Dear Professor Fischer,

We would like to thank the reviewers for their thoughtful and critical assessment of our paper. Below we address the reviewers' comments (in red) with details of how changes will be implemented in the paper and point to point replies to the reviewers comments. Please find the marked-up manuscript after the response to reviewers comments.

Best wishes,

Babette, Joy and Robin

Reply: Editor

Dear authors
Your manuscript has been reviewed by two referees, who stress the value of your paper, however, both raise important questions and ask for major changes in the manuscript before publication in CP.
I would like to encourage you to send a carefully revised manuscript (including a point-to-point reply to the reviews) to CP. In view of the criticisms by the referees, this manuscript will most likely be subject to a second round of reviews.
From an editor's point of view, there are two points in the reviews that I would like to stress:

- please, discuss more thoroughly the implication of your results on ocean (and atmospheric) d13C (see referee #1)

We have widened our discussion of the implications of our results on ocean and atmospheric d13C. For more details please see our point to point responses to reviewer 1 comments below.

- please, provide a more thorough discussion of the comparison between data and models and clarify any differences or overlaps to the paper by Sanchez-Goni & Harrison, QSR 2010 (see referee #2).

Differences and overlaps with Harrison and Sanchez-Goni (2010):
The Quaternary Science Review Special issue, edited by Harrison and Sanchez-Goni specifically deals with vegetation changes under millennial scale climate change, the Dansgaard-Oeschger cycles. Indeed, many records discussed in papers in Fletcher et al. (2010, Europe), Jiminez-Moreno et al. (2010, North America), Hessler et al. (2010, Africa and South America), and Takahara et al. (2010, for east Asian islands) also feature in our paper. In their papers Fletcher et al. (2010), Hessler et al. (2010), Takahara et al. (2010) do not apply the uniform biomization applied here; subtle subdivision were applied by all apart from Gonzales-Moreno et al. (2010). However, subtle subdivisions appear in Fletcher et al. (2010, eurothermic conifers, and xerophytic steppe), Jimenez-Moreno et al. (2010, southeastern pine forest). Furthermore, in their biomization approach Fletcher et al. (2010) used one biomization scheme for all European records, whereas in our approach we started off with the three original schemes for Southern Europe, the Alps and northeastern Europe, and merged the individual biomes into megabiomes. Similarly we first applied two regional biomization schemes for northern and northeastern America and for western America, and then merged those biomes into megabiomes. In our revised manuscript we now refer to the sites which are discussed in the QSR special issue. More details can be found in the response to reviewer 2. We have also provided details there about the author contributions to the paper.

Please note that while the QSR special issue specifically deals with vegetation changes over DO cycles, we purposely avoided those! Our biomizations were carried out at a 1ka resolution (this does not resolve millennial scale variability), and the time intervals discussed in the main text were choosen not to represent intervals of millennial scale change.

I am not in favor of supplementary text in a CP publication, so please include this discussion as separate chapter in the manuscript.

Additional changes:
1. Trevor Hill should have the same affiliation as Gemma Finch (at the moment this is wrong)
2. Granoszewski's address is wrong, as is the reference to Horoski Duze (T.2)
Added: Granoszewski W.: Late Pleistocene vegetation history and climatic changes at Horoszki Duże, Eastern Poland: a palaeobotanical study, Acta Palaeobotanica, Suppl. 4, 1-95, 2003.
3. Updated affiliation order.
4. Updated biomization record for Potato Lake.

Request to editor:
For visualization purposes, and following requests from both us and now the reviewers, please could the panels of Figure 3 (a and b) be on separate pages. Higher resolution vector graphics are available if necessary.

Reply: Reviewer 1

In their study Hoogakker et al. nicely compile BIOME maps using pollen records and model simulations. From the simulated biosphere changes they infer plant productivity and terrestrial carbon storage, and by using budget equations finally the ocean δ_{13}C . While I very much appreciate their effort in compiling BIOME maps and vegetation distributions over the past 120 kyr, I am not convinced by their conclusions on δ_{13}C changes. The manuscript itself is well organised and written. I thus encourage publication in CP after a major revision.

General:
The compiled BIOME maps from pollen data sets are very informative and useful for the paleo data and model community. In additon there are very few simulations over the past glacial-interglcial cycles with a fully coupled model. So, it is good to see that these simulations are evaluated against paleo data.
My main critics concern the interpretation of the model results. In my opinion the approach to reconstruct ocean δ_{13}C is too simplistic and without recognition of available evidence.
Therefore, I am not convinced that terrestrial carbon stock changes have the dominant role in ocean δ_{13}C changes over the past 120 kyr. It could well be true, but there are a lot of assumptions involved and other mechanism, e.g. ocean water mass changes (Bereiter et al., 2012) that possibly could explain the observations.

This is an interesting comment. With regards to the last paragraph, we are not dismissing water mass changes at all! We are fully aware of the changes in d13C and their link with nutrient inventories / water mass change interpretations, as well as inferences made using εNd. What we mean is that changes in the vegetation were likely to have changed ocean δ13C (as has been extensively shown for the LGM). Our study basically provides the first estimates of the possible extent of these changes. They are to be seen as baseline changes; water mass changes are on top of this. In our simulations we have not modelled the effect of meltwater release and millennial scale cooling events. In order to make this clearer we have added the following line to the introduction:

(Our) line 171-172 we added: ' The effects of millennial scale climate fluctuations were not simulated.'
The reason we are comparing with records that do not include the N Atlantic is because there dramatic changes do occur in bottom water, where AABW may have shoaled to about 2 km in the North Atlantic.

As a neutral reader I would expect a more thorough calculation and uncertainty consideration of carbon stock and δ_{13}C changes. Here my suggestions:

1. The Vostok CO2 record is outdated and often lower by 10-20 ppm than newer data. Use a composit record of newer data sets (see Figure below). Also use the common timescale AICC2012 (Veres et al. 2012). 20 ppm can greatly affect NPP and thus carbon storage.

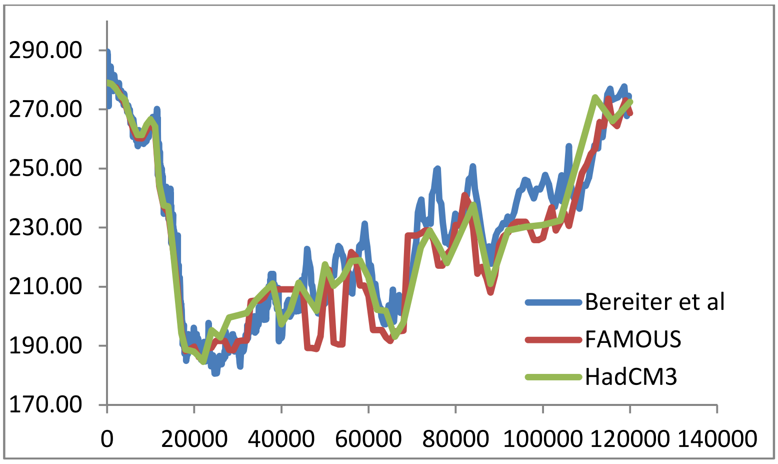

Fig 1.

Differences between prescribed CO2 in FAMOUS and HadCM3 simulations. FAMOUS used EPICA and HadCM3 runs used Vostok ice core reconstructions with the newer Bereiter composite curve. The largest discrepancies with the composite are between 70 and 100 kyr BP, and as the reviewer says, these are up to 20ppm and usually the composite is higher than the input CO2 to either HadCM3 or FAMOUS models and biome4. The timing of the peaks in CO2 in the new curve is more similar to the HadCM3 inputs than FAMOUS.
It is not feasible on the timescale and resources available to rerun the climate model simulations with the later composite CO2 as inputs. However, one could make the assumptions that 10-20ppm higher CO2 would not alter the simulated climate significantly to modify the NPP of the terrestrial biosphere in comparison with the CO2 fertilization effect on NPP. With this in mind we performed a sensitivity test whereby the CO2 prescribed to biome4 run with FAMOUS climate was increased by 20ppm (for all time steps). The following curve shows the increase in terrestrial carbon storage for the whole glacial cycle from the resulting CO2 fertilization effect.

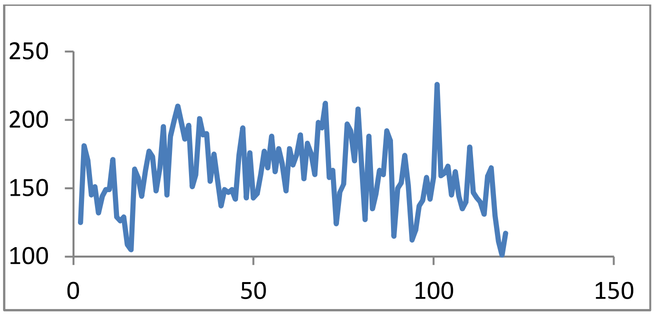

Fig. 2

The numbers are most relevant between 70 and 100 kyr, when the FAMOUS-biome4 CO2 input curves are most different from the composite. There is a ~150GtC increase (varying between 100 and 200GtC) or around 10% (average total modelled carbon storage during this time is ~1500GtC in the original FAMOUS-driven simulations). During the other time periods covered by the model simulations the CO2 inputs are similar to the composite and so there would be much smaller or negligible changes to NPP or carbon storage from running biome4 with the composite record.

We understand and agree with the reviewer that it would be a good idea to rerun the simulations with the composite CO2 curve forcing both the climate and vegetation, for completeness. However, as it is not possible to do this for the climate simulations (especially HadCM3) and as the sensitivity tests show that the impact would probably be maximum 10% increase in carbon storage and only really significant during MIS4 we would prefer to maintain the consistency between CO2 curves used for the climate forcing and the BIOME4 simulations presented in our original results

2. Show the uncertainty and impact of atmospheric $\delta^{13}C$ on ocean $\delta^{13}C$ using ice core records for the last 20 kyr (Schmitt et al., 2012) and MIS 5 (Schneider et al., 2013). Even though the majority of the $\delta^{13}C$ signal is transferred to the ocean it could give you an indication on the direction of change.

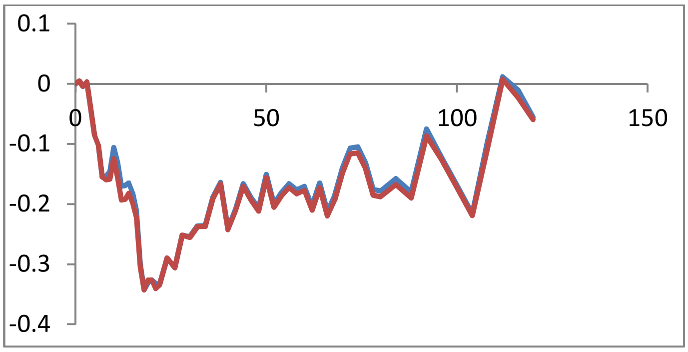

Fig. 3

Figure shows the impact of including time varying atmospheric δ13C based on ice core records on global ocean δ13C. The red line uses a constant δ13C of -6.5 per mil, and the blue line uses data from Lourantou et al, Schmitt et al, and Schneider et al with interpolation for the missing time period from 105 – 22 kyr BP. The difference is very small on the long term trends and while there could be some larger impacts on the smaller scale sub-glacial cycle patterning between ~90 and 40 kyr BP if there are also similar scale variations in δ13C, however there is no data for this time period.

3. One shortcoming of the $\delta^{13}C$ analysis is the missing of peatlands and permafrost carbon stocks in the model, as mentioned in the beginning of the paper. They act excactly on these long time scales that matter for the terrestrial carbon change over the observed period, and also have an opposite effect on carbon storage compared to e.g. forest ecosystems. According to Ciais et al., 2012, as you write, the inert carbon stock was larger by ~ 700 PgC during the LGM compared to PI. Assuming a linear increase in permafrost carbon between the previous interglacial and the LGM: How would the increasing carbon storage in permafrost areas affect the $\delta^{13}C$ budget? Please discuss and see below for more specific comments.

We have added to the discussion and included some additional exploratory plots on the impact of an increasing inert carbon pool during the glacial. See below for details.

4. The equations used to estimate carbon storage from NPP has underlying assumptions that are questionable. It is assumed that soil carbon is in steady state

at each time step in the past, which is wrong for ecosystems with a turnover time larger than the model time step (1000 years for FAMOUS I guess), i.e. for wetland ecosystems or again permafrost areas. Further, turnover times are estimated from present day soil carbon storage. Again it is assumed that for current conditions soils are in steady state, in a time of rising temperature, CO_2, and nutrient input. A discussion of the implications is needed here.

Although it is true that the heterogeneity of soil organic matter means that some soil carbon varies on millennial timescales, the soil response to changes in climate tends to be dominated by the more labile carbon pools. Effective residence times for soil carbon have been estimated as being decades near the equator and ~250 years in the high northern latitudes (Carvalhais et al., 2014). Moreover, our models do not include components such as wetlands or permafrost with the very long timescales suggested by the reviewer. The steady-state soil carbon assumption used in our study thus neglects a lag in total biosphere carbon response, although on the millennial timescales analysed here it is unlikely to introduce major inaccuracy compared to other assumptions used in the study.

The use of current, non-equilibrium soil conditions to estimate the turnover times for each biome is perhaps more of an issue. The difference in turnover constants (now listed in table 2) derived for the FAMOUS and HadCM3-forced runs partly reflects differences in assumptions for what level of simulated NPP is appropriate to compare with these modern carbon stocks. The uncertainty in turnover constants can introduce further uncertainty to the carbon storage calculations, on a similar scale (~10%) to those seen above related to the details of the CO_2 forcing curve used for the glacial cycle. On further investigation the rather large drop in pre-industrial to LGM terrestrial carbon storage seen in the FAMOUS-forced biome simulations seems to lie at the upper end of this uncertainty range. Some discussion of these issues is now included alongside our summary of the method of Wang et al. (2011).

Given the richness of BIOME data and the complexity of the climate models used in this study I think the analysis of $\delta^{13}C$ falls short. I don't think new climate simulations are needed, but additional simulations with BIOME4 for sensitivity tests and a thorough uncertainty estimate (1 sigma band for land and ocean $\delta^{13}C$) would considerably improve the statement of the paper.

We've added an uncertainty estimate in the $\delta13C$ ocean bit – where the largest uncertainty arises from the inert terrestrial carbon pool.

Specific:
p. 1039, l. 2: The Vostok CO_2 record is at least 16 years old and outdated by records with higher temporal resolution and measured by more accurate techniques (e.g. direct measurements by ice sublimation). Please replace it with data from newer ice cores (see Figure and References below).

See reply to comment above (estimated differences from using different CO_2, inclusion of comment that we are aware of newer CO_2 data available with higher temporal resolution). However, we also note that for the purpose of our paper, which primarily addresses smooth glacial-interglacial changes, significantly higher temporal resolution is not really needed.

p. 1943, l.2: should this be Fig. 1 or Table 1? Could not find reference to Fig. 1 in text.

P 1037, l 16. The reference to Table 2 is correct, as this also provides details of site elevations. Figure 1 shows the locations of the various pollen sites, with site details provided in Table 2. We have added a reference to Figure 1 in line 158 '(for locations see Figure 1)'.

p. 1049, l.11: Are HadCM3 surface temperatures absolutely 1°C colder at present or is the LGM-present anomaly 1°C colder? In the first case this should not matter, when you use anomalies for BIOME4. Please clarify.

The HadCM3 paleoclimate anomalies are, in general, a degree or so colder than the FAMOUS anomalies, so this is a significant difference in forcing.

p.1052, l. 19: The interpretation of the "sahara greening" in the model is at its limit, when only a hand full of grid cells swap color at this coarse resolution. In general the description for comparing model grid cell changes could be shortened and less speculative.

The Sahara greening reference has been scaled back.

p. 1060, l. 23: Is the CO_2 fertilization effect or the CO_2 climate effect more dominant for NPP? Could this be tested with a BIOME4 simulation with constant CO_2?

We have performed sensitivity tests where BIOME4 is driven by glacial-interglacial climate changes both with and without changes to CO_2 to influence CO_2 fertilization. The outcome is that CO_2 fertilization is the predominant driver of lower glacial NPP (around 85% of the impact at the LGM). We have added a sentence to reflect this in this paragraph.

p. 1061, l. 7: These numbers directly depend on prescribed CO_2. Using an updated CO_2 record (see Figure below) should result in e.g. smaller differences between the Eemian and the Holocene.

We have estimated the impact that using the composite CO_2 curve would have on the FAMOUS-forced BIOME4 simulations. Using the sensitivity experiment (described earlier) where CO_2 input to BIOME4 was increased by 20ppm for each timeslice we approximate the sensitivity to CO_2 of NPP and then use this to estimate NPP had the composite curve been used rather than the original CO_2 forcing in FAMOUS. This captures the impact of CO_2 fertilization, which is the primary driver (but can be considered conservative given that we do not have the CO_2-forced climate changes). The comparison can be seen below:

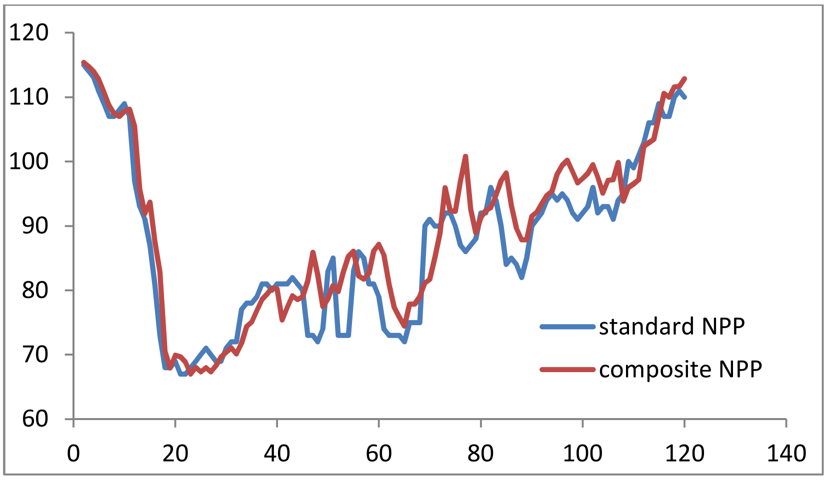

Fig. 4

The details described in the paragraph highlighted by the reviewer do change somewhat depending on CO2, as he/she says. The Eemian (at ~120kyr) is more similar to the Holocene, although still lower. The timing and magnitude of the large drops in productivity are modified slightly. We have altered the paragraph in the text to draw attention to the idea that the NPP will be quite sensitive to the CO2 inputs. However, we would prefer to leave the data as it is rather than use the composite curve so as to maintain climate and biome CO2-forcing consistency in the results we present.

p. 1092, l. 24: Which soil carbon data has been used for the calibration of the turnover times?

Modern soil and vegetation carbon inventory data by megabiome was taken from Table 3.2 of the IPCC TAR WG1 (Prentice et al. 2001). Prentice et al. cite Mooney, Roy and Saugier (2001) for vegetation carbon, and the IGBP-DIS soil carbon layer (Carter and Scholes, 2000) overlaid with De Fries et al. (1999) current vegetation map for average ecosystem soil carbon. As noted above, the turnover times and resultant terrestrial carbon storage are sensitive to the choice of carbon datasets – this has been noted in the paper.

Carter, A.J. and R.J. Scholes, 2000: Spatial Global Database of Soil Properties. IGBP Global Soil Data Task CD-ROM. International Geosphere-Biosphere Programme (IGBP) Data Information Systems. Toulouse, France.

De Fries, R.S., C.B. Field, I. Fung, G.J. Collatz, and L. Bounoua, 1999: Combining satellite data and biogeochemical models to estimate global effects of human-induced land cover change on carbon emissions and primary productivity. Global Biogeochemical Cycles, 13, 803-815

Mooney, H., J. Roy and B. Saugier (eds.) 2001. Terrestrial Global Productivity: Past, Present and Future, Academic Press, San Diego

p. 1063, l22: If I would argue that NPP is dominated by CO2 fertilization, as the curve in Fig. 5 visually correlates with the CO2 record, would you still get a precessional cycle in terrestrial carbon storage with constant CO2 in BIOME4? Using the updated CO2 record may change the periodicity. Please reassess.

We have used the sensitivity tests with higher CO_2 to produce a rough curve for terrestrial carbon storage had the Bereiter composite curve been used to drive BIOME4:

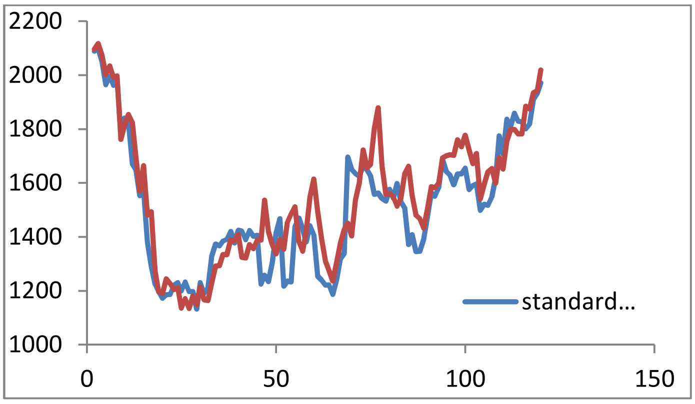

Fig. 5

Carbon storage has a greater proportional impact from climate than NPP – particularly the soil temperature dependence by the method of calculation used in this paper. The timing of the peaks and troughs in carbon storage are a balance between productivity and increased respiration (carbon release) with warmer temperatures. The timing and periodicity of these is roughly similar for BIOME4 in both scenarios, as in the figure. However, as we do not have the resources to rerun the climate model with the new composite curve, and because climate is more important in this case, we would prefer again to keep to the current CO_2 inputs for the climate and vegetation models.

p. 1064, l. 19: Replace 'decrease' by 'difference' as the former has a time direction associated. Time runs from LGM to PI.

We have changed this in the text.

p. 1065, l. 6: Please use updated CO2 (see Figure below) and δ_{13}C (Schmitt et al., 2012; Schneider et al., 2013) records for the atmospheric part of the budget.

We have used the updated and interpolated d13C records in the calculation, which makes very little difference to the calculation for the ocean budget (see figure 3). We have then estimated the changes to d13C for the global ocean from using the Bereiter et al composite curve by using the sensitivity experiment with FAMOUS-forced BIOME4 driven with higher CO2 to both as the atmospheric inventory input as well as the terrestrial carbon storage input. The result is given in Figure 6 below. The difference, as with terrestrial NPP and carbon storage, is largest between 70 and 100 kyr BP, where the Bereiter input produces a slightly isotopically heavier ocean at some time points (up to 0.05 per mil increase in most cases but larger than this at a couple of time slices only). However, it does not change the glacial-interglacial maximum change or the general characteristics of the glacial decline. The figure is produced for the reviewer but as before we would like to have the CO2 inputs to the climate, vegetation, and d13C budget calculations be consistent, and so keep them as they were in the paper.

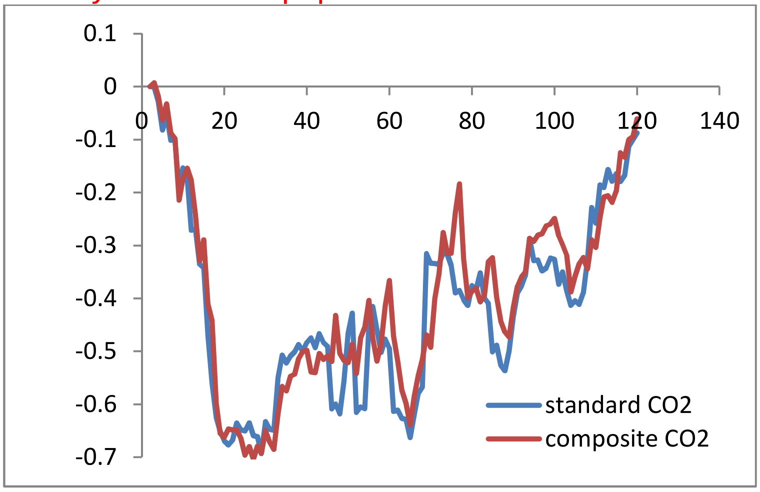

Fig. 6

p. 1066, l. 2: You could mention that biomes do not include permafrost (normally C3 plants) and peatlands (C3 plants and sphagnum moss with δ_{13}C = ~ -30 per mill). Having said that, please also clarify that the variability of terrestrial δ_{13}C in Fig. 6a is of secondary importance for ocean δ_{13}C. What matters are terrestrial carbon storage changes.

We have added a statement to this paragraph to reflect that changes in δ13C in the terrestrial biosphere are not as crucial as changes to the size of the terrestrial carbon pool.

p. 1066, l. 14: This is correct, but only because both models lack inert carbon pools. If you include them like in Ciais et al., 2012, then the FAMOUS model would agree better (see paragraph 4.3. in your own words).

We have estimated the effect of including an inert terrestrial carbon pool (permafrost, peatlands) of the size inferred by Ciais et al (2012). We used the figures of 1600GtC at pre-industrial and 2300GtC at LGM and then interpolated between. Given the lack of estimates for the Eemian, we used the same value as the pre-industrial at 120 ka BP and then interpolated linearly to the LGM value. Assuming a lighter δ13C signature (of -27 per mil) for the inert pool the impact on the FAMOUS global ocean δ13C is displayed in Fig. 7:

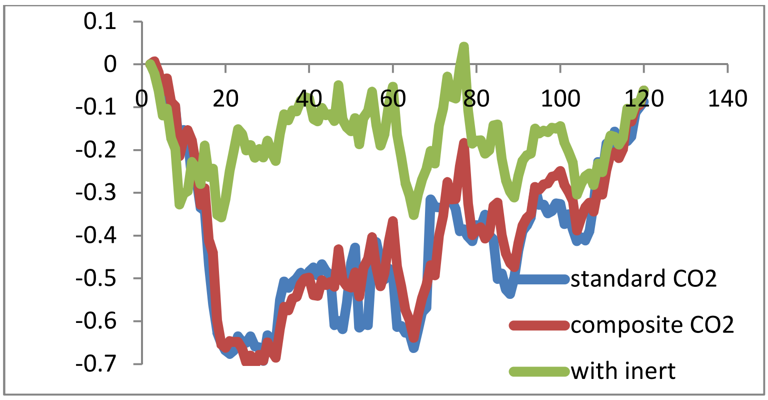

Fig. 7
For the FAMOUS-driven BIOME4 simulations, the inclusion of an inert terrestrial carbon pool improves the comparison of the ocean d13C with the data compilation by Oliver et al., and would make it match the data better than HadCM3-driven BIOME4 simulations, as the reviewer suggested. We have included discussion about this neglected carbon reservoir in section 4.4.

p. 1066, l. 24: Please also cite Bereiter et al., 2012.

OK

p. 1067, l. 5ff: This statement is too strong, I'm not convinced. I believe that the trend in modelled ocean $\delta^{13}C$ from MIS 5 to MIS 2 may be robust, but not the variability in between, e.g. the variability from HadCM3 climate is rather small.

We have toned this down and changed 'are' to 'may be'.

p. 1068, l. 25: Again, I'm not convinced by the presented material that the role of land $\delta^{13}C$ is "dominant" for ocean $\delta^{13}C$. See General comments.

We toned this down and changed 'dominant' to 'important'.

p. 1068, l. 13: This is very valuable and a good reason this paper deserves publication after a revision.

References: Ciais et al., 2011 should be Ciais et al., 2012 in the entire text.

We have changed this throughout the text.

Figure 2: What does (a) and (b) signify? Is there any difference between plots on top rightand left? Please enlarge this figure panel in two figures for better visibility.

Indeed, we requested that these panels be reproduced on separate pages to improve visibility in our initial submission to CPD - we will again ask the editor to make the panels as large as possible. a) simply denoted the panel of the more recent set of timeslices and b) to the earlier ones, but the distinction is not in fact used in the text and could be removed. The figure caption has been edited for clarity.

'Reconstructed biomes (defined through highest affinity score) superimposed on simulated biomes using FAMOUS (B4F, left) and HadCM3 (B4H, right) climates for selected marine isotope stages (denoted in ka BP). '

References:
Ahn J., Brook E. J. (2008) Atmospheric CO2 and climate on millennial time scales during the last glacial period. *Science* 322:83–85.
Ahn, J., et al. (2012), Abrupt change in atmospheric CO2 during the last ice age, Geophys. Res. Lett., 39, L18711, doi:10.1029/2012GL053018.
Bereiter, B., et al., (2012) Mode change of millennial CO2 variability during the last glacial cycle associated with a bipolar marine carbon seesaw, *Proceedings of the National Academy of Sciences of The United States of America, 109/25*, 9755-9760

Ciais, P., et al. (2012) Large inert carbon pool in the terrestrial biosphere during the Last Glacial Maximum, *Nat. Geosci.*, 5, 74–79, 2012.
MacFarling Meure, C., et al. (2006), Law Dome CO2, CH4 and N2O ice core records extended to 2000 years BP, *Geophys. Res. Lett.*, 33, L14810, doi:10.1029/2006GL026152.
Monnin E., et al. (2001) Atmospheric CO2 concentrations over the last glacial termination. *Science* 291:112–114.
Schmitt, J., et al. (2012) Carbon isotope constraints on the deglacial CO2 rise from ice cores, *Science*, 336, 711–714.
Schneider, R., et al. (2013) A reconstruction of atmospheric carbon dioxide and its stable carbon isotopic composition from the penultimate glacial maximum to the last glacialinception, *Climate of the Past, 9*, 2507-2523.
Veres, D., et al. (2013) The Antarctic ice core chronology (AICC2012): an optimized multiparameter and multi-site dating approach for the last 120 thousand years, Clim. Past, 9, 1733-1748, doi:10.5194/cp-9-1733-2013

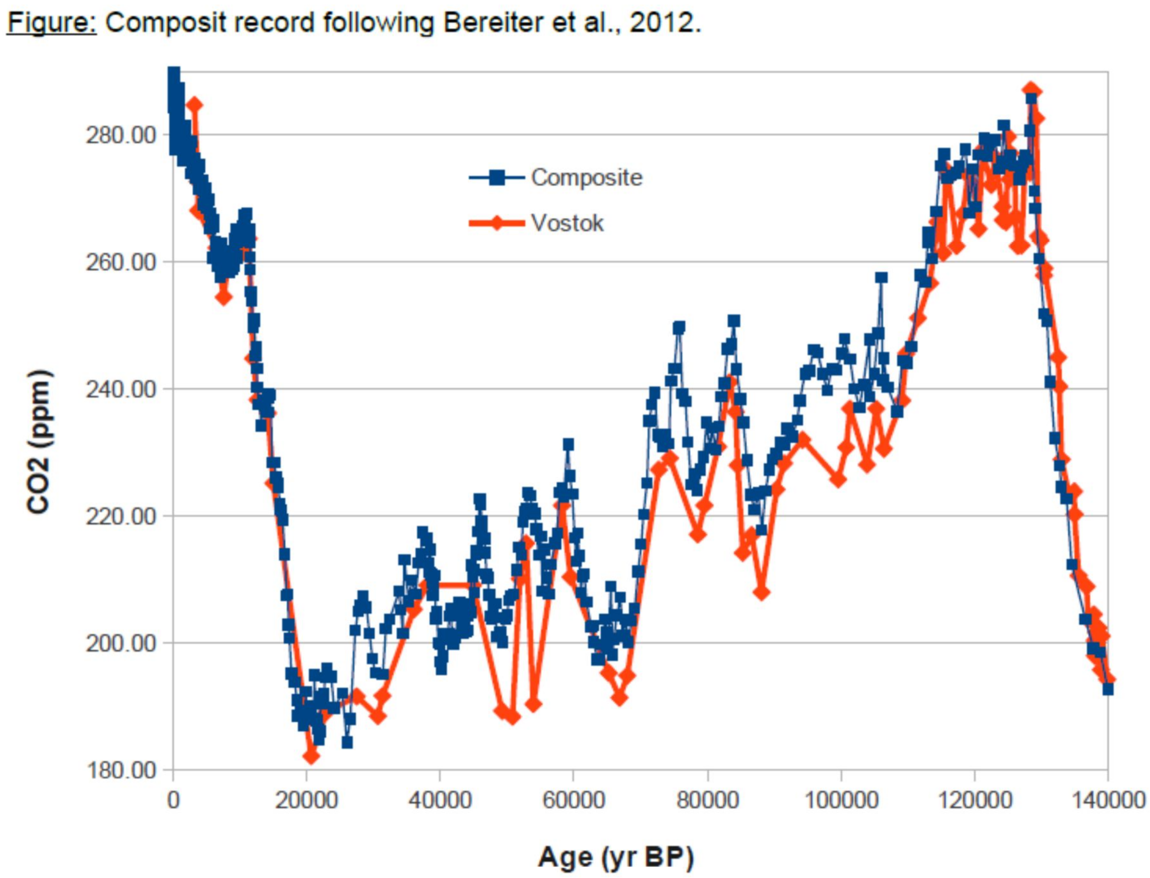

Figure: Composite record following Bereiter et al., 2012.
Composite CO2 record on AICC2012 (Veres et al., 2012)

-46 - 10 yr BP: Law Dome (MacFarling Meure et al., 2006)
0 - 1 kyr BP: WAIS (Ahn et al., 2012)
1 - 2 kyr BP: Law Dome (MacFarling Meure et al., 2006)
0 - 22 kyr BP: Dome C (Monnin et al. 2001)
22 - 24 kyr BP: Dome C Sublimation (Schmitt et al., 2011)
24 - 38 kyr BP: Byrd (Ahn et al., 2008)
38 - 60 kyr BP: TALDICE (Bereiter et al., 2012)
60 - 115 kyr BP: EDML (Bereiter et al.,2012)
105 - 155 kyr BP: Dome C Sublimation (Schneider et al., 2013

Reply: Reviewer 2

General comments
This objective of this paper is to use simulated paleoclimates over the past glacial/interglacial cycle to drive biome simulations, testing those simulations with the pollen data, and then applying the biome simulations to a simple terrestrial carbon/δ13C model in order to explain ocean δ13C variations over time.

The paper used the results of simulations from two climate models, biomes simulated from those climate-model outputs, and the "observed" record of biome variations inferred from fossil-pollen data to check to check the simulated biomes, and finally, calculations of terrestrial carbon-storage variations that in turn govern those δ13C variations.
There is considerable fuzziness in describing which model does what here, and the difference between simulations and reconstructions. The two climate models simulate climate, but not (as they are used here) elements of the carbon cycle (i.e. "interactive vegetation is not included" (in HadCM3), and "interactive vegetation was not used" (in FAMOUS)), so expressions like "The two climate models show good agreement in global and net primary productivity…" don't make sense. Also, the output of BIOME4 is simulated vegetation, as opposed to reconstructed vegetation, which is the product of the pollen synthesis.

We have rephrased throughout the manuscript to try to clearly denote the boundaries of the different reconstructions, simulations and calculations. In particular, the shorthand B4F (BIOME4 simulations forced by FAMOUS climate) and B4H (BIOME4 simulations forced by HadCM3 climate) have been introduced

The general experimental design applied here of using simulated climate to drive biome simulations, testing those simulations with the pollen data, and then applying the biome simulations to a simple model δ13C model emerges slowly in the paper (with the last step not really being discussed until 31 pages into the paper), and so the design might usefully be stated in a "here we use…" fashion in the abstract to get the reader off on the right track.

We have extended the abstract to outline the methods more clearly whilst still trying to be concise. We have also rewritten parts of the introduction to make the design of the paper clearer. At the end of line 159 we added ' In section 2.1 we outline the biomization procedures applied to reconstruct land biosphere changes.' Then at line 163 we added '). Details of the atmosphere ocean general circulation model (AOGCM) simulations are provided in section 2.2.' Line 165 and onwards has been rewritten to ' In section 3 we evaluate biome reconstructions based on these climate model outputs using the BIOME 6000 project (reference), and our new biomized synthesis of terrestrial pollen data records, focusing on the pre-industrial period, 6 ka BP (mid-Holocene), 21 ka BP (LGM), 54 ka BP (a relatively warm interval in the last glacial period), 64 ka BP, (a relatively cool interval in the glacial period), 84 ka BP (the early part of the glacial cycle), and 120 ka BP (the Eemian interglacial).' Finally the last sentence of the introduction has been rewritten to ' Finally in section 4 we apply the biome simulations to estimate net primary productivity and terrestrial carbon storage. Then, using a simple carbon isotope ($\delta^{13}C$) model, we assess the contribution of terrestrial biosphere and carbon storage changes to deep ocean $\delta^{13}C$

over the last 120 kyr and compare this by means of a comparison with deep ocean benthic foraminiferal carbon isotope records, representative for the $\delta^{13}C$ of deep ocean water.'

The data-model comparison (between simulated and "observed" biomes) is relatively lightweight, featuring only a few map comparisons with the relative sparse network of "long" records used here. I was expecting a comparison involving the full BIOME6000 0, 6 and 21 ka data set (which would not be hard to do). It is asserted that the hierarchy of models can successfully simulated the biomes inferred from the pollen data, but this "working hypothesis" as it's called, is never tested, although it could and should be.

This more complete comparison with the full BIOME6000 data for the relevant periods was in fact done, and is largely what is summarised in these subsections, rather than just referring to the much smaller number of longer-record biome sites we synthesise and use elsewhere in the paper for the whole glacial cycle. It was perhaps not clearly signposted that that is what was being discussed, and we have made this clearer in the revised manuscript.

There are three potential sources of data-model mismatches (or indeed accidental matches), 1) the model, 2) the data and 3) the experimental design. For example, disagreements between simulated biomes and observed ("biomized") biomes could be attributable to the hierarchy of models (AOGCMs and BIOME4), the biomization process itself, or to the experimental design (in the application of all of the models). It would be good to discuss those sources and the extent to which each could be influencing the results here.

We have discussed potential mismatches throughout the results and discussion sections. We rewrote section 4 'There is good general agreement between the modelling results and the pollen-synthesis (this paper and BIOME 6000). Below we calculate quantitative changes in the global terrestrial biosphere and carbon cycle, keeping in mind that these calculations carry some uncertainties relating to several mismatches. As is discussed in section 3.1 there are several occasions where the modern biomized pollen data do not agree with actual biome presence; for example Potato Lake and Lake Tulane in North America. In both cases high contributions of Pinus and some other taxa skewed the affinity scores towards drier biomes (grassland and dry woodland). For the past, not knowing whether a pollen distribution is representative for an area, puts restrictions on the biomization method. It is however noted, that in most cases the biomized modern pollen agree well pre-industrial biomes. The models produce some differences in climate and vegetation due to 1) difference in resolution, affecting the biome areal extent and altitude, 2) ice-sheet extent, affecting temperature (section 3.2). If we use the pre-industrial as a test-bed to compare model outputs and pollen (BIOME 6000) reconstructions, there are some biases that can be attributed to biases in BIOME4, the biomization method, and the models limiting geographical resolution.'

Overall, I don't think the case has been made that the hierarchy of models works well enough to use the BIOME4 output for carbon budget calculations. That the approach does work could be demonstrated using the BIOME6000 data, along with multimodel simulations of 6 and 21 ka; this would also help to evaluate the relative importance of the three sources of mismatch.

See above. We actually do compare the model simulation of the pre-industrial, 6 ka, and LGM with the BIOME 6000 data, and we have stated this more clearly. BIOME 6000 is mentioned throughout the manuscript: lines 147, 166, 614, 647 677, 679 etc. Table 1 lists the BIOME6000 studies that we compared our pre-industrial, 6 ka and LGM model simulations with. However in the text we previously referred to these as high-reolustion biomizations, and to emphasize they are part of BIOME6000 we now explicitly state this in the text.

There is a relatively large author list, which includes some but not all contributors of the original data, and which overlaps a lot with the authors of the individual papers in the Sanchez-Goñi and Harrison (2010) QSR special issue on millennial-scale climate variability and vegetation changes during the last glacial-interglacial cycle. It would be appropriate to provide an indication of author contributions.

Prof. Tzedakis initialized the collecting of long glacial-interglacial records for the Quaternary Quest project with which the first three authors as well as Prof. Harrison and Prentice are associated. The first three authors were responsible for the biomization of the pollen data (Hoogakker) and modelling of FAMOUS (Smith) and HadCM3 (Singarayer, who ran the model with Valdes) and the primary analysis and write-up. Some of the pollen data used in this study came from online databases, some we had access to from the main authors. During the setting up of the biomization matrices Dr. Hoogakker was assisted by the various biomization specialists and palynologists (essentially all the other authors), who critically assessed the procedure and results.

Differences and overlaps with Harrison and Sanchez-Goni (2010):
The Quaternary Science Review Special issue, edited by Harrison and Sanchez-Goni specifically deals with vegetation changes across millennial scale climate change, the Dansgaard-Oeschger cycles. In their paper Harrison and Sanchez-Goni (2010) only discuss certain stadial and interstadial intervals (e.g. their figures 3, 4 and 5). Parts of several of the records that feature in our study are also discussed in papers in Fletcher et al. (2010, Europe), Jiminez-Moreno et al. (2010, North America), Hessler et al. (2010, Africa and South America), and Takahara et al. (2010, for east Asian islands). There are differences in the biomization procedures applied, period covered, but also only a few records are actually shown in those studies. Tropical Asia and Australian records do not feature in this special publication. One major difference too is that all our biomized records are available in the supplementary information. Within section 3.1, where we discuss our biomization results, we also discuss overlaps and differences, with details below:

Line 341 and onwards ' For their study of biome response to millennial climate oscillations between 10 and 80 ka BP Jiminéz-Moreno et al. (2010) applied one scheme for the whole of North America, with a subdivsion for southeastern pine forest. All biomization matrices and scores for individual sites used in our study, generally at 1 kyr resolution, as well as explanatory files can be found in the Supplementary Information.'

Line 359 ' Interestingly, the temperature forest biome has highest affinity scores in a short interval (~15 ka BP) during the deglacation (Fig. 2a). In Jiminéz-Morene et al. (2010) Pinus does not feature in the grassland and dry shrubland biome, but comprises a major component of the southeastern pine forest; hence their biomized Lake Tulane records fluctuates between the 'grassland and dry shrubland' biome and 'southeastern pine forest biome'.'
Line 371 ' Again, In the Jiminéz-Morene et al. (2010) biomizations, Pinus does not feature in the grassland and dry shrubland biome, hence the forest biomes have highest affinity scores in their biomizations.'
Line 382 ' Biomizations for Carp Lake between 10 and 80 ka BP by Jiminéz-Morene et al. (2010) generally look similar to ours, apart from 36, 57-70 and 72-80 ka BP where the temperate forest biome shows highest affinity scores because Pinus undiff. is treated as insignificant in their biomization. Biomizations of Bear Lake between 10 and 80 ka BP are similar to Jiminéz-Morene et al. (2010).'
Line 389 ' Hessler et al. (2010) discuss the effects of millennial climate variability on the vegetation of tropical Latin America and Africa between 23N and 23S.'
Line 415 ' The biomized Colonia record of Hessler et al. (2010) generally shows the same features, apart from an increase in affinity scores for the dryer biomes between 10 and 18 ka BP.'
Line 447 ' Our results are similar to those obtained by Hessler et al. (2010).'
Line 479 ' Fletcher et al. (2010) use one uniform biomization scheme to discuss millennial climate in European vegetation records between 10 and 80 ka BP.'
Line 496 ' Instead of a desert and tundra biome Fletcher et al. (2010) define a xyrophytic steppe and eurythermic conifer biome in their biomizations, giving subtle differences in the biomization records, with the Fletcher et al. (2010) biomized records showing an important contribution of affinity scores to the xerophytic steppe biome. Characteristic species for the xerophytica shrub biome include artemisia, chenopodiaceae and ephedra, which in the Southern Europe biomization scheme of Elenga et al. (2000) feature in the dessert biome and grassland and dry shrubland biome (only ephedra).'
Line 509 ' In the Fletcher scheme characteristic pollen for the eurythermic conifer biome include pinus and juniperus. In our biomization pinus and juniperus contributes to all biomes except for the desert and tundra biome.'
Line 537 ' and Takahara et al. (2010).'

The figures need some work. The key figure is Fig. 2, which shows simulated ad observed biomes, but fuzzes up at the scale necessary to view the results for individual continents.

We have requested for Figures 2a and b to be plotted on separate pages, and also added more details to the Figure caption.

Zooming way in on Fig. 3 suggests that the curves may be “spikier” than they should (i.e. in the data), because it looks like they were constructed with “bevel-joined” line ends (which extrapolate the data, creating the sharp spikes), instead of the more appropriate, but inelegantly named, “butt-joined” line ends.

We have attempted to make the data curves look less spikey, within the limitations of the analysis software used.

Specific comments:
p. 1034/line 5: replace “Global …” distributions” with “Simulated (BIOME4) biome distributions at the global scale” (or something like that).
OK

1034/9: “modelled changes in vegetation” I think this should read “simulated changes in vegetation”—the modelling work got done as BIOME4 was developed; here the model is being applied to generate simulations.
OK

1034/25: “Quasi-periodic” What’s quasi about the periodicity?
We have deleted quasi.

1035/3: “…for the last ~0.8 million years…” What’s special about that interval? Orbital variations have never not influenced climate (and the biosphere, after it developed). It might be better to review the particular variations of climate and its controls over the last glacial cycle than to describe the general ice-sheet, sea-level, CO2, etc. (Quaternary 1010) relationships.
We have rewritten this bit to make it clearer: ' Periodic variations in the Earth’s orbital configuration (axial tilt with a ~41 kyr period, precession with ~19and 23 kyr periods, and eccentricity with ~100 kyr and longer periods) result in small variations in the seasonal and latitudinal distribution of insolation, amplified by feedback mechanisms (Berger, 1978). These are amplified by feedback mechanisms such that for the last ~ 0.8 million years long glacial periods have been punctuated by short interglacials on roughly a 100 kyr cycle.'

1035/9: “productivity and size of the terrestrial biosphere” “Size” could be interpreted a number of different ways, including areal extent, total biomass, etc.
OK, this has been rephrased to 'During glacial–interglacial cycles the productivity of, and carbon storage in, the terrestrial biosphere are influenced by orbitally forced climatic changes and atmospheric CO2 concentrations.'

1035/14: “… the terrestrial biosphere was significantly reduced as forests contracted.” Reduced in what sense? I think the area of the terrestrial biosphere varies rather little over time as icecovered areas seem to be roughly compensated for by exposed shelves. Does this mean instead that forested areas were reduced in area?
We deleted 'as forests contracted'.

1035/15: “21 kaBP” means “21,000 years ago before present”. Just “21 ka”.
Coming from a variety of backgrounds as the authors do, we find the conventions to seem a bit fuzzy as to the precise meaning and implication of various abbreviations. For clarity for all readers, we would like to stress the precise reference point (i.e 1950) of the timescale, so included the BP explicitly, then used ka separately as an SI-type notation for thousands of years. We were unaware that this could be taken with an implicit inclusion of the ‘BP’. Would the reviewer find (kyr BP) a suitable (and explicitly clear) compromise?
.

1036/4: “The data can be viewed through the prism of a global, physically based model that allows the point-wise data to be joined together in a coherent way.” Does that simply mean “interpolation” (which you’re not doing here). Or are you describing how to comparing a sparse network of reconstructions with gridded simulations? In any case this sounds like text from a proposal as opposed to a description of what was done here.
It does not mean interpolation. We have rewritten this sentence to 'The data can be interpreted in the context of a global, physically based model that allows the point-wise data to be seen in a coherent way.'

1036/6: “There are continuous, multi-millenial palaeoenvironmental records… that have not been previously brought together is a global synthesis.” Given the author overlap between this paper and those in the Sanchez-Goñi and Harrison (2010) QSR special issue, this statement is a little surprising. Also, only one kind of palaeoenvironmental data is being synthesized here.
We have rephrases this to ' There are continuous, multi-millennial pollen records that stretch much further back in time than the LGM but they have not previously been brought together in a global synthesis to study changes of the last glacial-interglacial cycle.' Further details of the extent of the overlap with Sanchez-Goñi and Harrison are given above.

1036/14: “We present quantitative estimates of changes in the terrestrial biosphere reconstructed from two atmosphere-ocean general circulation model (AOGCM) simulations over the last glacial cycle.” No you don’t—the “quantitative estimates” come out of BIOME4.
We deleted this and changed the last sentence of that section to ' Finally in section 4 we apply the biome simulations to estimate net primary productivity and terrestrial carbon storage. Then, using a simple $\delta^{13}C$ model, we assess the contribution of terrestrial biosphere and carbon storage changes to deep ocean $\delta^{13}C$ over the last 120 kyr and compare this with deep ocean benthic foraminiferal carbon isotope records, representative for the $\delta^{13}C$ of deep ocean water. '

1036/22: “We assess…” There’s a step missing here. How are biome simulations turned into δ13C values? (Actually the biome-simulation step is missing too.)
We have written a step-wise description of the work carried out, with reference to the various sections where this is being discussed.

1037/3: “Biomization assigns … based on biological and climatological ranges.” To a reader unfamiliar with this process, that might sound like some kind of calibration with climate data is involved.
Deleted ' based on basic biological and climatological ranges.'

1037/16: “megabiome score data…” Why are there blank rows in the spreadsheets? For example, there are pollen data for the Carp. L. sample at 6.12m, but no (mega)biome scores. (Also, why are there two age models for this record?)
We aimed to calculate affinity scores for every 1 ka, with smaller resolution in case the scores across the different biomes were close. We have improved the resolution to 1 ka at Carp Lake. We provide the age models that were originally provided. The

two age models provide some idea of range of ages, illustrating also that there can be large uncertainties.
Added to line 204 ' Sometimes more than one age model accompanies the data, illustrating the range of ages, and also that there can be large uncertainties.'

1038/4: “reconstructions” again
Changed to 'simulations'.

1038/8: “climate averages” “long-term monthly means”?
Rephrase to 'monthly climatologies'

Sections 2.2.2 and 2.2.3: How was land-surface cover specified (or calculated) in the simulations?
It was kept fixed at pre-industrial values, expressed in model variables that are standard for these versions of the MetOffice model (FAMOUS and HadCM3).

1039/10: “biogeochemistry-biogeography model” Should that aspect of the model be mentioned earlier.
Yes, added sentence ' Finally in section 4 we apply the BIOME 4 simulations to estimate net primary productivity and terrestrial carbon storage. Then, using a simple δ^{13}C model,'.

1039/20: “compare well with NGRIP…”
We have added a couple of sentences with references where comparisons to palaeodata and other models have been made, within this section. The model has been evaluated at high and low latitudes over a variety of time periods.

1039/24: “physically justified ice-sheet extents” Explain.
There is relatively little direct evidence to constrain the extent (as opposed to overall volume) of the northern hemisphere ice-sheets between the Eemian and the LGM, as the proxies on the ground are largely overwritten by the advancing ice, so specifying boundary conditions for this type of modelling work is a significant problem.

For the HadCM3 simulations, the pre-LGM ice sheet areas were obtained by looking at the sea-level change (largely ice-sheet volume) for the timeslice required and taking the ICE-5G extent (a reasonably well constrained reconstruction of the post-LGM ice-sheet collapse) at the time during deglaciation with the same sea-level. This is the extrapolation method we refer to from Eriksson et al (2012). Taken together the HadCM3 timeslices thus show the ice-sheets slowly collapsing in reverse as they grow to their maximum size, which is not physically realistic. The FAMOUS simulations directly used the ice-sheet states for the whole glacial cycle modelled from the icesheet modelling of Zweck and Huybrechts (2005), which produced a physically plausible evolution of the ice. The catch here is instead that such ice-sheet modelling cannot accurately know many of the relevant boundary conditions for the ice, not least the climate they see – it’s a rather chicken and egg problem.

We do not feel that a description at this level of detail is appropriate for the paper – the details are available in the cited papers for those who wish to know – but we have rephrased.

1040/20: “adjusting … to compensate for … biases” and (line 22) “Climate model anomalies …” Is this two separate steps (bias-correction, and then the calculation of anomalies)? What was the base period for the anomalies?
This has been rephrased for clarity. Climate anomalies are produced for a timeslice by subtracting the pre-industrial climate of the relevant model from the climate the model actually simulates for that timeslice. These anomalies are then added to the Leemans and Cramer observations (with the observations interpolated onto the relevant model grid – this appears to be a source of confusion, see later) to produce the climate that BIOME4 actually sees. By using the pre-industrial as a base period for the anomalies and modern observations we neglect differences between preindustrial and modern climate in the models, but these differences are in general small compared to the biases in these relatively low resolution climate models.

1040/22: “temperature and precipitation” What about sunshine, and how was changing insolation handled?
Sunshine anomalies were derived from the models using simulated cloudiness variables. The models did not include variation in either the total output of the sun, nor its spectral composition, which were assumed constant throughout the simulations.

1040/23: “Leemans and Cramer” This implies that BIOME4 was run over the 0.5-degree grid of this data set, but Fig. 3 shows simulated biomes on the grids of the AOGCMs. There’s a big step missing here.
The BIOME4 simulations were in fact conducted on the two different native grids of FAMOUS and HadCM3 respectively, rather than the common higher resolution grid of the climatology data. This has been explained more clearly in the revised manuscript.

1040/27: “model’s” Which one?
Both - corrected

1041/1: “no special correction…” How were modern climate values created for the exposed shelves?
The version of the Leemans and Cramer (1991) climatology included in the BIOME4 distribution includes climate values for these areas. We have not been able to find out their exact provenance.

1041/4: “BIOME4 was forced with appropriate CO2 … (same as used to force the climate model)” Does this mean that Vostok CO2 was used for the HadCM3-driven simulations and EPICA CO2 for the FAMOUS-driven simulations?
Yes, see response to reviewer 1 more details

1042/8: Southeastern? (also in line 15, San Felipe and Potato Lake would commonly be located in the Southwestern US).
Changed to Southeast. Yes.

1042/27: “Recent” as in “present day” or newer than Thompson and Anderson (2000)?
Changed to modern.

1042/29: "… those of the LGM also compare well." With what?
Move reference of Thompson and Anderson to end of sentence, and replace observations with reconstructions.

Section 3.1: I'm not sure this section serves the paper very well. Each subsection starts with an overview of the location of the sites, but then rapidly becomes anecdotal, describing some aspects of the record for some sites, and different aspects for others. One overall impression I got is that the biomes don't vary much over time, and another is that there are important differences between the (mega) biomizations here and what was produced in previous studies; neither impression increases confidence about the results.

This is likely more a consequence of the way this section was written than of real issues in the data. As the authors indicate (p. 1041, lines 14-15) only the main results are being presented, but there is no overarching summary—the paper just moves on to the simulation results.

Comparison, where possible, with other studies (generally showing good agreement), has been added, as explained above.

The paper promises a new synthesis, but all it delivers is a few dots on Fig. 2, and some spreadsheets that list the affinity scores, but not the actual reconstructed biomes that the paper is based on.
A new figure 2 has been added showing the affinity scores against time for all the records discussed.

I wonder if this section could be moved to supplemental information, where a more systematic discussion of the individual records could be done, and replaced in the main text with some kind of summary figure. Alternatively, the reader could simply be referred to the Harrison and Sanchez-Goñi summary article in the QSR issue, along with the individual regional articles in that issue.
We have added a new Figure 2, and the results of our biomizations are compared with those featureing in the QSR special issue where possible. (Editor not keen on adding this to supplement).

I'm going to skip commenting on the reset of this section.
1048/18: "where they disagree…" This paragraph starts out talking about the source codes of the climate models, and so it would be easy for the reader to surmise that the disagreement mentioned here is between the climate models and not between the BIOME4 simulations.
This has been rephrased.

1048/21: "coupled to BIOME4" That's not really happening here.
This has been rephrased.

1049/6: "Because of its lower resolution…" This is certainly true at the resolution of the GCMs, but earlier the experimental design was described as including the "apply-the-anomalies" approach to the 0.5-degree Leemans and Cramer data set

(and repeated on p. 1050/line 6), so presumably the modern "high-resolution" spatial climate variations are also present in the input data for BIOME4.
See above, concerning the grids used for BIOME4. This is what we did.

1049/13: "difference in temperature…" When? At present, or over the course of the climate simulations? (Same question for precipitation…)
This difference is present over much of the simulations - rephrased

1049/21: "warm bias" Again, when?
At the LGM – these has been rephrased.

1049/21: "Millennial-scale cooling events…are not features of our model runs…" Does this mean that they were not simulated, or that the experimental design of the climate simulations did not include the appropriate forcing?
We did not explicitly force the models to simulate millennial scale climate change, and no events of this type were spontaneously produced in the simulations

1049/28: Replace "modelled reconstructions" with "simulated biomes".
OK

1050/4: The caption for Fig. 2 should point out that it shows both simulated and reconstructed megabiomes. The caption should also explain what we're seeing on the grids of the two models.
We rephrased this to ' Reconstructed biomes (defined through highest affinity score) superimposed on simulated biomes using FAMOUS (left) and HadCM3 (right) climates for selected marine isotope stages (denoted in ka BP).'

One simulated biome at the grid point? The modal simulated biomes (on the 0.5-degree grid) within the area represented by each model grid cell?
See above, re: grids for BIOME4

1050/29: "additional warmth and sea level" "higher temperature and sea level"?
OK

1051/5: "Differences between our pre-industrial megabiome reconstructions [read "simulated biomes"] only arise from the way the pre-industrial climate forcing [Leemans and Cramer, right?] has been interpolated onto the model grids." How was the Leemans and Cramer data interpolated onto the model grids? More to the point, why was it necessary to do that? The anomalies of the pre-industrial simulated climate relative to themselves are zero, so there shouldn't be any difference in simulated biomes, unless something that hasn't been explained is going on.
See above, re: grids for BIOME4

1051/25: "… on the scale of the climate-model gridboxes." This makes me think that the biomes are being simulated only for each model grid point, and not for each 0.5-degree grid point in the Leemans and Cramer data set via the "apply-the-anomalies" approach. If that's the case, the poor agreement throughout between simulated and reconstructed biomes makes sense.
See above, re: grids for BIOME4

1052/9: "… this comparison gives reasonable support to our working hypothesis…." That hypothesis is testable, and indeed should be. It looks to me like there are as many sites with inferred biomes that differ from the simulated biomes as don't. If you can't convincingly show that biomes inferred from "modern" pollen data match those simulated by observed climate, then why should we believe the results for other times?
We do show this; through comparison with BIOME 6000. Discrepancies mainly occur near mountainous regions, and are discussed throughout the text.

1052/13: "For both the mid-Holocene and LGM periods, the high-resolution biomizations of the BIOME6000 project (see Table 1) provide a better base…" The same is true for the present.
Yes, as explained earlier we did do this comparison and have added some text.

1052/19: "a greening"?
This has been rephrased.

1052/24: "weak precipitation"?
rephrased

1052/25: "FAMOUS shows a smaller reduction"?
rephrased.

1052/27: "regional biome reconstructions" Do you mean yours here or the BIOME6000 ones?
BIOME6000 – this should now be clearer from the introduction to the section

1052/28: "magnitude of the rainfall" The magnitude of the rainfall or of the rainfall anomaly?
The anomaly

1053/5: "wetter anomalies" Wetter than what? (And it would be better to talk about changes in precipitation as opposed to "wetness".)
rephrased.

Sections 3.3.2 and 3.3.3: As was the case for the present day, it looks to me that (in the absence) of any quantitative measures, there are as many disagreements and agreements. It is asserted that the more abundant biome data from BIOME6000 shows that "… there is again good general agreement between the two different model reconstructions and the regional biomizations of the BIOME6000 project." (p. 1053, line 27) but there's no real evidence that such is the case.
As described above, this comparison has in fact been done and is described in sections 3.3.1 – 3.3.3.

1055/11: "The similar model-based reconstructions…" Similar to what? The LGM simulations? The biome reconstructions?
rephrased.

1055/23: "realistic two-dome pattern" Citation?

Rephrased to describe the ice differences more usefully.

1055/26: “limited vegetation extent” “Vegetation” in this paragraph seems to be equated with tree cover here, but was just used above in the context of land not covered by ice.
rephrased.

1055/27: “wetter climate in HadCM3” Wetter than what?
Wetter than FAMOUS - rephrased

1056/1: “cooler in FAMOUS” Cooler than what?
Cooler than HadCM3 - rephrased

Sections 3.3.3-3.3.5: The main “take away” message I get from these sections is that there is almost no change in simulated or reconstructed biomes over this 40,000 year-long interval, with the ice/land mask accounting for most of any change in the simulations. Is that right?
No, I don’t think that’s really what we’re saying. It’s true that the reconstructed biomes from our pollen records don’t show very much change over this period. Only two of these sites change their highest affinity score between 21 and 54 ka, and only really one between 54 and 64 ka. The global biome simulations however do show significant changes, especially between 21 and 54 ka – see figure 3 (was fig 2 in the first draft). In particular, differences in the different climate anomalies from HadCM3 and FAMOUS through this period can be seen to be significant in their impact on how the simulated biomes evolve. This is true well away from the immediate area of the icesheets, which are specified quite differently for the two models at 54ka.

However, the geographical locations, and sparseness of the pollen records that we have cannot show the quivalent evolution of these biomes over this period, or tell us which of the simulations is more realistic. We have tried to emphasise some of these points.

1056/25: “similar affinity scores to the 64 ka..” “similar affinity scores to those at 64 ka”?
OK .

1056/26: “they are sparse” Sites in general, or those with similar affinity scores at 64 and 84 ka?
Rephrased to 'there are not many sites'.

1057/1: Warmer than what?
The climate at 84 ka BP is simulated as generally warmer than 64 ka BP - rephrased

1057/7: “poorly modelled Mediterranean storm-tracks…” What’s the basis for that assertion?
Mediterranean stormtracks have been shown to be poorly modelled in GCMs of this era/resolution – see e.g.
Brayshaw, D. J., Hoskins, B. and Black, E. (2010) Some physical drivers of changes in the winter storm tracks over the North Atlantic and Mediterranean during the

Holocene. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 368 (1931). pp. 5185-5223

1057/9: “Although there are still differences….” I don’t understand “still”
Deleted still.

1057/12: “larger areas of forest”?
Rephrased.

1057/13: “a dry anomaly … that reduces vegetation” Again I think you’re equating “vegetation” with “forest”.
Deleted that reduces vegetation, especially in the HadCM3 reconstruction.

1057/25: “regional climate feedbacks” Explain.
This would take a few sentences to explain and would take away attention of our main message and have therefore rephrased this to ' The affinity scores for temperate forest are almost as high for this site, and neither climate model has the resolution to reproduce the local climate for this altitude well (Bush et al., 2010), although both do reflect dry conditions near the coast here.'

1057/28: “in line with … each other” I’m not sure what this means. Simply “both models”?
Rephrased.

1058/3: Both models increase the extent of their tropical forests…” Does this refer to the BIOME4 simulations? Throughout this section the climate simulations from the GCMs and the biome simulations from BIOME4 keep being conflated.
Rephrased

1058/11: “Quantitative estimates … can thus be drawn…” Yes, but are they meaningful?
Error estimates for this have been calculated and can be seen above in the reply to reviewer 1.
1058/16: “their overall effects” Overall effects of what? From proximity, “their” would refer to “areas and periods with significant regional differences” but that doesn’t make sense.
Changed to 'the effect'.

1058/18: Fig 3. There are three curves shown in each panel. I’m guessing “_S” means shelves and “_NS” means no shelves, but this isn’t explained
The naming conventions throughout have been changed for greater clarity - the new versions (N4F, B4H and B4H_NS) have been explained more clearly

1058/23: “The changes in atmospheric CO2 levels … are common to all BIOME4 runs.” Two things: 1) CO2 changes over time, so it makes no sense that the same levels were used for all runs. 2) CO2 levels presumably don’t vary within a single simulation.
rephrased

1059/3: “FAMOUS also neglects the additional area of land ...” What’s the argument here?
Simply that the FAMOUS-forced BIOME4 run has a smaller area available to be colonised by vegetation than the HadCM3-forced run does at certain periods

1059/5: “global total areas of biomes”?
Added 'of biomes'.

1059/14: “several sites (Fig. 4)” Curves for only one site area plotted in Fig. 4.
A new figure has been made that shows scores for relevant biomes for all sites

1059/16: “~ 70 to 75 PgCyr-1” Which is which? (Later you discuss the NPP values simulated by the two different simulated climates.)
We have now explicitly given the values as estimated separately for B4F and B4H in the text.

1059/23: “… BIOME4 is driven solely by an observational climate dataset…” (for the PI), so on
Added 'for the pre-industrial'.

line 28, the “lower resolution topography” being referred to is that in the 0.5-degree data, right? I find it hard to believe that there is enough smoothing in those data (relative to elevation in the real world) to account for all of the positive NPP bias.
See above, re: grids for BIOME4

1060/6: “In the LGM simulations….”
Rephrased 'The LGM simulations ..'

1060/20: “Further analysis with HadCM3 suggests…” What kind of analysis?
This sentence has been deleted and further detail added towards the end of the paragraph. We were able to separate out the impact of continental shelf exposure, CO_2 fertilization, and CO_2 forcing of climate by sensitivity experiments with BIOME4 driven with modern or time-slice appropriate CO_2, as well as excluding/including the continental shelf areas in global total NPP calculations.

1060/28: “Some differences in the timing of some events… are apparent…” What events?
By events we mean the timing of peaks and troughs on multi-millennial time-scales. These differ somewhat between B4F and B4H. This is mostly a result of the different CO_2 forcings used. The text has been changed to reflect this and we have deleted the perhaps misleading term ‘events’.

1061/7: “lower NPP” Than what?
lower NPP compared with pre-industrial times; this has been changes in the text

1061/22: Prentice et al. (1993). Not in references.
Added.

1062/13: Wang et al. (2011). Not in references.

Added

1062/11 – 1063/2: This discussion is really methods, not results. Are the turnover times for different biomes tabulated anywhere? Where does the exponential decay multiplier come from?
Turnover values are now given in Table 3. The decay multiplier is a global, generic estimate from Mahecha et al. 2010, and corresponds to a Q10 of 1.4

Mahecha, Miguel D. and Reichstein, Markus and Carvalhais, Nuno and Lasslop, Gitta and Lange, Holger and Seneviratne, Sonia I. and Vargas, Rodrigo and Ammann, Christof and Arain, M. Altaf and Cescatti, Alessandro and Janssens, Ivan A. and Migliavacca, Mirco and Montagnani, Leonardo and Richardson, Andrew D., Global Convergence in the Temperature Sensitivity of Respiration at Ecosystem Level, Science 2010 doi: 10.1126/science.1189587

1063/3: “The differences in modern NPP by biome between HadCM3 and FAMOUS (related resolution differences…” Please explain. Is “modern” different from “PI”? If so, there’s a whole set of simulations that haven’t been described anywhere (see also comments about p.1051). If not, why should there be differences?
Pre-industrial was indeed meant. Differences are down to the fact the BIOME4 is run on the two different model grid/resolutions, with some differences in soil properties, atmospheric CO2 levels and how accurately the minimum annual temperature could be calculated from the data available for each model. The resultant global scale NPP calculated is sensitive enough to these differences in each model to make it worth addressing each separately, we feel.

1063/14: “greater retention” Retained from what? (Sounds like from present…)
We intended this to mean that a greater area of forest biomes was maintained going into the last glacial with B4H due to its wetter/warmer climate. The sentence has been changed to clarify this.

1063/23: “greater level of periodicity” I think you’re confusing the amplitude with the presence or absence of variations at the ~ 23 kyr time scale.
We have altered the wording.

1063/26: “For the biome scores … (Fig. 3).” Figure 3 shows simulated biome areas.
Rephrased

1063/28: “The largest impact…” On what? The areas? The periodicity of the variations?
We have altered the wording to clarify that we meant the largest contribution to the 23-kyr variations is…

1064/8: “… because other forest types are not compensating periodicities in grassland variation…” No idea what this means.
Deleted this part of the sentence as being confusing and not necessary.

1064/15: I wonder at this point how much of the variation in Fig. 5 is related to the differences in the simulated climates and how much to the turnover times.

We have done some further sensitivity studies on this matter. As noted above, the turnover times derived from the modern carbon/PI NPP for each model are sensitive to the different model setups, and a range of timescales could be equally well justified (see also reply to reviewer1 regarding the NPP-carbon stock equilibrium assumption used in this method). The timescale uncertainty alone feeds through to an uncertainty in terrestrial soil carbon change from the PI to the LGM of order of 10 -20%. The rather large drop in terrestrial carbon reported for the FAMOUS-forced BIOME4 simulations appears to be at the upper end of the possible scale, so the inter-model difference is potentially a little exaggerated in our full results. Even allowing for this, there is still a significant contribution from the different model climates, especially in the smaller scale features in the curves rather than the headline PI to LGM difference. The discussion of figure 5 has been amended in the revised paper.

1064/17: This section has a lot of methods in it, and is rather late in the paper.
There is some method in this section. However as it is a stand on its own feature, derived from the model simulations it features better in its own section; otherwise readers have to make big leaps from this section to a new section with in the methods section 2 (around 25 pages before).

1065/10: “by the model output δ13C for each grid cell” Where do those values come from?
Added 'from BIOME4'.

1065/14: “did not estimate δ13C values” “did not vary (atmospheric) δ13C values”?
We have revisited this section, and are now interpolating atmospheric d13C between the time periods of the available ice core records, so this sentence is no longer relevant.

1065/16: “the calculated δ13C ocean changes would not change” “would not vary”?
Reworded.

1065/20: “total ocean δ13C was calculated for the last 120 kyr (Fig. 6b). Fig. 6b look like it shows anomalies from present day.
The wording has been changed to reflect the fact that we are calculating anomalies.

1066/ 18: “FAMOUS variation is nearly twice the magnitude” Twice the amplitude?
We changed magnitude with amplitude.

1066/21: “deep Pacific δ13C records” Where are those shown?
Rephrased records to stack.

1067/21: “Estimates of global carbon storage reduction are significantly greater if continental shelf exposure is not included…” But the shelves were exposed, so I’m not sure why this is even worth talking about.
Agreed – removed from conclusions

1068/4: “regional climate biases” Biases weren’t ever assessed. The simulated climates differ from one another, but they were never compared with climate reconstructions.

We rephrased this to 'differences in climates between the models…'

Terrestrial biosphere changes over the last 120 kyr and their impact on ocean $\delta^{13}C$

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Abstract

A new global synthesis and biomization of long (> 40 kyr) pollen-data records is presented, and used with simulations from the HadCM3 and FAMOUS climate models and the BIOME4 vegetation model to analyse the dynamics of the global terrestrial biosphere and carbon storage over the last glacial-interglacial cycle. ~~Global modelled (BIOME4)~~Simulated biome distributions using BIOME4 driven by HadCM3 and FAMOUS at the global scale over time generally agree well with those inferred from pollen data. The ~~two climate models~~simulations show good agreement in global net primary productivity (NPP). NPP is strongly influenced by atmospheric carbon dioxide (CO_2) concentrations through CO_2 fertilization. The combined effects of ~~modelled changes in~~simulated vegetation changes and (via a simple model) soil carbon result in a global terrestrial carbon storage at the Last Glacial Maximum that is 210-470 PgC less than in pre-industrial time. Without the contribution from exposed glacial continental shelves the reduction would be larger, 330-960 PgC. Other intervals of low terrestrial carbon storage include stadial intervals at 108 and 85 ka BP, and between 60 and 65 ka BP during Marine Isotope Stage 4. Terrestrial carbon storage, determined by the balance of global NPP and decomposition, influences the stable carbon isotope composition ($\delta^{13}C$) of seawater because terrestrial organic carbon is depleted in ^{13}C. Using a simple carbon-isotope mass balance equation, which combines the BIOME4 model derived terrestrial carbon store and carbon isotope discrimination with values for the atmosphere from ice core records, we find agreement in trends between modelled ocean $\delta^{13}C$ based on modelled land carbon storage, and palaeo-archives of ocean $\delta^{13}C$, confirming that terrestrial carbon storage variations may be important drivers of ocean $\delta^{13}C$ changes.

1. Introduction

The terrestrial biosphere (vegetation and soil) is estimated to contain around 2000 Pg C (Prentice et al., 2001) plus a similar quantity stored in peatlands and permafrost (Ciais et al., 2014). Variations in global climate on multi-millennial time scales have caused substantial changes to the terrestrial carbon pools. ~~Quasi-periodic~~Periodic variations in the Earth’s orbital configuration (axial tilt with a ~41 kyr period, precession with ~19and 23 kyr periods, and eccentricity with ~100 kyr and longer periods) result in small variations in the seasonal and latitudinal distribution of insolation~~ (Berger, 1978). These are~~, amplified by feedback mechanisms ~~such that for~~(Berger, 1978). For the last ~ 0.8 million years long glacial periods have been punctuated by short interglacials on roughly a 100 kyr cycle. Glacial periods are associated with low atmospheric CO_2 concentrations, lowered sea level and extensive continental ice-sheets; interglacial periods are associated with high (similar to pre-industrial) CO_2 concentrations, high sea level and reduced ice-sheets (Petit et al., 1999; Peltier et al., 2004).

During glacial-interglacial cycles the productivity of, and ~~size of~~carbon storage in, the terrestrial biosphere are influenced by orbitally forced climatic changes and atmospheric CO_2 concentrations. Expansion of ice-sheets during glacial periods caused a significant loss of land area available for colonization, but this was largely compensated by the exposure of continental shelves due to lower sea level. During the last glacial period the terrestrial biosphere was significantly reduced~~ as forests contracted.~~. It has been estimated that the terrestrial biosphere contained 300 to 700 Pg C less carbon during the Last Glacial Maximum (LGM; 21 ka BP) compared with pre-industrial times (Bird et al., 1994; Ciais et al., ~~2011~~2012; Crowley et al., 1995; Duplessy et al., 1988; Gosling and Holden, 2011; Köhler and Fischer, 2004; Prentice et al., 2011). As first noted by Shackleton et al. (1977), the oceanic inventory of carbon isotopes ($\delta^{13}C$) is influenced by terrestrial carbon storage because terrestrial organic carbon has a negative signature, due to isotopic discrimination during photosynthesis. Many of the estimates of the reduction in terrestrial carbon storage at the LGM have therefore been based on the observed LGM lowering of deep-ocean $\delta^{13}C$. A reduction in the terrestrial biosphere of this size would have contributed a large amount of CO_2 to the atmosphere, although ocean carbonate compensation would have reduced the expected CO_2 increase to 15 ppm over about 5 to 10 kyr (Sigman and Boyle, 2000).

Many palaeoclimate data and modelling studies have focused on the contrasts between the LGM, the mid-Holocene (6 ka BP) and the pre-industrial period. The BIOME 6000 project (http://www.bridge.bris.ac.uk/resources/Databases/BIOMES_data) synthesized palaeovegetation records from many sites to provide global datasets for the LGM and mid-Holocene. Data syntheses are valuable in allowing researchers to see the global picture from scattered, individual records, and to enable model-data comparisons. The data can be ~~viewed through~~ interpreted in the ~~prism~~context of a global, physically based model that allows the point-wise data to be ~~joined together~~seen in a coherent way. There are continuous, multi-millennial ~~palaeoenvironmental~~pollen records that stretch much further back in time than the LGM but they have not previously been brought together in a global synthesis~~.~~ to study changes of the last glacial-interglacial cycle. These records can provide a global picture of transient change in the biosphere and the climate system. Here we have synthesized and biomized (Prentice et al., 1996) a number of these records~~,~~ (for locations see Figure 1), providing a new dataset of land biosphere change that covers the last glacial-interglacial cycle. In section 2.1 we outline the biomization procedures applied to reconstruct land biosphere changes.

To improve understanding of land biosphere interactions with the ocean-atmospheric reservoir, we have modelled the terrestrial biosphere for the last 120 kyr ~~(e.g.~~, from the previous ~~—~~(Eemian~~—~~) interglacial to the pre-industrial period~~). We present quantitative estimates~~. Details of ~~changes in~~ the ~~terrestrial biosphere reconstructed from two~~ atmosphere~~-~~ ocean general circulation model (AOGCM) climate and vegetation model simulations ~~over the last glacial cycle. We~~are provided in section 2.2. In section 3 we evaluate biome reconstructions based on ~~these climate~~ our model outputs using the BIOME 6000 project (www.bridge.bris.ac.uk/resources/Databases/BIOMES_data), and our new biomized synthesis of terrestrial pollen data records, focusing on the pre-industrial period, 6 ka BP (mid-Holocene), 21 ka BP (LGM), 54 ka BP (a relatively warm interval in the last glacial period), 64 ka BP, (a relatively cool interval in the glacial period), 84 ka BP (the early part of the glacial cycle), and 120 ka BP (the Eemian interglacial). ~~We~~The effects of millennial scale climate fluctuations were not simulated. Finally in section 4 we use our biome simulations to estimate net primary productivity and terrestrial carbon storage. Using a simple $\delta^{13}C$ model, we then assess the contribution of terrestrial biosphere and carbon storage changes to deep ocean $\delta^{13}C$ over the last 120 kyr ~~by means of a comparison~~and compare this with deep ocean benthic foraminiferal carbon isotope records, representative for the $\delta^{13}C$ of deep ocean water.

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2 Methods

2.1 Biomization

Biomization assigns pollen taxa to one or more plant functional types (PFTs~~)~~ ~~based on basic biological and climatological ranges.~~). The PFTs are assigned to their respective biomes and affinity scores are calculated for each biome (sum of the square roots of pollen percentages contributed by the PFTs in each biome). This method was first developed for Europe (Prentice et al., 1996) and versions of it have been applied to most regions of the world (Jolly et al., 1998; Elenga et al., 2000; Takahara et al., 1999; Tarasov et al., 2000; Thompson and Anderson, 2000; Williams et al., 2000; Pickett et al., 2004; Marchant et al., 2009). We apply these regional PFT schemes (Table 1) to pollen records that generally extend > 40 kyr, assigning the pollen data to megabiomes (tropical forest, warm temperate forest, temperate forest, boreal forest, savannah/dry woodland, grassland/dry shrubland, desert and tundra) as defined by Harrison and Prentice (2003), in order to harmonize regional variations in PFT to biome assignments and to allow globally consistent model-data comparisons.

Table 2 lists the pollen records used. Biomization matrices and megabiome score data can be found in the Supplementary Information. For taxa with no PFT listing, the family PFT was used if part of the regional biomization scheme. ~~d.~~ Plant taxonomy was checked using itis.gov, tropicos.org, and the African Pollen Database. Pollen taxa can be assigned to more than one PFT either because they include several species in the genus or family, with different ecologies, or because they comprise species that can adopt different habitats in different environments.

Age models provided with the individual records were used. However, in cases where radiocarbon ages were only provided for specific depths (e.g. Mfabeni, CUX), linear interpolations between dates were used to estimate ages for the remaining depths. Some age models may be less certain, especially at sites which experience variable sedimentation rates and/or erosion. Sometimes more than one age model accompanies the data, illustrating the range of ages and also that there can be large uncertainties. To aid comparison, for several Southern European sites (e.g. Italy and Greece) it has been assumed that vegetation changes occurred synchronously within the age uncertainties of their respective chronologies, for which there is evidence (e.g. Tzedakis et al., 2004b).

2.2 Model simulations

Global ~~reconstructions~~ simulations of vegetation changes over the last glacial cycle were produced using a vegetation model (BIOME4) forced offline using previously published climate simulations from two AOGCMs~~.~~ (HadCM3 and FAMOUS). By using two models we ~~could~~ test the robustness of the reconstructions to different climate forcings.

2.2.1 HadCM3

HadCM3 is a general circulation model, consisting of coupled atmospheric model, ocean, and sea ice models (Gordon et al., 2000; Pope et al., 2000). The resolution of the atmospheric model is 2.5 degrees in latitude by 3.75 degrees in longitude by 19 unequally spaced levels in the vertical. The resolution of the ocean is 1.25 by 1.25 degrees with 20 unequally spaced layers in the ocean extending to a depth of 5200 m. The model contains a range of parameterisations, including a detailed radiation scheme that can represent the effects of minor trace gases (Edwards and Slingo, 1996). The land surface scheme used is the Met Office Surface Exchange Scheme 1 (MOSES1; Cox et al., 1999). In this version of the model, interactive vegetation is not included. The ocean model uses the Gent–McWilliams mixing scheme (Gent and McWilliams, 1990), and sea ice is a thermodynamic scheme with parameterisation of ice-drift and leads (Cattle and Crossley, 1995).

Multiple ‘‘snap-shot’’ simulations covering the last 120 kyr have been performed with HadCM3. The boundary conditions and set-up of the original set of simulations have been previously documented in detail in Singarayer and Valdes (2010). The snap-shots were done at intervals of every 1 ka between the pre-industrial (PI) and LGM (21 ka BP), every 2 ka between the LGM and 80 ka BP, and every 4 ka between 80 and 120 ka BP. Boundary conditions are variable between snap-shots but constant for each simulation. Orbital parameters are taken from Berger and Loutre (1991). Atmospheric concentrations of CO_2 were taken from Vostok (Petit et al., 1999) and CH_4, and N_2O were taken from EPICA (Spahni et al., 2005; Loulergue et al., 2008), all on the EDC3 timescale (Parrenin et al., 2007). The prescription of ice-sheets was achieved with ICE-5G (Peltier (2004) for 0-21 ka BP, and extrapolated ~~beyond 21 ka BP~~ to ~~120 ka BP~~the pre-LGM period from the ICE-5G reconstruction using the method described in Eriksson et al (2012). The simulations were each spun up from the end of previous runs described in Singarayer and Valdes (2010) to adjust to the modified ice-sheet boundary conditions for 470 years. The ~~climate averages~~monthly climatologies described hereafter are of years 470-499. The ~~climate averages were subsequently used to drive the BIOME4 biogeochemistry-biogeography~~ model performs reasonably well in ~~order to simulate~~terms of glacial ~~terrestrial ecosystem changes.~~ interglacial global temperature anomaly (HadCM3 is in the middle of the distribution of global climate models and palaeoclimate reconstructions), high latitude temperature trends (although as with all models, the magnitude of the temperature anomalies in the glacial is underestimated), as well as at lower latitudes (Singarayer and Valdes, 2010; Singarayer and Burrough, 2015).

2.2.2 FAMOUS

FAMOUS (Smith, 2012) is an Earth System Model, derived from HadCM3. It is run at approximately half the spatial resolution of HadCM3 to reduce the computational expense associated with atmosphere-ocean GCM simulations without fundamentally sacrificing the range of climate system feedbacks of which it is capable. Pre-industrial control simulations of FAMOUS have both an equilibrium climate and global climate sensitivity similar to that of HadCM3. A suite of transient FAMOUS simulations of the last glacial cycle, conducted with specified atmospheric CO_2, ice-sheets and changes in solar insolation resulting from variation in the Earth's orbit, compare well with the NGRIP, EPICA and MARGO proxy reconstructions of glacial surface temperatures (Smith and Gregory, 2012). ~~Although of a lower spatial resolution than HadCM3, these FAMOUS simulations have the benefit of being transient, and representing low-frequency variability within the climate system, as well as using more physically justified ice-sheet extents before the LGM.~~ For the present study, we use the most realistically-forced simulation of the Smith and Gregory (2012) suite (experiment ALL-ZH), forced with northern hemisphere ice-sheets ~~derived from~~taken from the physical ice-sheet modelling work of Zweck and Huybrechts (2005), atmospheric CO_2, CH_4 and N_2O concentrations from EPICA and orbital forcing from Berger (1978). Although of a lower spatial resolution than HadCM3, these FAMOUS simulations have the benefit of being transient, and representing low-frequency variability within the climate system, as well as using more physically plausible ice-sheet extents before the LGM than were used in the HadCM3 simulations. To allow the transient experiments to be conducted in a tractable amount of time, these forcings were all “accelerated” by a factor of ten, so that the 120 kyr of climate are simulated in 12model kyr – this method has been shown to have little effect on the surface climate (Timm and Timmerman, 2007; Ganapolski et al., 2010) although it does distort the response of the deep ocean. In addition, we did not include changes in sea level, Antarctic ice volume, or meltwater from ice-sheets to enable the smooth operation of the transient simulations. The impact on the terrestrial carbon budget of ignoring the continental shelves exposed by lower sea-levels will be discussed later; the latter two approximations are unlikely to have an impact over the timescales considered here. Although within the published capabilities of the model, interactive vegetation was not used during this simulation~~.~~, with (icesheets aside) the land surface characteristics of the model being specified as for a preindustrial simulation.

2.2.3 BIOME4

BIOME4 (Kaplan et al. 2003) is a biogeochemistry-biogeography model that predicts the global vegetation distribution based on monthly mean temperature, precipitation and sunshine fraction, as well as information on soil texture, depth and atmospheric CO_2. It derives a seasonal maximum leaf area index that maximises NPP for a given PFT by simulating canopy conductance, photosynthesis, respiration and phenological state. Model gridboxes are then assigned biome types based on a set of rules that use dominant and sub-dominant PFTs, as well as environmental limits. ~~Reconstructions~~

Two reconstructions of ~~glacial~~ the evolution of the climate ~~states~~over the last glacial cycle were obtained by ~~adjusting~~ calculating monthly climate anomalies with respect to the simulated pre-industrial for the HadCM3 and FAMOUS glacial climate simulations ~~to compensate for their individual pre-industrial climate biases in surface temperature~~respectively, then adding these anomalies, on the native FAMOUS and ~~precipitation on monthly timescales. Climate model anomalies were superimposed on~~HadCM3 grids, to an area averaged interpolation of the Leemans and Cramer (1991) observed climatology ~~(Kaplan et al., 2003).~~provided with the BIOME4 distribution. These climate reconstructions were then used to force ~~the~~two BIOME4 ~~model. This process~~simulations. The climate anomaly method allows us to correct for known errors in the climates of HadCM3 and FAMOUS and produce more accurate results from BIOME4, although the method assumes that the ~~model’s modern-day~~

~~errors are systematically present, unchanged over ice-free regions, throughout the whole glacial cycle. Soil properties on exposed shelves are~~pre-industrial errors in each model are systematically present, unchanged over ice-free regions, throughout the whole glacial cycle. We chose to use the actual climate model grids for the BIOME4 simulations, rather than interpolating onto the higher-resolution observational climatology grid, to avoid concealing the significant impact that the climate model resolution has on the vegetation simulation, and to highlight the differences between the physical representation of the climate between the two different models. Because of its lower resolution, FAMOUS cannot represent geographic variation at the same scale as HadCM3, which not only affects the areal extent of individual biomes, but also how altitude is represented in the model, which can have a significant effect on the local climate and resulting biome affinity. The frequency of data available from the FAMOUS run also limits the accuracy of the minimum surface air temperature it can force BIOME4 with, as only monthly average temperatures were available. This results in some aspects of the FAMOUS-forced BIOME4 simulation seeing a less extreme climate than it should, and artificially favours more temperate vegetation in some locations.

Soil properties on exposed shelves were extrapolated from the nearest pre-industrial land points. There is no special correction for the input climate ~~model temperatures~~anomalies over this exposed land, which results in a slightly subdued seasonal cycle at these points (due to smaller inter-seasonal variation of ocean temperatures). ~~BIOME4 was forced with appropriate CO_2 levels for each time slice simulation (same as used to force the climate model), derived from the ice core records~~The version of the observational climatology distributed with BIOME4 includes climate values for these areas. The BIOME4 runs used the time-varying CO_2 records that were used to force the corresponding climate models, as described in sections 2.2.1 and 2.2.2. As well as affecting productivity, the lower CO_2 concentrations found during the last glacial favour the growth of plants that use the C_4 photosynthetic pathway (Ehleringer et al., 1997), which can affect the distribution of biomes as well. All other BIOME4 parameters as well as soil characteristics were held constant at pre-industrial values.

The results of the HadCM3-forced BIOME4 simulation will be referred to in this paper as B4H, and those from the FAMOUS-forced BIOME4 simulation as B4F.

3. Results

In this section, the results of both the pollen-based biomization for individual regions and the biome reconstructions based on the GCM climate simulations will be outlined. ~~To limit the length of the paper, only main results are covered; the full synthesis dataset and model-based reconstructions are available from the authors.~~The biomized records and biomization matrix can be found in supplementary information. Biome changes relating to millennial scale climate oscillations are discussed elsewhere (e.g. Harrison and Sanchez Goñi, 2010 and references therein).

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3.1 Biomization

This method translates fossil pollen assemblages into a form that allows direct data-model comparison and allows the reconstruction of past vegetation conditions.

3.1.1 North America

Two regional PFT schemes were used for sites from North America: the scheme of Williams et al. (2000) for northern and eastern North America and the scheme of Thompson and Anderson (2000) for the western USA. ~~No weighting was~~For their study of biome response to millennial climate oscillations between 10 and 80 ka BP Jiminéz-Moreno et al. (2010) applied ~~to trees and shrub pollen data as proposed by Thompson and Anderson (2000) to be able to reconstruct woodland,~~one scheme for the whole of North America, with a subdivsion for southeastern pine forest~~ and desert biomes.~~. All biomization matrices and scores for individual sites used in our study, generally at 1 kyr resolution, as well as explanatory files can be found in the Supplementary Information. The Arctic Baffin Island sites (Amarok and Brother of Fog) have highest affinity scores for tundra during the ice-free Holocene and last interglacial.

At Lake Tulane (Florida) the *grassland and dry shrubland* biome has the highest affinity scores for the last 52 kyr, apart from two short intervals (~14.5 to15.5 ka and ~36.5 to 37.5 ka) where *warm-temperate forest* and *temperate forest* have highest scores~~.~~ (Fig. 2a). According to Williams et al. (2000), present day, 6 ka BP, and LGM records of most of Florida and the ~~Southwest~~Southeast of America should be characterized by highest affinity scores for the *warm-temperate forest* biome (Williams et al., 2000). The discrepancy of our biomization results with those of the regional biomization results of Williams et al. (2000) is due to high percentages of *Quercus*, *Pinus* undiff (both are in the *grassland and dry shrubland* and *warm-temperate forest* biomes), and Cyperaceae and Poaceae that contribute to highest affinity scores of the *grassland and shrubland* biome. Intestingly, the temperature forest biome has highest affinity scores in a short interval (~15 ka BP) during the deglacation (Fig. 2a). In Jiminéz-Morene et al. (2010) Pinus does not feature in the grassland and dry shrubland biome, but comprises a major component of the southeastern pine forest; hence their biomized Lake Tulane records fluctuates between the 'grassland and dry shrubland' biome and 'southeastern pine forest biome'.

In Northwest America pollen data from San Felipe (16 to 47 ka), Potato Lake (last 35 ka), and Bear Lake (last 150 kyr) all show highest scores for the *grassland and dry shrubland* biome. Potato Lake is currently situated within a forest (Anderson, 1993). In our biomizations *Pinus* pollen equally contribute to scores of *boreal forest*, *temperate forest*, *warm-temperate forest* and the *grassland and dry shrubland* biomes. In addition, high contributions of Poaceae occur so that the *grassland and dry shrubland* biome has highest affinity scores throughout the last 35 kyr. ~~-~~Again, in the Jiminéz-Morene et al. (2010) biomizations Pinus does not feature in the grassland and dry shrubland biome, hence the forest biomes have highest affinity scores in their biomizations. At Carp Lake the Holocene is characterized by alternating highest affinity scores between the *temperate forest* and *grassland and dry shrubland* biomes whereas during the glacial the *grassland and dry shrubland* biome attains highest affinity scores. The age model of Carp Lake suggests this record goes back to the Eemian, and if so, then last interglacial climate was lacking the alternation between the *temperate forest* and *grassland and dry shrubland* biomes as was the case during the late Holocene. ~~Recent~~Modern biomizations at Carp Lake and Bear Lake are similar to modern ~~biome observations (Thompson and Anderson, 2000)~~ and those of the LGM also compare well~~.~~ (Thompson and Anderson, 2000). Biomizations for Carp Lake between 10 and 80 ka BP by Jiminéz-Morene et al. (2010) generally look similar to ours, apart from 36, 57-70 and 72-80 ka BP where the temperate forest biome shows highest affinity scores because Pinus undiff. is treated as insignificant in their biomization. Biomizations of Bear Lake between 10 and 80 ka BP are similar to Jiminéz-Morene et al. (2010).

3.1.2 Latin America

The regional biomization scheme of Marchant et al. (2009) was used for Latin American locations. ~~Eleven~~Hessler et al. (2010) discuss the effects of millennial climate variability on the vegetation of tropical Latin America and Africa between 23N and 23S, using similar biomization schemes. In our studyeleven sites from

Central and South America are considered~~ here~~ covering a latitudinal gradient of 49^{o} (from 20 to -29^{o}) and an elevation range of 3900 m (from 110-4010 m asl [above sea level]) (Table 2). Five of the sites are from relatively low elevations (<1500 m asl), from north to south these are: Lago Quexil and Petén-Itzá in Guatamala and Salitre, and Colonia and Cambara in South East Brazil. The high elevation records (>1500 m asl), with the exception of the most northerly site in Mexico (Lake Patzcuaro), are distributed along the Andean chain: Ciudad Universitaria X (Colombia), Laguna Junin (Peru), Lake Titicaca (Bolivia/Peru) and Salar de Uyuni (Bolivia).

The five lowland sites indicate the persistence of forest biomes for much of the last 130 kyr (Fig. ~~2~~2bi). In Central American the Lago Quexil record stretches back to 36 ka ~~BPand~~BP and has highest affinity scores for the *warm-temperate forest* biome during the early Holocene. During glacial times the *temperate forest* biome dominates, intercalated with mainly the *grassland and dry shrubland* and *desert* biomes during the LGM and last deglaciation. At Lago Petén-Itzá (also Guatamala) highest affinity scores for the warm-temperate forest biome are recorded for the last 86 kyr. The Salitre and Colonia records are the only Latin American sites that fall within the *tropical forest* biome today. The majority of the Salitre record shows high affinities for *tropical forest* from ~64 ka BP –to modern; apart from an interval coinciding with the Younger Dryas which displays highest affinity scores for the *warm-temperate forest* biome. The southern~~-~~-most Brazilian record, at Colonia, has highest affinity scores for *tropical forest* for the last 40 kyr, except between 28 and 21 ka BP (~coincident with the LGM) when scores were highest for the *warm-temperate forest* biome. Between 120 and 40 ka BP highest affinity scores alternate between the *tropical forest* and *warm-temperate forest* biome at Colonia. The biomized Colonia record of Hessler et al. (2010) generally shows the same features, apart from an increase in affinity scores fo the dryer biomes between 10 and 18 ka BP. To the south, at Cambara (Brazil), highest affinity scores are found for *warm-temperate forest* during the Holocene and between 38 and 29 ka BP, whilst during the interval in between they alternate between *warm temperate forest* and *grassland and dry shrubland*.

Apart from Laguna Junin, higher elevation sites (>1500 m: Lake Patzcuaro, Titicaca, , Uyuni, and CUX) do not show a strong glacial-interglacial cycling in their affinity scores; Mexican site Lake Patzcuaro (2240 m) and Colombian site CUX (2560 m) have highest affinity scores mainly for *warm-temperate forest* over the last

35 kyr, although they alternate between *warm- temperate forest* and *temperate forest* during the Holocene and at CUX also during the LGM~~.~~ (Fig. 2bii). Lake Patzcuaro and CUX biomization results for the Holocene, 6 ka BP and LGM compare well with those derived by Marchant et al. (2009). At Uyuni (3643 m) highest affinity scores are for *temperate forest* and *grassland and dry shrubland* between 108 and 18 ka BP. At Titicaca (3810 m) high affinity scores are found for *temperate forest* over the last 130 kyr, apart from during the previous interglacial (Eemian) when highest affinity scores for the *desert* biome occur. Finally at ~~Ljunin~~Lago junin highest affinity scores alternate between *warm-temperate forest* and *temperate forest* during the Holocene and *temperate forest* and *grassland and dry shrubland* during the glacial.

3.1.3 Africa

For the biomization of African pollen records the scheme of Elenga et al. (2004) was applied. What is specifically different from Southern European biomizations is that Cyperaceae is not included as this taxon generally occurs in high abundances in association with wetland environments where it represents a local signal (Elenga et al., 2004). It is noted that most African sites are from highland or mountain settings, with the exception of Mfabeni (11 m.a.s.l.).

At the mountain site Kashiru swamp in Burundi the Holocene is characterized by an alternation of highest affinity scores for *tropical forest*, *warm temperate forest* and the *grassland and dry shrubland* biomes. During most of the glacial, scores are highest for the *grassland and dry shrubland* biome, preceded by an interval where *warm temperate forest* showed highest scores~~.~~ (Fig. 2c). Our results are similar to those obtained by Hessler et al. (2010). Highest affinity scores for *tropical forest* and *warm forest* were found during the Holocene at the Rusaka Burundi mountain site, whereas those of the last glacial again had highest scores for *grassland and dry shrubland biome*. At the Rwanda Kamiranzovy Site the *grassland and dry shrubland* biome displayed highest scores during the last glacial (from ~30 ka BP) and deglaciation, occasionally alternating with the *warm temperate forest* biome. In Uganda at the low mountain site Albert F (619 m) the Holocene and potentially Bølling Allerød is dominated by highest affinity scores for *tropical forest*, whereas the Younger Dryas and last glacial show highest affinity scores for the *grassland and dry shrubland* biome~~.~~ (Fig. 2c). In the higher-elevation Ugandan mountain site Mubwindi swamp (2150 m), the Holocene pollen record shows alternating highest affinity scores between *tropical forest* and the *grassland and dry shrubland* biome, whereas the glacial situation is similar to the Albert F site (e.g. dominated by highest scores for the *grassland and dry shrubland* biome). In South Africa, the Mfabeni Swamp record shows highest affinity scores for the *grassland and dry shrubland* biome for the last 46 kyr years occasionally, alternated with the *savanna and dry woodland* biome, and tropical forest during the late Holocene. At the Deva Deva Swamp in the Uluguru Mountains highest affinity scores are for *grassland and dry shrubland* for the last ~48 kyr. At Saltpan the grassland and dry shrubland biome dominates throughout the succession, including the Holocene and glacial. At Lake Tritrivakely (Madagascar) the grassland and dry shrubland biome dominates, apart from between 3 and 0.6 ka BP when the tropical forest biome dominates~~.~~ (Fig. 2c). Our results compare well with those of Elenga et al. (2004) who show a LGM reduction in tropical rainforest and lowering of mountain ~~vegetations~~vegetation zones in major parts of Africa.

3.1.4 Europe

For European pollen records three biomization methods were used that are region specific. For Southern Europe the biomization scheme of Elenga et al. (2004) was used, where Cyperaceae is included in the biomization as it can occur as 'upland' species characteristic of tundra. For sites from the Alps the biomization scheme of Prentice et al. (1992) was used, and for Northern European records the biomization scheme of Tarasov et al. (2000). Fletcher et al. (2010) use one uniform biomization scheme to discuss millennial climate in European vegetation records between 10 and 80 ka BP.

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In Southern Europe at the four Italian sites (Monticchio, Lago di Vico, Lagaccione and Valle di Castiglione) the Holocene and last interglacial show highest affinity scores for *warm temperate forest* and *temperate forest*. During most of the glacial and also cold interglacial substages the *grassland and dry shrubland* biome has highest affinity scores, whereas during warmer interstadial intervals of the last glacial the *temperate forest* biome had highest affinity scores again~~.~~ (Fig. 2di). At Tenaghi Phillipon and Ioannina a similar biome sequence may be observed, with highest affinity scores for *temperate forest* and *warm temperate forest* during interglacials. During the last glacial and last interglacial cool substages the *grassland and dry shrubland* biome showed highest affinity scores at Tenaghi Philippon. At Ioannina the LGM and last glacial cool stadial intervals have highest affinity scores for *grassland and dry shrubland*, whereas affinity scores of glacial interstadial periods are highest for *temperate forest*~~.~~ (Fig. 2di). Our biomization results for Southern European sites agree well with those of Elenga et al. (2004) who also found a shift to dryer grassland and dry shrubland biomes~~.~~ during glacial times. Instead of a desert and tundra biome Fletcher et al. (2010) define a xyrophytic steppe and eurythermic conifer biome in their biomizations, giving subtle differences in the biomization records, with the Fletcher et al. (2010) biomized records showing an important contribution of affinity scores to the xerophytic steppe biome. Characteristic species for the xerophytica shrub biome include artemisia, chenopodiaceae and ephedra, which in the Southern Europe biomization scheme of Elenga et al. (2000) feature in the dessert biome and grassland and dry shrubland biome (only ephedra).

All four alpine sites are from altitudes between 570 and 670 m and for all four sites the last interglacial period was characterized by having highest scores for the *temperate forest* biome~~.~~ (Fig. 2dii). At Füramoos the last glacial ~~(note hiatus between 15 and 41 ka BP)~~ showed highest affinity scores for the *tundra* biome, whilst during the Holocene the *temperate forest* biome shows highest affinity scores (Fig. 2dii). In the Fletcher scheme characteristic pollen for the eurythermic conifer biome include pinus and juniperus. In our biomization pinus and juniperus contributes to all biomes except for the desert and tundra biome.

Most Northern European sites are mainly represented for the last interglacial period, apart from Horoszki Duze in Poland. At most sites the *temperate forest* biome and *boreal forest* biome show highest affinity scores during the last interglacial (Eemian), whereas cool substages and early glacial (Butovka, Horoszki Duze) show high affinity scores for the *grass and dry shrubland* biome These results compare well with Prentice et al. (2000), who suggest a southward displacement of the Northern hemisphere forest biomes and more extensive tundra and steppe like vegetation during the LGM.

3.1.5 Asia

For the higher latitude site Lake Baikal the biomization scheme of Tarasov et al. (2000) was used. For the two Japanese pollen sites we used the biomization scheme of Takahara et al. (1999). At Lake Baikal, during the Eemian the highest affinity scores~~-~~ are for *boreal* and *temperate forest*; the penultimate deglaciation and cool substage show highest affinity scores for *grassland and dry shrubland*, similar to Northern European Sites. Pollen taxa such as *Carpinus*, *Pterocarya*, *Tilia cordata* and

Quercus have probably been redeposited or transported over a large distance; however they all make up less than 1% of the pollen spectrum and therefore did not influence the biomization much.

At Lake Suigetsu in Japan the *warm-temperate forest* biome shows highest affinity scores over the last 120 kyr; those of other biomes (including *tundra*) do show increasing affinity scores during glacial times but never exceeding those of the *warm-temperate forest* biome. At lake Biwa the *warm-temperate forest* biome shows highest affinity scores during interglacial times, whilst in-between they alternate between the *warm-temperate forest* biome and the *temperate forest* biome. These results agree well with those of Takahara et al. (1999~~).~~) and Takahara et al. (2010).

3.1.6 East Asia/Australasia

For East Asian and Australasian sites the scheme of Pickett et al. (2004) was used. In Thailand the Khorat Plateau site shows highest affinity scores for the *tropical forest* biome over the last ~40 kyr. At New Caledonia's Xero Wapa, the *warm-temperate forest* and *tropical forest* biomes show highest affinity scores over the last 127 kyr. In Australia's Caledonian Fen interglacial times (Holocene and previous interglacial) the *savanna and dry woodland* biome has highest affinity scores. During the glacial the *grassland and dry shrubland* biome generally shows highest affinity scores, occasionally alternated with highest scores for the *savanna and dry woodland* biome during the early part of Marine Isotope Stage (MIS) 3 and what would be MIS 5a (ca. 80-85 ka BP). Over most of the last glacial –interglacial cycle highest affinity scores at Lynch's Crater are for the *tropical forest* and *warm temperate forest* biomes with the *savannah and dry forest* biome important during MIS 4 to 2 and generally having the highest affinity scores between 40 and 7 ka BP, probably the result of increased biomass burning (human activities) causing the replacement of dry rainforest by savannah. In addition, the significance of what is considered to be tundra from MIS 4 is due to an increase in Cyperaceae with the expansion of swamp vegetation over what was previously a lake. At Okarito (New Zealand), the temperate *forest biome* has highest affinity scores throughout (occasionally alternated with *warm-temperate forest*), apart from during the LGM and deglaciation (~25to 14ka BP), where those of *savanna and dry woodland*, and *grassland and dry shrubland* show highest affinity scores. Biomization results for the Australian mainland and Thailand agree well with those obtained by Pickett et al. (2004) for the Holocene and LGM.

3.2 HadCM3/FAMOUS model comparison

Although the source codes of HadCM3 and FAMOUS are very similar, differences in the resolution of the models and the setup of their simulations results in a number of differences in both the ~~climate~~ climates they produce and the vegetation patterns ~~they produce for~~seen in B4H and B4F over the last glacial cycle. Specific regions and times where they disagree on the dominant biome type will be discussed later, but there are a number of features that apply throughout the simulations.

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~~Coupled to BIOME4, both models~~Both B4H and B4F keep the underlying soil types constant as for the ~~modern~~pre-industrial throughout the glacial cycle. In terms of the global land carbon budget, the largest difference between the ~~models~~simulations comes from whether sea-level changes are included or not. The HadCM3 ~~allows~~snapshot simulations allowed for the exposure of coastal shelves as sea-level ~~changes~~changed through the glacial cycle, with reconstructions based on Peltier and Fairbanks (2006) who used the SPECMAP $\delta^{18}O$ record (Martinson et al., 1987) to constrain ice volume/sea level change from the last interglacial to the LGM. FAMOUS, on the other hand, ~~keeps~~kept global mean sea level as for the present day throughout the whole transient simulation. As a consequence the area of land available to vegetation expands and contracts with falling and rising sea level in ~~HadCM3~~B4H but remains unchanged in ~~FAMOUS~~B4F. Inclusion of changing land exposure with sea level therefore allows for significant additional vegetation changes and represents a potentially major factor in the global carbon budget. This difference will be discussed further later.

~~Because of its lower resolution, FAMOUS does not represent geographic variation at the same scale as HadCM3. This not only affects the areal extent of individual biomes, but also altitude changes, which can have a significant effect on the local climate and resulting biome affinity.~~

Full details of the climates produced by FAMOUS and HadCM3 in these simulations can be found in Smith and Gregory (2012) and Singarayer and Valdes (2010). In general, land ~~surfaces in~~surface temperature anomalies in the HadCM3 simulations are a degree or so colder than in FAMOUS. This difference in temperature, present in some degree/we throughout most of the simulation is attributed mainly to differences in surface height and ice-sheet ice extent. FAMOUS model results are also, on average, slightly drier compared with those of HadCM3.

This is related to the model resolution, with HadCM3 showing much more regional variation (some areas become wetter and some drier), whilst FAMOUS produces a more spatially uniform drying as the climate cools. A notable exception to this general difference is in ~~northwestern~~north-western Europe, where FAMOUS more closely reproduces the temperatures reconstructed from Greenland ice-cores (Masson-Delmotte et al., 2005), compared to which the HadCM3 simulations used here have a significant warm bias at the LGM. Millennial scale cooling events and effects of ice-rafting are not features of our model runs, which present a relatively temporally smoothed simulation of the last glacial cycle.

3.3 Data-model comparison.

We present here an overview of the vegetation reconstructions for the last glacial-interglacial cycle ~~produced by the climate anomalies from HadCM3~~simulated in B4H and ~~FAMOUS~~B4F. We ~~focus on specific periods, since reviewing every detail present in this comparison is unfeasible. We thus compared the modelled reconstructions~~compare the simulated biomes in B4H and B4F with each other and with the dominant megabiome derived from the pollen-based biomizations~~ and each other~~, restricting our description of the results to major areas of agreement and disagreement. Maps of the dominant megabiomes produced by ~~BIOME4 using the climate anomalies from HadCM3~~B4H and ~~FAMOUS~~B4F for these periods can be seen in Figure ~~2~~3.

We focus on a few specific periods, detailed below, since reviewing every detail present in this comparison is unfeasible. The pre-industrial period serves as a test-bed to identify biases inherent in our model setup, before climate anomalies have been added. The 6 ka BP mid-Holocene period represents an orbital and ice-sheet configuration favouring generally warm northern hemisphere climate (Berger and Loutre, 1991). The LGM simulation at 21 ka BP is at the height of the last glacial cycle, when ice-sheets were at their fullest extent, orbital insolation seasonality was similar to present and CO_2 was at its lowest concentration (~185 ppm), and the resulting climate was cold and dry in most regions. These three time periods form the basis of the standard PMIP2 simulations and were used in the BIOME 6000 project. We thus additionally compare our simulations with the BIOME 6000 results for these time periods. The 54 ka BP interval is representative of peak warm conditions during Marine Isotope Stage 3 (MIS 3), where both the model climates and some proxy evidence suggest relatively warm conditions, at least for Europe (Voelker et al., 2002), associated with temporarily higher levels of greenhouse gases, an orbital configuration that favours warmer northern-hemisphere summers, and northern hemisphere ice sheet volume roughly half that of the LGM. The time slice 64 ka BP represents MIS 4, both greenhouse gases and northern-hemisphere insolation were lower, and northern hemisphere ice volume was two-thirds higher than at 54 ka BP, resulting in significantly cooler global climate. 84 ka BP is representative of stadial conditions of the early part of the glacial (at the end of MIS 5), after both global temperatures and atmospheric concentrations of CO_2 have fallen significantly and the Laurentide ice-sheet has expanded to a significant size but before the Fennoscandian ice-sheet can have a major influence on climate. The 84 ka BP period can be compared with the Eemian (120 ka BP, the earliest climate simulation used here), which represents the end of the last interglacial warmth (MIS 5e), before glacial inception. The Eemian period (120 ka BP) differs from the pre-industrial mainly in insolation. The earlier parts of the Eemian (e.g. 125 ka BP) are often studied due to their ~~additional warmth~~higher temperature and sea level compared to the Holocene (Dutton and Lambeck, 2012), but 120 ka BP is the oldest point for which both FAMOUS and HadCM3 climates were available.

3.3.1 Pre-industrial

Our BIOME4 ~~is~~simulations were forced using anomalies from the pre-industrial ~~climate~~climates produced by HadCM3 and FAMOUS. Differences between ~~our pre-industrial megabiome reconstructions~~B4H and B4F for this period thus only arise from the way the pre-industrial climate forcing has been interpolated onto the two different model grids we used. Differences between ~~the model~~ B4H and B4F and the pollen-based reconstructions for this period highlight biases that are not ~~to do with the~~directly derived from climates of HadCM3 and FAMOUS, but are inherent to BIOME4, the pollen-based reconstruction method, or simply the limitations of the models' geographical resolution.

Although few of the long pollen records synthesised in this study extend to the modern period and their geographical coverage is sparse, a comparison with previous high-resolution biomizations of BIOME6000 (see Table 1 for details; these studies include the sites synthesised here amongst many others) and Marchant et al. (2009)) show that they are generally representative of the regionally dominant biome. The biomized records of Carp Lake and Lake Tulane in North America are exceptions, showing dry grassland conditions rather than the forests (conifer and warm-mixed, respectively) that are more typical of their regions (Williams et al., 2000).

There is generally very good agreement between ~~the BIOME4 output~~B4H and B4F for this period and the high-resolution ~~biomization~~BIOME6000 and Marchant et al. (2009) studies. A notable exception, common to both ~~models~~B4H and B4F, can be seen in the south-west US being misclassified compared to the regional biomization of Thompson and Anderson (2000). The open conifer woodland they assign to sites in this region appears to be sparsely distributed (their figure 2) amongst larger areas likely to favour grassland and desert, and thus may be unrepresentative of areas on the scale of the climate model gridboxes. The limitations of HadCM3 and FAMOUS's spatial resolution appear most evident in South America, where the topographically-influenced mix of forest and grassland biomes found by Marchant et al. (2009) cannot be correctly reproduced, with disagreement at the grid-box scale between ~~FAMOUS~~B4F and ~~HadCM3~~B4H. Eurasia is generally well reproduced, although the Asian boreal forest does not extend far enough north, and overruns what should be a broad band of steppe around 50°N on its southern boundary. Australia, with a strong gradient in climate from the coasts to the continental areas also shows the influence of the coarse model resolutions, with ~~the translation to the FAMOUS grid~~B4F more accurately reproducing the southern woodlands but neither ~~model~~simulation reproducing the full extent of the desert interior. Both Australian records are from the eastern coastal ranges; there are no long continuous records in the interior because of the very dry conditions. Overall, ~~this~~our comparison with the full BIOME6000 dataset gives reasonable support to our working hypothesis that BIOME4, operating on the relatively coarse climate model grids we use here, is capable of producing a realistic reconstruction of global biomes.

3.3.2 6 ka BP mid-Holocene

~~For~~As for the pre-industrial, in both the mid-Holocene and LGM periods~~,~~ the high resolution biomizations of the BIOME6000 project (see Table 1) provide a better base for comparison of our model results than the relatively sparse, long time-series pollen records synthesised in this study. A common thread in the BIOME 6000 studies is the global similarity between the reconstructions for 6 ka BP and the pre-industrial, and this is, by and large, also the ~~message of our BIOME4 reconstructions using both FAMOUS and HadCM3 climate anomalies. A greening~~result seen in B4H and B4F. An increase in vegetation on the northern boundary of the central Africa vegetation band is the most notable difference compared to the pre-industrial in the regional biomizations (Jolly et al., 1998), which is also suggested by the long central African pollen records synthesised here. Both climate model-based reconstructions show grassland on the borders of pre-industrial desert areas in North Africa, although the additional ~~precipitation~~amount of rainfall in both models is too ~~weak~~low, and ~~is held a little~~the model resolution too ~~far~~low to ~~the south to "green"~~represent any significant "greening" of the desert~~ more fully. FAMOUS~~. B4F shows a ~~limited reduction~~smaller change in ~~the central African~~ tropical forest area in central Africa than ~~the HadCM3-based reconstruction~~B4H does, agreeing better with the regional biome reconstructions. Both ~~models~~HadCM3 and FAMOUS predict similar patterns and changes in precipitation for this period, but the magnitude of the rainfall anomaly in FAMOUS is slightly lower. The reduction in forest biomes at the tip of South Africa in ~~the FAMOUS reconstruction~~B4F has some support from Jolly et al. (1998), although ~~BIOME4 on the FAMOUS grid~~B4F initially overestimates forest in this area.

~~The model-based reconstructions~~B4H and B4F show limited changes elsewhere too. In North America, FAMOUS's ~~wetter~~increase in rainfall anomalies produce more woodland in the west in B4F compared to the pre-industrial, which ~~HadCM3 does~~is not seen in B4H. This is not a widespread difference shown in the regional biomization, although individual sites do change. Marchant et al. (2009) suggest drier biomes than the pre-industrial for some northern sites in Latin America, agreeing with ~~FAMOUS~~B4F but not ~~HadCM3~~B4H. For Eurasia and into China, Prentice (1996), Tarasov et al. (2000) and Yu et al. (2000) all suggest greater areas of warmer forest biomes to the north and west across the whole continent, with less tundra in the north. Neither ~~model-based reconstruction~~BIOME4 simulation shows these differences, however, with some additional grassland at the expense of forest on the southern boundary in ~~HadCM3~~B4H, and ~~FAMOUS~~B4F predicting more tundra in the north. Although both ~~models~~FAMOUS and HadCM3 produce warmer summers for this period, in line with the increased seasonal insolation from the obliquity of the Earth's orbit at this time, the colder winters they also predict for Eurasia skew annual average temperatures to a mild cooling which appears to ~~be preventing~~prevent the additional forest growth to the north and west seen in the pollen-based reconstructions.

3.3.3 21 ka BP (Last Glacial Maximum)

For the LGM, both ~~models~~the BIOME4 simulations and pollen-data-based reconstructions predict a global increase in grasslands at the expense of forest, with more tundra in northern Eurasia and desert area in the tropics than during the Holocene. Along with the cooler, drier climate, lower levels of atmospheric CO_2 also favour larger areas of these biomes. Our long pollen records do not have sufficient spatial coverage to fully describe these differences, showing only smaller areas of forest biomes in southern Europe, central Africa and Australia, but there is again good general agreement between ~~the~~our two ~~different model reconstructions~~BIOME4 simulations and the regional biomizations of the BIOME6000 project.

The ~~model~~FAMOUS and HadCM3 grids do not seem to have sufficient resolution to reproduce much of the band of tundra directly around the Laurentide ice-sheet in either B4H or B4F, but the forest biomes ~~they~~the simulations show for North America are largely supported by Williams et al. (2000). However, Thompson and Anderson (2000) suggest larger areas of the open-conifer biome in the southwestern US than in the Holocene that the ~~models~~BIOME4 simulations again do not show. Both ~~models~~B4H and B4F predict a smaller Amazon rainforest area. Marchant et al. (2009) suggest that the Holocene rainforest was preceded by cooler forest biomes, whereas both ~~models produce a climate~~HadCM3 and FAMOUS simulate climates that favours grasslands. Marchant et al. (2009) also provide evidence for cool, dry grasslands in the south of the continent; FAMOUS follows this climatic trend but B4F suggests desert or tundra conditions, whilst ~~HadCM3~~B4H shows a smaller area of the desert biome. For Africa, Elenga et al. (2000) show widespread grassland areas where the Holocene has forest, with which the ~~models~~simulations agree, and dry woodland in the southeast, with ~~which the models do not agree; they~~neither B4H or B4F show; HadCM3 and FAMOUS appear to be too cold for BIOME4 to retain this biome. Elenga et al. (2000) also shows increased grassland area in southern Europe, which is not strongly indicated by ~~the models having~~either B4H or B4F, which have some degree of forest cover here.

The large areas of tundra shown by Tarasov et al. (2000) in northern Eurasia to the east of the Fennoscandian ice-sheet are well reproduced by the ~~models~~BIOME4 simulations, although HadCM3's slightly wetter conditions produce more of the boreal forest in the centre of the continent in B4H. The generally smaller amounts of forest cover in Europe in ~~FAMOUS~~B4F agree with the distribution of tree populations in Europe at the LGM proposed by Tzedakis et al (2013) better than those from ~~HadCM3~~B4H, possibly due to HadCM3's warm bias at the glacial maximum. Both ~~models~~B4H and B4F agree with the smaller areas of tropical forest in China and southeast Asia reconstructed by Yu et al. (2000) and Pickett et al. (2004) compared to the Holocene, but have too much forest area in China compared to the biomization of Yu et al. (2000). Neither ~~model~~BIOME4 simulation reproduces the reconstructed areas of xerophytic biomes in south Australia, or the tropical forest in the north (Pickett et al., 2004).

3.3.4 54 ka BP (Marine Isotope Stage 3)

There are fewer published biomization results for periods before the LGM, so our model-data comparison is restricted to the pollen-based biomization results at sites synthesised in this paper. Of these sites, only two sites show a different megabiome affiliation ~~with respect~~when compared to the LGM: in South America Uyuni shows highest affinity scores for the forest biome, and in Australia, Caledonian Fen shows highest affinity scores for the dry woodland biome (both sites show highest affinity score for grassland during the LGM). Overall, the few sites where data are available show little differences compared with the LGM. This is perhaps a surprise given the evidence that this was relatively warm interval in the glacial, in Europe at least (Voelker et al., 2002). ~~The similar~~These mostly unchanged biome assignments derived from our pollen data records are supported by ~~the model~~our BIOME4 simulations in that, although both FAMOUS and HadCM3 do produce relatively warm anomalies compared to the LGM, ~~the model-based reconstructions for~~both B4H and B4F simulations at 54 ka BP are similar to the LGM ~~biomizations at~~local to the pollen sites in the Americas, most of southern Europe (apart from Ioannina where the data show highest affinity scores for temperate forest) and east Africa.

In other parts of the world, the biomes simulated at 54 ka BP ~~by the model~~in B4H and B4F do differ significantly from those of the LGM. Both ~~model~~BIOME4 simulations show increased vegetation in Europe and central Eurasia due to the climate influenced by the smaller Fennoscandian ice-sheet, as well as reduced desert areas in North Africa and Australia, generally reflecting a warmer and wetter climate under higher CO_2 availability~~. The models~~ than at the LGM. However our simulations disagree on ~~climates and~~both the climate anomalies and the likely impact on the vegetation in several areas in this period. These include differences, both local and far-field, related to prescribed ice-sheets, particularly in North America where the ice-sheet configuration in FAMOUS shows ~~a realistic two dome pattern. Further afield, HadCM3 model~~largely separate Cordilleran and Laurentide ice-sheets compared to the more uniform ice coverage of the continent in HadCM3. Further afield, B4H has significantly more tropical rainforest, especially in Latin America, and predicts widespread boreal forest cover right across Eurasia. ~~FAMOUS,~~B4F however, reproduces a more limited ~~vegetation~~forest extent, with more grassland in central Eurasia. The differences in the tropics appear to be linked to a ~~wetter climate~~larger rainfall anomalies in HadCM3 than FAMOUS, possibly due to a stronger response to precessional forcing, whilst the west and interior of northern Eurasia is cooler in FAMOUS than HadCM3, with a greater influence from the Fennoscandian ice-sheet.

3.3.5 64 ka BP (Marine Isotope Stage 4)

There are only a few differences between biomized records at the LGM, 54 ka BP, and 64 ka BP (Figure ~~2~~3). Apart from one southern European site (Ioannina), which has a highest affiliation with grassland (compared with temperate forest during the LGM), the pollen biome affiliations are much the same as at the LGM for the sites presented here. The two sites in northern Australasia show a highest affiliation with the warm-temperate forest biome during this period, compared with tropical forest at 54 ka BP, however affinity scores between the two types are close, so this is unlikely to be related to different climates. The ~~model-based reconstructions~~BIOME 4 simulations support this as they also ~~don't~~do not show major differences at the pollen sites~~-~~.

Both ~~model-based biome reconstructions~~B4H and B4F are, in general, similar ~~to those reproduced~~ for ~~54kyr.~~64 and 54ka BP. The 64ka BP climate ~~of 64kyr simulated~~ in HadCM3 is cooler and drier than for ~~54kyr,~~54ka BP, with B4H producing larger areas of tundra in north and east Eurasia and patchy tropical forests. There is less difference between ~~64kyr~~64ka BP and ~~54kyr~~54ka BP in the FAMOUS reconstructions, which simulates a cooler climate at ~~54kyr~~54ka BP compared to HadCM3, so ~~the FAMOUS~~B4F and ~~HadCM3 biome reconstructions~~B4H agree better in this earlier period~~.~~ than at 54ka BP. North American vegetation distributions primarily differ between ~~the models~~B4H and B4F in this period due to the different configurations of the Laurentide ice-sheet imposed on the climate models.

3.3.6 84 ka BP (Marine Isotope Stage 5b)

The pollen-based biomization for 84 ka ~~BPclearly~~BP clearly reflects the warmer and wetter conditions with more CO_2 available than at 64 ka BP, especially in

Europe, with the majority of sites showing highest affinity scores for the temperate forest biomes. Sites in other parts of the world show similar affinity scores to ~~the~~those at 64 ka BP timeslice, although ~~they~~there are ~~sparse~~not many sites and it is less clear whether they reflect widespread climatic conditions.

The ~~model-based reconstructions~~BIOME4 simulations reflect the warmer European climate resulting from the ~~small~~smaller Fennoscandian ice-sheet at 84ka BP than 64ka BP, with ~~FAMOUS~~B4F showing some European forest cover, and ~~HadCM3~~B4H extending Eurasian vegetation up to the Arctic coast. ~~The HadCM3-based reconstruction~~B4H shows more of this vegetation to be grassland rather than forest however, probably a result of a slightly cooler climate in ~~the model~~HadCM3. Around the southern European pollen sites themselves, however, ~~HadCM3~~B4H shows little ~~differences~~difference and ~~FAMOUS~~B4F predicts dry woodlands, perhaps a result of poorly modelled Mediterranean storm-tracks that would bring moisture inland.

Although there are ~~still~~ differences in the configuration of the Laurentide ice-sheet between the ~~models~~HadCM3 and FAMOUS, both ~~now~~B4H and B4F reproduce dry vegetation types in Midwest America and significant boreal forest further north at 84 ka BP. Both ~~models~~BIOME4 simulations show significantly smaller desert areas in North Africa and larger areas of forest in the tropical belt than at 64 ka BP, reflecting significant precipitation and higher CO_2 levels here, although both also show a dry anomaly over Latin America~~ that reduces vegetation, especially in the HadCM3 reconstruction.~~. Because of increased rainfall in Australia, ~~HadCM3 simulations show~~B4H shows a smaller desert compared with 54 ka BP.

3.3.7 120 ka BP (last interglacial period, Marine Isotope Stage 5e)

This time-slice represents the previous interglacial, and ~~should~~would be expected to have the smallest anomalies from the pre-industrial control climate of the climate models. The pollen-based biomization shows widespread forest cover for Eurasia, with the only other difference from both the 84 ka ~~BPperiod~~BP period and the pre-industrial control being Lake Titicaca, which has the highest affinity toward desert for this period. The affinity scores for temperate forest are almost as high for this site, and neither ~~climate model~~HadCM3 nor FAMOUS has the resolution to reproduce the local climate for this altitude well~~,~~ (Bush et al., 2010), although both do reflect dry conditions near the coast here~~, possibly as a result of regional climate feedbacks (Bush et al., 2010).~~.

The models do indeed produce relatively small climate anomalies and vegetation ~~in line with~~similar to the pre-industrial control and each other. Both models produce widespread forest cover north of 40N, much as for the pre-industrial climate, although FAMOUS is slightly too wet over North America for B4F to produce mid-west grasslands as seen in ~~HadCM3~~B4H. Both ~~models~~B4H and B4F increase the extent of their tropical forests, although FAMOUS has a relative dry anomaly over central Africa, ~~with~~and B4F has less tropical forest than for the pre-industrial or ~~HadCM3~~B4H, which once again appears to have a stronger response to precessional forcing.

4 Global terrestrial vegetation changes

~~The general agreement of the modelling results above across the two climate models and the pollen-based synthesis provides confidence in our global biome reconstructions for the last glacial cycle, although with qualifications as described above. Quantitative estimates of changes in the global terrestrial biosphere and the glacial carbon cycle can thus be drawn from our reconstructions.~~

There is good general agreement between our BIOME 4 simulations and pollen-synthesis, from both this paper and BIOME 6000. Below we calculate quantitative changes in the global terrestrial biosphere and carbon cycle, keeping in mind that these calculations carry some uncertainties relating to several mismatches. As is discussed in section 3.1 there are several occasions where the modern biomized pollen data do not agree with actual biome presence; for example Potato Lake and Lake Tulane in North America. In both cases high contributions of Pinus and some other taxa skewed the affinity scores towards drier biomes (grassland and dry woodland). For the past, not knowing whether a pollen distribution is representative for an area puts restrictions on the biomization method. It is however noted that in most cases the biomized pre-industrial pollen agree well pre-industrial biomes. The climate models produce some differences in climate forcing due to 1) difference in resolution, affecting the biome areal extent and altitude and 2) ice-sheet extent, affecting temperature (section 3.2). We can use the pre-industrial as a test-bed to compare model outputs and pollen-reconstructions (using the BIOME 6000 database): there are some biases that can be attributed to biases in BIOME4, some to the biomization method, and some to the models' limiting geographical resolution.

4.1 Biome areas

Whilst there is general agreement between ~~the biome reconstructions from the FAMOUS~~B4H and ~~HadCM3 climate anomalies~~B4F, there are also areas and periods with significant regional differences. A clearer picture of ~~their overall~~the effect on the global biosphere can be seen by using the global total areas of each megabiome for the two ~~models~~simulations (Figure ~~3~~4). Cooler temperatures, reduced moisture, and lower levels of CO_2 through the glacial result in a general reduction of forest biomes and increases in grassland, desert, and tundra. Lower levels of atmospheric CO_2 also preferentially favour plants using the C4 photosynthetic pathway (Ehleringer et al., 1997), contributing to the expansion of the grassland and desert biomes during the glacial. The changes in atmospheric CO_2 levels through the glacial cycle are common to all the BIOME4 ~~runs~~simulations, so CO_2 fertilisation effects and C3/C4 competition are not responsible for differences in vegetation response between ~~the FAMOUS-~~B4F and ~~HadCM3-forced simulation. FAMOUS~~B4H. B4F predicts consistently lower areas of warm-temperate and boreal forest than ~~HadCM3~~B4H, and higher amounts of grassland and desert. FAMOUS also neglects the additional area of land ~~available to~~that HadCM3 sees as continental shelves are exposed, reducing the area of land available to the biosphere, although some of this additional land is occupied by the northern hemisphere ice-sheets in HadCM3. The global total areas ~~highlight~~of biomes highlights a significant oscillation in the areas of the different megabiomes of ~20 kyr in length – this is particularly notable between 60 and 120 ka BP in the grassland megabiome and results from the 23 kyr cycle in the precession of the Earth's orbit. The precession cycle exerts a significant influence on the seasonality of the climate, as noted in tropical precipitation records (e.g. the East Asian monsoon; Wang et al., 2008). Such variations are not explicitly evident in the dominant megabiome types at any of the pollen sites, but the precession oscillation does appear in the individual biome affinity scores of several sites (Fig. ~~4~~2), lending support to this feature of the model reconstructions.

4.2 Net Primary Productivity

Net Primary Productivity (NPP) is the net flux of carbon into green plants (in this case terrestrial plants) due to photosynthesis, after accounting for plant respiration. Global NPP derived from our BIOME4 ~~reconstructions~~simulations for the PI is ~~~70-75~~74 PgC year^{-1}~~. This is~~ for B4H and 78 PgC year^{-1} for B4F. These values are somewhat higher than previously estimated present-day range of 46-62 PgC year^{-1}

(Tinker and Ineson, 1990; Nemani et al., 2003). Recent estimates using eddy covariance flux data estimate global NPP as ~62 PgC year^{-1} (assuming 50% carbon use efficiency to convert from GPP to NPP; Beer et al. 2010).

Some other model estimates for the PI are also lower (e.g. Prentice et al., 2011: 59.2 PgC year^{-1}). As mentioned in section 3.3.1, BIOME4 is driven solely by an observational climate dataset for the pre-industrial due to the anomaly approach used to reduce the impact of climate model biases (see methods section 2.1.3). Therefore, any overestimate in NPP is not a result of the climate model forcing but possibly due to biases in the vegetation model, and/or biases in the observational climatology used to drive the model, and ~~low~~the spatial resolution used. For example, the lower resolution topography does not represent mountainous regions such as the Andes well nor its topographically-induced variation in vegetation (see section 3.3.1), which may positively skew NPP values. The model may also overestimate NPP compared to observationally based techniques for the modern or pre-industrial partly because it does not contain any representation of non-climatically induced changes, e.g. cultivation or land degradation.

~~In the~~The LGM BIOME4 simulations show a global NPP ~~declines~~decline to ~42 PgC year^{-1} in ~~FAMOUS~~B4F and 48 PgC year^{-1} in ~~HadCM3~~B4H. While these are also higher than some other model-based estimates of 28-40 PgC year^{-1} (e.g. François et al., 1999; 2002), the relative decrease in the LGM in our ~~models~~simulations to approximately two-thirds of PI is consistent with several previous studies. A calculation based primarily on isotopic evidence has produced an even lower estimate of LGM NPP of 20 ± 10 PgC year^{-1} (Ciais et al., ~~2011~~2012); with LGM primary productivity approximately 50% lower than their PI estimate.

The PI-LGM difference is greater in ~~FAMOUS~~B4F than in ~~HadCM3~~B4H (Fig. 5a) primarily due to the fact that HadCM3's glacial land area increases as sea-level lowers, enabling additional NPP on continental shelf regions, whereas FAMOUS land area remains the same. This is demonstrated by recalculating global NPP for ~~HadCM3~~B4H neglecting exposed shelf regions (~~HadCM3~~B4H_NS), which then matches the values from ~~FAMOUS~~B4F (Fig. 5a, green line). The effect of vegetating continental shelves on global NPP is small in comparison to the overall decrease during the glacial period; NPP reduction at the LGM is 40% for ~~HadCM3_NS and 35% for HadCM3_S compared to the PI. Further analysis with HadCM3 suggests that CO_2 fertilization and CO_2 forcing of climate are the main~~

~~driving forces of the glacial NPP decrease – both of these factors are included in our model setups. By comparison, the~~B4H_NS and 35% for B4H compared to the PI. The impact of large continental ice-sheets reducing the land surface area available for primary production ~~is~~has a negligible~~, as these~~ effect on NPP compared to reduced CO_2 and glacial climate change. These high-latitude areas only contribute a small fraction of global NPP in any case~~;~~ and if the area covered in ice at the LGM is excluded from NPP calculations of the PI, global NPP only decreases by a maximum of ~5 PgC yr^{-1}. In addition, sensitivity tests with B4H, with and without CO_2, variation suggests that CO_2 fertilization, rather than climate, is the primary driver of lower glacial NPP (accounting for around 85% of the reduction in global NPP at the LGM).

Some differences in the timing of some ~~events~~multi-millennial peaks/troughs in NPP between ~~the HadCM3~~B4H and ~~FAMOUS-forced runs~~B4F are apparent, especially in the earlier half of the simulation. These ~~phase shifts~~differences, all of the order of a few thousand years, can largely be ascribed to the different CO_2 forcings used for B4H and B4F as well as the multiple snap-shot setup of the HadCM3 run, which only produces simulations at 2 or 4 ka intervals, compared to the 1 ka resolution of ~~the FAMOUS-forced biome reconstruction.~~B4F. Differences in the forcing provided by the ice-sheet reconstructions used in the models, as well as in the strength of their responses to orbital forcing in the early part of the glacial (see Figure ~~3~~4) may also play a role.

Both ~~models~~BIOME4 simulations predict slightly lower NPP during the previous interglacial, the Eemian ~~(–~~(3-5 PgC yr^{-1}~~).~~ lower) compared with pre-industrial times. The first large-scale decrease in NPP occurs during the initial glaciation following the Eemian~~, estimated at about 10 PgC yr^{-1} (~~, between 120 ka BP and 110 ka BP (in both ~~models). NPP values~~simulations). There is then ~~go up and down by ~ 2 to 5 PgC year^{-1} until another~~a second large drop of –10 PgC yr^{-1} (HadCM3_S) to –20 PgC yr^{-1} (~~HadCM3-~~B4H_NS, ~~FAMOUS _NS) ~70~~B4F) between 75 ka BP and 60 ka BP, associated with MIS 4. ~~NPP than recovers to similar values as between 105 and 70 ka BP (MIS 5d to 5a)~~NPP then increases during MIS 3, followed by the final reduction (–10 PgC year^{-1}) to lowest values during the LGM (Figure ~~5).~~6). We note here that the details of the magnitude and timing of the NPP variations will be highly dependent on the prescribed CO_2 curve given that CO_2 fertilization is the predominant factor driving the changes. A recent composite CO_2

curve derived from several ice core records (Bereiter et al., 2013) has CO_2 that is 5-20ppm higher during MIS4 than either Vostok or EDC records. Further sensitivity tests with B4F forced with higher CO_2 levels suggest that NPP could be up to 8 PgC/yr higher at certain time slices (see supplementary Figure 1).

4.3 Terrestrial carbon storage

Early modelling studies and data-based reconstructions produced a range of 270-1100 PgC decrease in terrestrial carbon storage during the LGM compared with pre-industrial time (see summary table 1 in Kohler and Fischer, 2004). These estimates were based on various techniques including isotopic mass balance based on known marine and atmospheric $\delta^{13}C$ values (Bird et al., 1994), and either data-based or simple model-based reconstructions where constant carbon storage per unit area of each biome was assumed (e.g. Prentice et al., 1993; Crowley, 1995). These early estimates were unreliable, however, because (a) they do not account for variation in carbon storage within biomes and (b) they neglect the substantial influence of atmospheric CO_2 concentration on carbon storage (see Prentice and Harrison, 2009, for a fuller discussion). More recent studies have narrowed the range of LGM terrestrial carbon storage decreases to 300-700 PgC. Prentice et al. (2011) estimated a 550-694 PgC decrease at the LGM using the LPX dynamic vegetation model forced by four Palaeoclimate Modelling Intercomparison Project Phase II climate model runs for the LGM. Using isotopic and modelling methods Ciais et al. (~~2011~~2012) suggested that only 330 PgC less carbon was stored in the terrestrial biosphere at the LGM than PI Holocene. While this is of the same order as other estimates it represents a reduction of only 10% from PI. Ciais et al. (~~2011~~2012) also included a large inert carbon pool to represent permafrost and peatland carbon storage (which are not included in most dynamic vegetation models). Their optimization procedure suggested that this inert carbon pool was larger by 700 PgC at the LGM than PI, meaning the reduction in their active terrestrial biosphere was therefore larger than most other studies have suggested, at approximately 1000 PgC.

As BIOME4 does not compute the size of the terrestrial carbon reservoir, here we estimate carbon storage over the last glacial cycle using the method of Wang et al. (2011). Consistent with BIOME4's assumption of steady states for its reconstructed vegetation, this method assumes that the carbon storage for each gridpoint is in balance with the modelled NPP, via turnover times ~~characteristic of the soil and~~

~~vegetation. Total terrestrial carbon storage is then the sum of vegetation carbon, C_{veg}, and soil carbon, C_{soil} derived using equations 1 and 2 below:~~that are characteristic of the soil and vegetation. Although the heterogeneity of soil organic matter means that some soil carbon varies on millennial timescales, the soil response to changes in climate tends to be dominated by the more labile carbon pools, with effective residence times for soil carbon being measured in decades rather than centuries (Carvalhais et al., 2014). The steady-state soil carbon assumption used here neglects a lag in total biosphere carbon response, although on the millennial timescales analysed here it is unlikely to introduce major inaccuracy.

$$\cancel{C_{veg} = \sum_{biome} NPP_{biome} \cdot \tau^{v}_{biome}} \qquad \cancel{[1]}$$

$$\cancel{C_{soil} = \sum_{biome} NPP_{biome} \cdot \tau^{s}_{biome} \cdot \exp\left[-k\left(T - T_{ref}\right)\right]}$$

We estimate total terrestrial carbon storage as the sum of vegetation carbon, C_{veg}, and soil carbon, C_{soil} derived using equations 1 and 2 below:

$$C_{veg} = \sum_{biome} NPP_{biome} \cdot \tau^{v}_{biome} \qquad [1]$$

$$C_{soil} = \sum_{biome} NPP_{biome} \cdot \tau^{s}_{biome} \cdot \exp\left[-k\left(T - T_{ref}\right)\right] \qquad [2]$$

where ~~τ^{v}_{biome}~~ τ^{v}_{biome} is the turnover time of vegetation carbon, which is assumed to depend primarily on vegetation type, and is therefore kept constant for each mega-biome. The turnover time of soil is heavily dependent on temperature and therefore ~~τ^{s}_{biome}~~ τ^{s}_{biome} is modified by the multiplier ~~$\exp\left[-k\left(T - T_{ref}\right)\right]$,~~ $\exp\left[-k\left(T - T_{ref}\right)\right]$, where T is the surface temperature at each grid cell, T_{ref} is the temperature for the PI, and k=0.034~~.~~ (corresponding to a Q_{10} value of 1.4) following Wang et al. (2011). The time constants ~~τ^{v}_{biome}~~ τ^{v}_{biome} and ~~τ^{s}_{biome}~~ τ^{s}_{biome} were estimated separately for the ~~FAMOUS~~B4F and ~~HadCM3 biome reconstructions~~B4H by dividing modern carbon storage by the model's reconstructed ~~modern~~pre-industrial NPP, using carbon storage values for each megabiome from Table 3.2 (MRS and IGBP columns) in Prentice et al (2001). The values for the derived turnover times are given in Table 3.

The small differences in ~~modern~~ pre-industrial NPP by biome between ~~HadCM3~~B4H and ~~FAMOUS~~B4F (related to both model setup and resolution differences between HadCM3 and FAMOUS) result in differences in ~~τ^{v}_{biome} and τ^{s}_{biome}~~

τ^{v}_{biome} and τ^{s}_{biome} values used to calculate carbon storage, and hence different sensitivities to changes in NPP. The assumption of equilibrium between carbon storage and simulated NPP inherent to this method means that the calculation of these time constants, and the resultant estimates of terrestrial carbon storage, are rather sensitive to small differences in the setups of the models and the choice of modern carbon storage data used for comparison. This leads to an additional uncertainty of around 10% on the terrestrial carbon storage numbers thus derived.

During the interglacials ~~FAMOUS~~B4F and ~~HadCM3~~B4H estimate high terrestrial carbon storage: 2100 PgC during the pre-industrial period and 2000 PgC during the last interglacial (Fig. 5b). However, entering the glacial, ~~FAMOUS predicted~~B4F predicts larger carbon storage decreases than ~~HadCM3~~B4H. During the LGM, the terrestrial carbon reduction of 800 PgC is nearly twice as large in ~~FAMOUS~~B4F compared with ~~HadCM3_S~~B4H (470 PgC). Roughly one third of the difference between ~~FAMOUS~~B4F and ~~HadCM3 results from~~B4H can be accounted for by the increase in continental shelf area in HadCM3 that are not included in FAMOUS. The ~~other two thirds results~~rest comes partly from the wetter and warmer climate in glacial HadCM3 than FAMOUS~~. This~~, which enables a greater retention of forest ~~biomes,~~biome areas into the glacial in ~~particular warm temperate and boreal forest~~B4H (Figures 2 and 3~~).~~), and partly from differences in the carbon turnover times derived for each model. In particular the timescales derived for B4F likely give an upper bound on the change in terrestrial carbon that might be expected from the FAMOUS glacial climate anomalies.

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Both ~~HadCM3~~B4H and ~~FAMOUS~~B4F give Holocene total terrestrial carbon storage estimates similar to previous studies including Ciais et al.'s (~~2011~~2012) estimates for the active land biosphere. The reduction in carbon storage at the LGM compared to pre-industrial time according to ~~HadCM3~~B4H is within the range given previously, whereas the estimate from ~~FAMOUS~~B4F is larger than most estimates, but more similar to Ciais et al.'s estimated (~~2011~~2012) decrease for the active terrestrial biosphere.

Closer examination of the trends during the last glacial cycle reveals that modelled terrestrial carbon storage (Fig. 5b) displays ~~a greater level of periodicity on~~variation at the ~23 kyr time-scale ~~than~~that is not evident for NPP (Fig. 5a), in both ~~FAMOUS~~B4F and ~~HadCM3~~B4H for the early glacial. The prevalence of a ~23 kyr cycle relates to the precession of the Earth's orbit, changing the seasonality of climate. ~~For the biome scores this~~This periodicity is particularly notable between 60 and 120 ka BP (when eccentricity modulation of precession is largest) in the grassland and temperate forest megabiome areas (Fig. ~~3~~4). The largest ~~impact~~contributor to this multi-millennial variability in carbon storage is~~ from~~ the extent to which northern hemisphere mid-latitudes are forested (temperate forest vs. grassland). This variation at 23-kyr periodicity is more evident in ~~FAMOUS~~B4F than ~~HadCM3~~B4H, even though both models drive similar sized periodical changes in megabiome coverage. In ~~HadCM3~~B4H, slightly wetter glacial conditions result in greater overall forested areas; a decline in temperate and tropical forest is compensated for by an increase in warm-temperate and boreal forest (Fig. ~~3). FAMOUS~~4). B4F, on the other hand, shows declines in all forest types through the glacial. This drives a greater glacial decline in ~~FAMOUS~~B4F carbon storage, as well as slightly larger precessional variation in carbon storage~~, because other forest types are not compensating periodicities in grassland variation, as they do in HadCM3~~.

The first large-scale reduction in terrestrial carbon storage occurs shortly after the previous interglacial, where both models (including ~~HadCM3_S~~B4H) show a 500 PgC decrease (Figure ~~5~~6). Predicted sizes of the terrestrial biosphere then vary around a 1800 PgC mean by about ±100 PgC for ~~HadCM3_S~~B4H and B4H_NS, whereas ~~FAMOUS~~B4F shows another large decrease at ~ 65 ka BP by another 500 PgC, providing terrestrial carbon storage estimates in MIS 4 that are similar to the LGM.

4.4 Implications for ocean carbon

Changes in ocean carbon storage have been calculated here by combining the modelled changes in terrestrial biosphere carbon storage with changes in atmospheric carbon dioxide recorded in ice cores. The ~~decrease~~difference in atmospheric carbon between the PI and LGM is approximately 180 PgC (Barnola et al., 1987) which when added to the decrease in terrestrial carbon storage, equates to an increase in total ocean carbon storage of 1050 PgC for ~~FAMOUS~~B4F and 650 PgC for ~~HadCM3_S~~B4H.

Globally decreased LGM deep ocean stable carbon isotope ratios ($\delta^{13}C$), as recorded by benthic foraminifera at –0.3 to –0.4‰, suggests that global LGM terrestrial carbon storage was decreased by 500 to 700 Pg compared with the PI (assuming vegetation and soil $\delta^{13}C$ of –25‰) (e.g. Broecker and Peng, 1993;

Duplessy et al., 1988, Bird et al, 1996; Kaplan et al., 2002; Beerling et al, 1999). A more recent estimate derived from a compilation of 133 ocean cores is –0.34 ± 0.13‰ (Ciais et al., ~~2011~~2012). An ensemble of ocean circulation model simulations suggests a similar decrease of -0.31 ± 0.2‰ (Tagliabue et al., 2009).

Using our modelled glacial-interglacial terrestrial carbon storage changes the above approach may be inverted to estimate global ocean $\delta^{13}C$ changes over the same time period. The mass balance approach of Bird et al. (1996) was followed to estimate ocean $\delta^{13}C$ at any point from 120 ka BP to the PI. Using the modelled terrestrial biosphere carbon mass and that of the atmosphere (from the ice core record), contributions to global ocean mass changes were estimated. First, changes in total terrestrial biosphere $\delta^{13}C$ were estimated by multiplying the terrestrial carbon storage calculated at each grid point (described above in section 3.4.3) by the model output $\delta^{13}C$ for each grid cell~~.~~ from BIOME4 (the model outputs discrimination, which is then subtracted from the atmospheric $\delta^{13}C$). These were then averaged to produce a global terrestrial biosphere $\delta^{13}C$ (Fig. 6a). ~~We then assumed a constant atmospheric $\delta^{13}C$. An ice~~Ice core records suggests variations in atmospheric $\delta^{13}C$ between –6.~~5~~4 to –7‰ but the time ~~period~~periods covered only extends ~~to~~from the LGM through the deglaciation (Leuenberger et al., 1992; Lourantou et al., 2010; Schmitt et al., 2012~~), so we chose~~) and the penultimate deglaciation (Schneider et al, 2013), but does not ~~to have to estimate $\delta^{13}C$~~cover the last glacial period. Comparison of the two time periods shows that the LGM was around 0.4‰ heavier than the penultimate glacial maximum, suggestive of a long-term trend (Schneider et al., 2013). We use the values from the ice core records for the available time periods and interpolate between ~~-~~22 and ~~120 ka~~105 kyr BP ~~and instead kept all values at –6.5‰.~~to echo the long-term trend. Sensitivity tests (not shown) demonstrated that the calculated $\delta^{13}C$ ocean changes would not ~~change~~be significantly different whether constant modern (-6.5‰) or varying atmospheric $\delta^{13}C$ was used~~ (the maximum difference at LGM was 2% on total ocean $\delta^{13}C$ depending on whether –6.5 or –7‰ was assumed). Combining~~. Differences in calculated ~~terrestrial and atmospheric $\delta^{13}C$ and~~ocean $\delta^{13}C$ were generally less than 4% (0.02‰) and were a maximum of 15% during the Younger Dryas (~12-11 kyr BP) from either prescribing a modern –6.5‰ or measured –7‰. In other words, global ocean $\delta^{13}C$ is not particularly sensitive to atmospheric $\delta^{13}C$. Calculated terrestrial and atmospheric $\delta^{13}C$ were combined and, assuming total isotopic mass balance over time, total ocean $\delta^{13}C$ ~~was~~anomalies from pre-industrial were calculated for the last 120 kyr (Fig. 6b).

The modelled terrestrial biosphere $\delta^{13}C$ (Fig. 6a) displays the largest increase during the LGM when atmospheric CO_2 was at its lowest concentrations, due to changes in C_4 vegetation input (C_4 vegetation discriminates against ^{13}C less than C_3 vegetation when carbon is incorporated by photosynthesis). Consequently, $\delta^{13}C$ increases (becomes less negative) when C_4 vegetation is more prevalent. The differences in biome area between ~~FAMOUS~~B4F and ~~HadCM3-driven output~~B4H (Fig. ~~3~~4), in particular warm temperate and boreal forest coverage, do not result in large differences in terrestrial biosphere $\delta^{13}C$. The extent of C_4 type vegetation is similar between the models and differences in other biomes have little impact on overall isotopic signature.

The reconstructed total ocean $\delta^{13}C$ of the two models mimics the trends in total terrestrial carbon storage; when carbon storage is reduced, ocean $\delta^{13}C$ decreases and when carbon storage is increased, ocean $\delta^{13}C$ increases (Figure ~~5, ~~6~~).~~, 7). Changes to terrestrial biosphere $\delta^{13}C$ are of secondary importance compared to the size of the terrestrial carbon pool. The total ocean LGM to PI change in $\delta^{13}C$ as estimated using this method is –0.34‰ for ~~HadCM3_S~~B4H and –0.65‰ for ~~FAMOUS~~B4F (Fig. 6b). The additional exposed continental shelf areas available in HadCM3 account for ~~only a small proportion~~less than half of the difference between the two (compare ~~HadCM3_S~~B4H and ~~HadCM3~~B4H_NS in Fig. 6b). Even though ~~FAMOUS~~B4F and ~~HadCM3~~B4H display similar trends in terrestrial biosphere $\delta^{13}C$, the larger decrease in terrestrial carbon from ~~FAMOUS~~B4F results in almost double the change in ocean $\delta^{13}C$~~. The predicted PI to LGM decrease in total ocean~~ ~~$\delta^{13}C$~~ ~~from HadCM3~~, although as noted above this is ~~similar to that inferred e.g.~~ likely at the extreme end of the uncertainty~~by Ciais et al. (2011) and Tagliabue et al. (2009) whereas FAMOUS seems be outside the~~ range of ~~recent estimates.~~ the consequences of the FAMOUS climate anomalies.

The predicted PI to LGM decrease in total ocean $\delta^{13}C$ from B4H is similar to that inferred e.g. by Ciais et al. (2012) and Tagliabue et al. (2009) whereas B4F seems be outside the range of recent estimates. Recently compiled deep ocean records of Oliver et al. (2010), covering the last glacial cycle, display similar trends to our modelled ocean $\delta^{13}C$ over the entire glacial cycle (Fig. 6b and c). The absolute magnitude of glacial-interglacial variation in ~~HadCM3~~B4H is closer to that in the

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reconstructions, whereas ~~FAMOUS~~B4F variation is nearly twice the ~~magnitude~~amplitude. However, the temporal variation in ~~FAMOUS~~B4F has some features that are more similar to the data compilation, such as lighter values in MIS4 that are similar to the LGM values (Fig. 6b and c). The $\delta^{13}C$ excursion of deep Pacific $\delta^{13}C$ ~~records~~stack ~ 64 ka BP (coincident with Marine Isotope Stage 4 or the early Wisconsin glacial advance) is as large as, or larger than that of the LGM (Oliver et al., 2010), and is not notable in the ~~HadCM3~~ B4H-derived estimates~~.~~ (Fig. 6). The very low deep Pacific values might not be completely due to changes in terrestrial carbon storage and perhaps partly relate to reorganisation of water masses and/or ocean productivity (Kohfeld et al., 2005; Leduc et al., 2010~~).~~, Bereiter et al., 2012). Most longer benthic foraminiferal $\delta^{13}C$ records show even lower values during the penultimate glaciation, as part of a longer timescale trend in increasing ocean $\delta^{13}C$ since ca. 250 ka BP (Hoogakker et al., 2006; Piotrowski et al., 2009; Oliver et al., 2010), which is not captured here. This may be related to longer-term in carbon reservoirs changes that may be linked to changes in ocean ventilation and/or productivity (Wang et al., 2001; Hoogakker et al., 2006; Rickaby et al., 2007), not represented in our modelling approach.

Our model estimates assume a constant inert terrestrial carbon pool (permafrost and peatlands). As described in section 4.3, Ciais et al (2012) infer that this carbon pool was larger by around 700GtC at the LGM compared with the pre-industrial. We have estimated the impact on ocean $\delta^{13}C$ of including this estimate and its uncertainty (700GtC ± 600 GtC; Ciais et al, 2012), assuming that the inert terrestrial carbon pool was the same size at the last interglacial as the PI with an average $\delta^{13}C$ of -27‰, linearly interpolating to the LGM estimate. While there are large uncertainties on the inert terrestrial pool, in general its inclusion improves the B4F comparison to data (Supplementary Figure 2) and results in poorer simulated changes from B4H. Including uncertainties in the size of the inert terrestrial carbon store, atmospheric CO2, atmospheric $\delta^{13}C$, and discrimination in permafrost, the PI to LGM decline in global ocean $\delta^{13}C$ from the B4F model is -0.4 ± 0.2‰, and -0.1 ± 0.2‰ for B4H.

While the distribution of $\delta^{13}C$ in oceans is affected by several factors such as reorganisation of water masses (especially in the North Atlantic), ocean productivity and export (Brovkin et al., 2002; Kohfeld and Ridgwell, 2009) and nutrient utilisation, the modelled results presented here suggest that the large-scale trends in ocean $\delta^{13}C$ ~~are~~may be dominated by terrestrial carbon storage variation, as Shackleton (1977) first proposed.

5. Conclusions

We have used a new global synthesis and biomization of long pollen records in conjunction with model simulations to analyse the sensitivity of the global terrestrial biosphere to climate change over the last glacial-interglacial cycle. Model output and biomized pollen data generally agree, lending confidence to our global-scale analysis of the carbon cycle derived from the model simulations. We used the models to estimate changes in global terrestrial net primary production and carbon storage. Carbon storage variations have a strong 23-kyr (precessional) cycle in the first half of the glacial cycle in particular. Estimates of global carbon storage by a BIOME4 simulation forced by HadCM3 climate at the LGM are ~470 PgC below modern levels~~ if~~, taking the contribution of exposed continental shelves and their colonisation are taken into account.~~ Estimates of global carbon storage reduction are significantly greater if continental shelf exposure is not included, with FAMOUS showing the largest changes.~~ Other intervals of significant reductions in terrestrial carbon storage include stadial conditions ~115 and 85 ka BP and between 60 and 65 ka BP during Marine Isotope Stage 4. Comparison of modelled ocean $\delta^{13}C$, using output of ~~HadCM3 (shelves or no shelves)~~B4H, B4H_NC and ~~FAMOUS~~B4F, and compiled palaeo-archives of ocean $\delta^{13}C$ suggest ~~a dominant~~an important role of terrestrial carbon storage changes in driving ocean $\delta^{13}C$ changes. Modelled ocean $\delta^{13}C$ changes derived with ~~FAMOUS~~B4F are larger because of larger ~~simulated~~glacial decreases changes in terrestrial carbon storage. The differences in terrestrial carbon storage between the models in turn derive from differences in the variability of ice-sheet prescription (Fig. ~~3) and regional climate biases~~4) and differences in climates between the models, where HadCM3 is generally wetter and slightly warmer in the glacial than FAMOUS, which means productivity and extent of warm temperate and boreal forests does not decrease in B4H as it does into the glacial in ~~FAMOUS~~B4F.

Existing data coverage is still low, and so there are still large areas of uncertainty in our knowledge of the palaeo-Earth system. Better spatial and temporal coverage for all parts of the globe, especially lowland areas, are required, and for this we need data from new sites incorporated into global datasets that are easily accessible by the scientific community.

The synthesised biomized dataset presented in this paper can be downloaded as supplementary material to this paper, or may be obtained by contacting the authors. Output from the climate and biome model simulations are also available from the authors.

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Table 1. Details of the various biomization schemes applied for the different regions.

Africa	Jolly et al. (1998)
Southeast Asia, Australia	Pickett et al. (2004)
Japan	Takahara et al. (1999)
Southern Europe	Elenga et al. (2000)
North East Europe	Tarasov et al. (2000)
North America: Western North	Thompson and Anderson (2000)
North America: East and North East	Williams et al. (2000)
Latin America	Marchant et al. (2009)

Table 2: Details of the locations of pollen-data records synthesised in this study.

	Core	Latitude	Longitude	A.S.L. (m)	Age ~ / (ka BP)	Reference	Biome reference
North America							
Canada (short)	Brother-of-Fog	67.18	-63.25	380	Last interglacial	Frechette et al., 2006	Williams et al., 2000
Canada (short)	Amarok	66.27	-65.75	848	Holocene and last interglacial	Frechette et al., 2006	Williams et al., 2000
USA	Carp Lake	45.92	-120.88	714	0 to ca 130	Whitlock and Bartlein, 1997	Thompson and Anderson, 2000
USA	Bear Lake	41.95	-111.31	1805	0 to 150	Jiménez-Moreno et al. 2007	Thompson and Anderson, 2000
USA	Potato lake	34.4	-111.3	2222	2 to ca 35	Anderson et al., 1993	Thompson and Anderson, 2000
USA	San Felipe	31	-115.25	400	16 to 42	Lozano-Garcia et al., 2002	Thompson and Anderson, 2000
USA	Lake Tulane	27.59	-81.50	36	0 to 52	Grimm et al., 2006	Williams et al., 2000
Latin America							
Mexico	Lake Patzcuaro	19.58	-101.58	2044	3 to 44	Watts and Bradbury, 1982	Marchant et al., 2009
Guatamala	Lake Petén-Itzá	16.92	-89.83	110	0-86	Correa-Metrio et al., 2012	Marchant et al., 2009
Colombia	Ciudad Universitaria X	-4.75	-74.18	2560	0 to 35	van der Hammen and González, 1960	Marchant et al., 2009
Peru	Laguna Junin	-11.00	-76.18	4100	0 to 36 (LAPD1?)	Hansen et al., 1984	Marchant et al., 2009
Peru/Bolivia	Lake Titicaca	-15.9	-69.10	3810	3-370 (shown until 140)	Gosling et al., 2008; Hanselman et al., 2011; Fritz et al., 2007	Marchant et al., 2009
Guatamala	Lago Quexil	16.92	-89.88	110	9 to 36	Leyden, 1984; Leyden et al., 1993; 1994	Marchant et al., 2009

Brazil	Salitre	-19.00	-46.77	970	2 to 50 (LAPD1)	Ledru, 1992; 1993; Ledru et al., 1994, 1996	Marchant et al., 2009
Brazil	Colonia	-23.87	-46.71	900	0 to 120	Ledru et al., 2009	Marchant et al., 2009
Brazil	Cambara	-29.05	-50.10	1040	0 to 38	Behling et al., 2004	Marchant et al., 2009
Peru/Bolivia	Lake Titicaca	~-16 to -17.5	~-68.5 to -70	3810	3-138	Hanselman et al., 2011; Fritz et al., 2007	Marchant et al., 2009
Bolivia	Uyuni	-20.00	-68.00	653	17 to 108	Chepstow Lusty et al., 2005	Marchant et al., 2009
Europe							
Russia	Butovka	55.17	36.42	198	Holocene, early glacial and Eemian	Borisova, 2005	Tarasov et al., 2000
Russia	Ilinskoye	53	37	167	early glacial & Eemian	Grichuk et al. 1983, Velichko et al., 2005	Tarasov et al., 2000
Poland	Horoszki Duze	52.27	23		~75 to Eemian	Granoszewski, 2003	Tarasov et al., 2000
Germany	Klinge	51.75	14.51	80	early glacial, Eemian & Saalian (penultimate glacial)	Novenko et al. 2008	Tarasov et al., 2000
Germany	Füramoos	47.59	9.53	662	0 to 120	Muller et al., 2003	Prentice et al., 1992
Germany	Jammertal	48.10	9.73	578	Eemian	Muller, 2000	Prentice et al., 1992
Germany	Samerberg	47.75	12.2	595	Eemian and early Würmian	Grüger, 1979a, b	Prentice et al., 1992
Germany	Wurzach	47.93	9.89	650	Eemian and early Würmian	Grüger and Schreiner, 1993	Prentice et al., 1992
Italy	Lagaccione	42.57	11.85	355	0 to 100	Magri, 1999	Elenga et al., 2004
Italy	Lago di Vico	42.32	12.17	510	0 to 90	Magri and Sadori, 1999	Elenga et al., 2004
Italy	Valle di Castiglione	41.89	12.75	44	0 to 120	Magri and Tzedakis 2000	Elenga et al., 2004
Italy	Monticchio	40.94	15.60	656	0 to 120	Allen et al., 1999	Elenga et al. , 2004
Greece	Ioannina	39.76	20.73	470	0 to 120	Tzedakis et al., 2002; 2004a	Elenga et al., 2004
Greece	Tenaghi Philippon	41.17	24.30	40	0 to 120	Wijmstra, 1969; Wijmstra and Smith, 1976; Tzedakis et al., 2006	Elenga et al.

Africa							
Uganda	ALBERT-F	1.52	30.57	619	0 to 30	Beuning et al. 1997	Jolly et al., 1998
Uganda	Mubwindi swamp3	-1.08	29.46	2150	0 to 40	Marchant et al., 1997	Jolly et al., 1998
Rwanda	Kamiranzovy swamp 1	-2.47	29.12	1950	13 to 40	Bonnefille and Chalie, 2000	Jolly et al., 1998
Burundi	Rusaka	-3.43	29.61	2070	0 to 47	Bonnefille and Chalie, 2000	Jolly et al., 1998
Burundi	Kashiru Swamp A1	-3.45	29.53	2240	0 to 40	Bonnefille and Chalie, 2000	Jolly et al., 1998
Burundi	Kashiru Swamp A3	-3.45	29.53	2240	0 to 40	Bonnefille and Chalie, 2000	Jolly et al., 1998
Tanzania	Uluguru	-7.08	37.62	2600	0 to >45	Finch et al., 2009	Jolly et al., 1998
Madagascar	Lake Tritrivakely	-19.78	46.92	1778	0 to 40	Gasse and Van Campo, 1998	Jolly et al., 1998
South Africa	Tswaing (Saltpan) Crater	-25.57	28.07	1100	0 to 120 (although after 35 probably less secure based)	Scott 1988b; Partridge *et al.* 1993; Scott 1999a; 1999b	Jolly et al., 1998
South Africa	Mfabeni swamp	-28.13	32.52	11	0 to 43	Finch and Hill, 2008	Jolly et al., 1998
Australasia							
Russia	Lake Baikal	53.95	108.9		114 to 130		
Japan	Lake Biwa	35	135	85.6	0 to 120	Nakagawa et al., 2008	Takahara et al., 1999
Japan	Lake Suigetsu	35.58	135.88	~0	0 to 120	Nakagawa	Takahara et al., 1999
Thailand	Khorat Plateau	17	103	~180	0 to 40	Penny, 2001	Pickett et al., 2004
Australia	Lynch's Crater	-17.37	145.7	760	0 to 120	Kershaw, 1986	Pickett et al., 2004
New Caledonia	Xero Wapo	-22.28	166.97	220	0 to 120	Stevenson and Hope, 2005	Pickett et al., 2004
Australia	Caldeonia fen	-37.33	146.73	1280	0 to 120	Kershaw et al., 2007	Pickett et al., 2004
New Zealand	Okarito	-43.24	170.22	70	0 to 120	Vandergoes et al., 2005	Pickett et al., 2004

Table 3: values for τ^{v}_{biome} and τ^{s}_{biome} (years) by megabiome derived for B4F and B4H

B4F	TrF	WTeF	TeF	BoF	SDW	GDS	De	Tn
τ^{v}_{biome}	13.1	11.2	11.2	12.4	15.5	1.47	4.7	1.1
τ^{s}_{biome}	8.2	12.3	12.3	73.6	48.3	11.3	75	62.5
B4H								
τ^{v}_{biome}	11.7	9.0	9.0	11.0	8.1	2.1	4.7	1.1
τ^{s}_{biome}	7.4	9.9	9.9	65.5	25.4	16.0	74.0	62.8

TrF: tropical forest; WTeF: warm-temperate forest; TeF: temperate forest; BoF: boreal forest; SDW; savannah and dry woodland; GDS: grass and dry shrubland; De: desert; Tn: tundra

Figure 1: Locations and altitudes of pollen records superimposed on pre-industrial HadCM3 orography (m).

~~Figure 2: Biome reconstructions from FAMOUS and HadCM3 climates for selected marine isotope stages (denoted in ka BP). The biome with the highest affinity score for each site in our synthesis where there is pollen during this stage is superimposed.~~

~~Figure 3:~~ Figure 2: Biome affinity scores for the various regions. (ai) For Northeast America, using the Williams et al. (2000) biomization scheme, (aii) For North and Northwest America using the Thompson and Anderson (2000) biomization scheme. (2b) For Latin America using the Marchant et al. (2009) biomization scheme. (2c) For Africa using the Elenga et al. (2004) biomization scheme. (2di) For Southern Europe using the Elenga et al. (2004) biomization scheme, (2dii) Alps using the Prentice et al. (1996) biomization scheme, and (2diii) northern Europe using the Tarasov et al. (2000) biomization scheme. (2e) Lake Baikal using the Tarasov et al. (2000) biomization scheme, (2fi) Japan using the Takahara et al. (2000) biomization scheme. (2fii) East Asia/Australasia using the Pickett et al. (2004) biomization scheme.

Figure 3: Reconstructed biomes (defined through highest affinity score) superimposed on simulated biomes using FAMOUS (B4F, left) and HadCM3 (B4H, right) climates for selected marine isotope stages (denoted in ka BP).

Figure 4: Global area coverage of megabiome types in the model reconstructions.

~~Figure 4: Affinity scores for the 4 dominant biome types at the Ioannina site (20.73E, 39.76N) from Greece~~ S indicates the inclusion of potentially-vegetated continental shelves after sea level lowering, NS indicates no vegetated continental shelves following sea level lowering.

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Figure 5: Net Primary Production and carbon storage throughout the last glacial cycle derived from the model-based biome reconstructions. ~~HadCM3_S~~B4H includes the

additional influence of land exposed by sea-level changes, ~~HadCM3~~B4H _NS and ~~FAMOUS_NS~~B4F do not.

Figure 6: (a) modelled $\delta^{13}C$ for terrestrial biosphere; (b) change in modelled total ocean $\delta^{13}C$ (c) benthic foraminifera deep ocean $\delta^{13}C$ compiled by Oliver et al (2010).