 PgC (Brovkin et al., 2012), -597 PgC (O'ishi and Abe-Ouchi, 2013) and

15   -330 PgC (Ciais et al., 2012).

However, the exact size of the terrestrial carbon emissions is uncertain. Other carbon stores not accounted for here are potentially important, for example methane during sea level rises or permafrost melting. Our model does not have a process based permafrost component, and particularly the carbon stored in deep permafrost soils in Northern peatlands. Saito et al. (2013) show that, based on the temperature changes, there is a substantial expansion of permafrost area during glacial times

20   but cannot estimate any changes in carbon storage. Zimov et al. (2006, 2009) have argued that permafrost storage could be a major source of carbon through the deglaciation, and Ciais et al. (2012) argue that there was a large extra pool of inert carbon at the LGM. Similarly, Köhler et al. (2014) have argued that large amounts of carbon were locked into permafrost which were then released rapidly at the Bolling-Allerod.

Research has also suggested that waterlogging and flooding as sea level rises during the Holocene could cause rapid anaer-

25   obic decomposition of vegetation, causing methane emissions (Ridgwell et al., 2012). This could account for emissions of as much as 25 PgC for 10 meters sea level rise (ibid). Since our simulations do not account for methane or this effect of inundation, it is likely it there is a slight underestimation of equivalent CO_2 effect of the carbon emissions (as methane is a stronger greenhouse gas than carbon dioxide).

5   Conclusions

30   Using a fully coupled atmosphere-ocean-vegetation model with static and dynamic vegetation, we find that over the last 120 ka the net effect of vegetation feedbacks on global, annual mean 1.5m air temperature is a cooling, which can be as much as -0.66°C (Figure 2b). For the vast majority of the last glacial-interglacial cycle, cooling associated with biogeophysical feedbacks dominate over the biogeochemical warming associated with reduced terrestrial carbon storage. The biogeophysical

cooling effect is mainly due to the role that vegetation plays in changing surface albedo and particularly related to snow cover and the taiga/tundra transition (Gallimore and Kutzbach, 1996; de Noblet et al., 1996) and we believe is relatively robust. The biogeochemical contribution to atmospheric carbon dioxide is small (~20ppmv) and hence the temperature contribution is small (on average 0.26°C with a maximum of 0.33°C).There are significant uncertainties in this calculation which would

5   further diminish the net temperature impact of the terrestrial biosphere by cancelling out the biogeophysical impact. In this analysis, the only time periods where the effects are comparable are at times when additional mechanisms operate, such as changes in ocean circulation, but these mechanisms may be model specific.

The key uncertainties in this study originate in the biogeochemistry, especially the soil carbon build-up in newly exposed land, the fate of soil carbon in glacial systems, and the amount of carbon in permafrost (not calculated in this study). Further

10   research is needed to fully understand the functioning of these systems and how they can be best incorporated into climate models. In addition, the technique we use for inferring the biogeochemical effects of terrestrial carbon changes has limitations and is potentially model dependent. However, the smaller estimate of terrestrial carbon emissions may make the low LGM atmospheric carbon dioxide somewhat easier to reconcile (Montenegro et al., 2006).

Our work confirms previous results using EMICs Brovkin et al. (2012) that found the net terrestrial biosphere effect to

15   be primarily biogeophysical and that the terrestrial carbon contribution to atmospheric carbon is comparatively small. Our findings also represent a clear illustration of the net climatic effect of vegetation is highly dependent on the timescale, with the biogeophysical response dominating in the longer term in contrast to century-scale future changes.

6   Code availability

The model code is currently available to view at http://cms.ncas.ac.uk/code_browsers/UM4.5/UMbrowser/index.html.

20 ## 7   Data availability

The GCM simulation data is available at http://www.paleo.bris.ac.uk/ummodel/scripts/papers/Davies-Barnard_et_al_2017. html.

Appendix A

Author contributions. PJV and JSS ran the climate model simulations. TDB did the analysis and wrote the manuscript. AR ran the cGENIE

25 model simulations. All the authors provided comments and contributed to the manuscript.

Competing interests. The authors have no competing interests to declare.
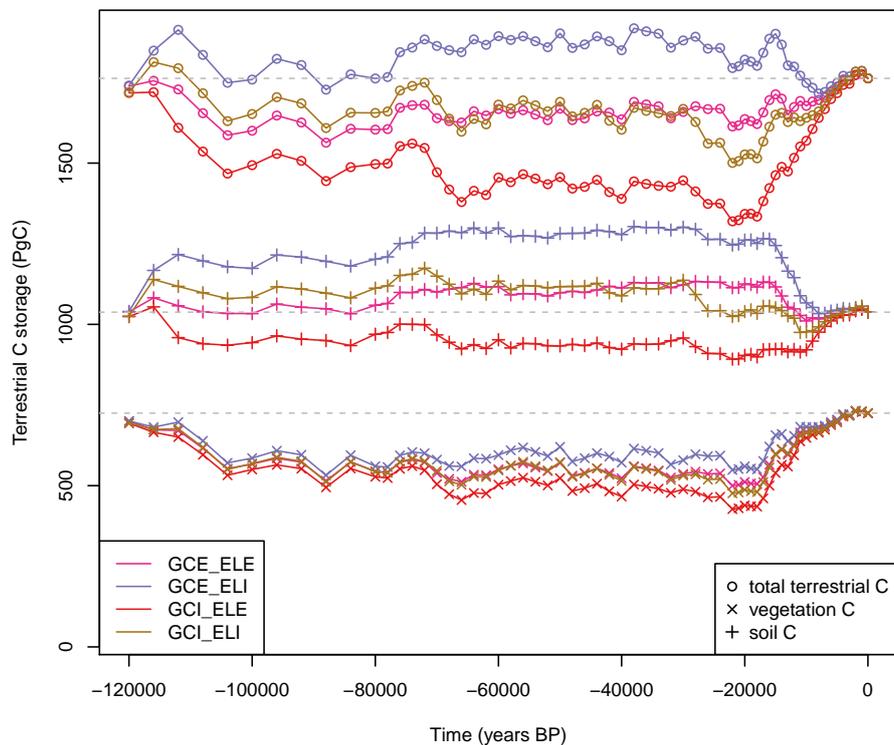
Figure 8. Absolute changes of carbon stores (vegetation and soil) over time. The four scenarios are as detailed in Table 1.

Table A1. Terrestrial carbon storage at the LGM.

Carbon storage Scenarios	Soil C (PgC)	Vegetation C (PgC)	Total C (PgC)
GCI_ELE Carbon under ice sheets released to atmosphere. No carbon on expanded land area.	893	430	1323
GCE_ELE Carbon under ice sheets remains stored under the ice. No carbon on expanded land area.	1114	502	1617
GCE_ELI Carbon under ice sheets remains stored under the ice. Modelled carbon storage on new land included.	1249	552	1800
GCI_ELI Carbon under ice sheets released to atmosphere. Modelled carbon storage on new land included.	1027	479	1506

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