1 Terrestrial biosphere changes over the last 120 kyr and their 2 impact on ocean $\delta^{13}C$

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- 87 Abstract

88 89 A new global synthesis and biomization of long (> 40 kyr) pollen-data records 90 is presented, and used with simulations from the HadCM3 and FAMOUS climate 91 models and the BIOME4 vegetation model to analyse the dynamics of the global 92 terrestrial biosphere and carbon storage over the last glacial-interglacial cycle. 93 Simulated biome distributions using BIOME4 driven by HadCM3 and FAMOUS at 94 the global scale over time generally agree well with those inferred from pollen data. 95 The simulations show good agreement in global net primary productivity (NPP). NPP 96 is strongly influenced by atmospheric carbon dioxide (CO_2) concentrations through CO₂ fertilization. The combined effects of simulated vegetation changes and (via a 97 98 simple model) soil carbon result in a global terrestrial carbon storage at the Last 99 Glacial Maximum that is 210-470 PgC less than in pre-industrial time. Without the 100 contribution from exposed glacial continental shelves the reduction would be larger, 101 330-960 PgC. Other intervals of low terrestrial carbon storage include stadial intervals 102 at 108 and 85 ka BP, and between 60 and 65 ka BP during Marine Isotope Stage 4. 103 Terrestrial carbon storage, determined by the balance of global NPP and 104 decomposition, influences the stable carbon isotope composition (δ^{13} C) of seawater 105 because terrestrial organic carbon is depleted in ¹³C. Using a simple carbon-isotope 106 mass balance equation, which combines the BIOME4 model derived terrestrial carbon store and carbon isotope discrimination with values for the atmosphere from ice core 107 records, we find agreement in trends between modelled ocean δ^{13} C based on modelled 108 land carbon storage, and palaeo-archives of ocean δ^{13} C, confirming that terrestrial 109 carbon storage variations may be important drivers of ocean δ^{13} C changes. 110 111

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113 **1. Introduction**

114 The terrestrial biosphere (vegetation and soil) is estimated to contain around 115 2000 Pg C (Prentice et al., 2001) plus a similar quantity stored in peatlands and 116 permafrost (Ciais et al., 2014). Variations in global climate on multi-millennial time 117 scales have caused substantial changes to the terrestrial carbon pools. Periodic 118 variations in the Earth's orbital configuration (axial tilt with a ~41 kyr period, 119 precession with ~19and 23 kyr periods, and eccentricity with ~100 kyr and longer 120 periods) result in small variations in the seasonal and latitudinal distribution of 121 insolation, amplified by feedback mechanisms (Berger, 1978). For the last ~ 0.8 122 million years long glacial periods have been punctuated by short interglacials on 123 roughly a 100 kyr cycle. Glacial periods are associated with low atmospheric CO_2 124 concentrations, lowered sea level and extensive continental ice-sheets; interglacial 125 periods are associated with high (similar to pre-industrial) CO₂ concentrations, high sea level and reduced ice-sheets (Petit et al., 1999; Peltier et al., 2004). 126

127 During glacial-interglacial cycles the productivity of, and carbon storage in, 128 the terrestrial biosphere are influenced by orbitally forced climatic changes and 129 atmospheric CO₂ concentrations. Expansion of ice-sheets during glacial periods 130 caused a significant loss of land area available for colonization, but this was largely 131 compensated by the exposure of continental shelves due to lower sea level. During the 132 last glacial period the terrestrial biosphere was significantly reduced. It has been 133 estimated that the terrestrial biosphere contained 300 to 700 Pg C less carbon during 134 the Last Glacial Maximum (LGM; 21 ka BP) compared with pre-industrial times 135 (Bird et al., 1994; Ciais et al., 2012; Crowley et al., 1995; Duplessy et al., 1988; Gosling and Holden, 2011; Köhler and Fischer, 2004; Prentice et al., 2011). As first 136 noted by Shackleton et al. (1977), the oceanic inventory of carbon isotopes (δ^{13} C) is 137 138 influenced by terrestrial carbon storage because terrestrial organic carbon has a 139 negative signature, due to isotopic discrimination during photosynthesis. Many of the 140 estimates of the reduction in terrestrial carbon storage at the LGM have therefore been based on the observed LGM lowering of deep-ocean δ^{13} C. A reduction in the 141 terrestrial biosphere of this size would have contributed a large amount of CO₂ to the 142 143 atmosphere, although ocean carbonate compensation would have reduced the 144 expected CO₂ increase to 15 ppm over about 5 to 10 kyr (Sigman and Boyle, 2000).

145 Many palaeoclimate data and modelling studies have focused on the contrasts 146 between the LGM, the mid-Holocene (6 ka BP) and the pre-industrial period. The 147 BIOME 6000 project (http://www.bridge.bris.ac.uk/resources/Databases/BIOMES data) 148 synthesized palaeovegetation records from many sites to provide global datasets for 149 the LGM and mid-Holocene. Data syntheses are valuable in allowing researchers to 150 see the global picture from scattered, individual records, and to enable model-data comparisons. The data can be interpreted in the context of a global, physically based 151 152 model that allows the point-wise data to be seen in a coherent way. There are 153 continuous, multi-millennial pollen records that stretch much further back in time 154 than the LGM but they have not previously been brought together in a global 155 synthesis to study changes of the last glacial-interglacial cycle. These records can 156 provide a global picture of transient change in the biosphere and the climate system. 157 Here we have synthesized and biomized (Prentice et al., 1996) a number of these 158 records (for locations see Figure 1), providing a new dataset of land biosphere change 159 that covers the last glacial-interglacial cycle. In section 2.1 we outline the biomization 160 procedures applied to reconstruct land biosphere changes.

161 To improve understanding of land biosphere interactions with the ocean-162 atmospheric reservoir, we have modelled the terrestrial biosphere for the last 120 kyr, 163 from the previous (Eemian) interglacial to the pre-industrial period. Details of the 164 atmosphere ocean general circulation model (AOGCM) climate and vegetation model simulations are provided in section 2.2. In section 3 we evaluate biome 165 166 reconstructions based on our model outputs using the BIOME 6000 project 167 (www.bridge.bris.ac.uk/resources/Databases/BIOMES data), and our new biomized 168 synthesis of terrestrial pollen data records, focusing on the pre-industrial period, 6 ka 169 BP (mid-Holocene), 21 ka BP (LGM), 54 ka BP (a relatively warm interval in the last 170 glacial period), 64 ka BP, (a relatively cool interval in the glacial period), 84 ka BP 171 (the early part of the glacial cycle), and 120 ka BP (the Eemian interglacial). The 172 effects of millennial scale climate fluctuations were not simulated. Finally in section 4 173 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 174 terrestrial biosphere and carbon storage changes to deep ocean $\delta^{13}C$ over the last 120 175 176 kyr and compare this with deep ocean benthic foraminiferal carbon isotope records, representative for the $\delta^{13}C$ of deep ocean water. 177

178 **2 Methods**

179 2.1 Biomization

180 Biomization assigns pollen taxa to one or more plant functional types (PFTs). 181 The PFTs are assigned to their respective biomes and affinity scores are calculated for 182 each biome (sum of the square roots of pollen percentages contributed by the PFTs in 183 each biome). This method was first developed for Europe (Prentice et al., 1996) and 184 versions of it have been applied to most regions of the world (Jolly et al., 1998; 185 Elenga et al., 2000; Takahara et al., 1999; Tarasov et al., 2000; Thompson and 186 Anderson, 2000; Williams et al., 2000; Pickett et al., 2004; Marchant et al., 2009). We 187 apply these regional PFT schemes (Table 1) to pollen records that generally extend > 188 40 kyr, assigning the pollen data to megabiomes (tropical forest, warm temperate 189 forest, temperate forest, boreal forest, savannah/dry woodland, grassland/dry 190 shrubland, desert and tundra) as defined by Harrison and Prentice (2003), in order to 191 harmonize regional variations in PFT to biome assignments and to allow globally 192 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. 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.

200 Age models provided with the individual records were used. However, in 201 cases where radiocarbon ages were only provided for specific depths (e.g. Mfabeni, 202 CUX), linear interpolations between dates were used to estimate ages for the 203 remaining depths. Some age models may be less certain, especially at sites which 204 experience variable sedimentation rates and/or erosion. Sometimes more than one age 205 model accompanies the data, illustrating the range of ages and also that there can be 206 large uncertainties. To aid comparison, for several Southern European sites (e.g. Italy 207 and Greece) it has been assumed that vegetation changes occurred synchronously 208 within the age uncertainties of their respective chronologies, for which there is 209 evidence (e.g. Tzedakis et al., 2004b).

210 **2.2 Model simulations**

Global 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 test the robustness of the reconstructions to different climate forcings.

216 2.2.1 HadCM3

217 HadCM3 is a general circulation model, consisting of coupled atmospheric 218 model, ocean, and sea ice models (Gordon et al., 2000; Pope et al., 2000). The 219 resolution of the atmospheric model is 2.5 degrees in latitude by 3.75 degrees in 220 longitude by 19 unequally spaced levels in the vertical. The resolution of the ocean is 221 1.25 by 1.25 degrees with 20 unequally spaced layers in the ocean extending to a 222 depth of 5200 m. The model contains a range of parameterisations, including a 223 detailed radiation scheme that can represent the effects of minor trace gases (Edwards 224 and Slingo, 1996). The land surface scheme used is the Met Office Surface Exchange 225 Scheme 1 (MOSES1; Cox et al., 1999). In this version of the model, interactive 226 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 227 228 parameterisation of ice-drift and leads (Cattle and Crossley, 1995).

229 Multiple "snap-shot" simulations covering the last 120 kyr have been 230 performed with HadCM3. The boundary conditions and set-up of the original set of 231 simulations have been previously documented in detail in Singarayer and Valdes 232 (2010). The snap-shots were done at intervals of every 1 ka between the pre-industrial 233 (PI) and LGM (21 ka BP), every 2 ka between the LGM and 80 ka BP, and every 4 ka 234 between 80 and 120 ka BP. Boundary conditions are variable between snap-shots but 235 constant for each simulation. Orbital parameters are taken from Berger and Loutre 236 (1991). Atmospheric concentrations of CO_2 were taken from Vostok (Petit et al., 237 1999) and CH₄, and N₂O were taken from EPICA (Spahni et al., 2005; Loulergue et 238 al., 2008), all on the EDC3 timescale (Parrenin et al., 2007). The prescription of ice-239 sheets was achieved with ICE-5G (Peltier (2004) for 0-21 ka BP, and extrapolated to 240 the pre-LGM period from the ICE-5G reconstruction using the method described in 241 Eriksson et al (2012). The simulations were each spun up from the end of previous 242 runs described in Singarayer and Valdes (2010) to adjust to the modified ice-sheet 243 boundary conditions for 470 years. The monthly climatologies described hereafter are 244 of years 470-499. The model performs reasonably well in terms of glacial-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).

250 **2.2.2 FAMOUS**

251 FAMOUS (Smith, 2012) is an Earth System Model, derived from HadCM3. It 252 is run at approximately half the spatial resolution of HadCM3 to reduce the 253 computational expense associated with atmosphere-ocean GCM simulations without 254 fundamentally sacrificing the range of climate system feedbacks of which it is 255 capable. Pre-industrial control simulations of FAMOUS have both an equilibrium 256 climate and global climate sensitivity similar to that of HadCM3. A suite of transient 257 FAMOUS simulations of the last glacial cycle, conducted with specified atmospheric 258 CO₂, ice-sheets and changes in solar insolation resulting from variation in the Earth's 259 orbit, compare well with the NGRIP, EPICA and MARGO proxy reconstructions of 260 glacial surface temperatures (Smith and Gregory, 2012). For the present study, we use 261 the most realistically-forced simulation of the Smith and Gregory (2012) suite 262 (experiment ALL-ZH), forced with northern hemisphere ice-sheets taken from the 263 physical ice-sheet modelling work of Zweck and Huybrechts (2005), atmospheric 264 CO₂, CH₄ and N₂O concentrations from EPICA and orbital forcing from Berger 265 (1978). Although of a lower spatial resolution than HadCM3, these FAMOUS 266 simulations have the benefit of being transient, and representing low-frequency 267 variability within the climate system, as well as using more physically plausible ice-268 sheet extents before the LGM than were used in the HadCM3 simulations. To allow 269 the transient experiments to be conducted in a tractable amount of time, these forcings 270 were all "accelerated" by a factor of ten, so that the 120 kyr of climate are simulated 271 in 12model kyr - this method has been shown to have little effect on the surface 272 climate (Timm and Timmerman, 2007; Ganapolski et al., 2010) although it does 273 distort the response of the deep ocean. In addition, we did not include changes in sea 274 level, Antarctic ice volume, or meltwater from ice-sheets to enable the smooth 275 operation of the transient simulations. The impact on the terrestrial carbon budget of 276 ignoring the continental shelves exposed by lower sea-levels will be discussed later; 277 the latter two approximations are unlikely to have an impact over the timescales 278 considered here. Although within the published capabilities of the model, interactive

vegetation was not used during this simulation, with (icesheets aside) the land surfacecharacteristics of the model being specified as for a preindustrial simulation.

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282 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.

290 Two reconstructions of the evolution of the climate over the last glacial cycle 291 were obtained by calculating monthly climate anomalies with respect to the simulated 292 pre-industrial for the HadCM3 and FAMOUS glacial climate simulations 293 respectively, then adding these anomalies, on the native FAMOUS and HadCM3 294 grids, to an area averaged interpolation of the Leemans and Cramer (1991) observed 295 climatology provided with the BIOME4 distribution. These climate reconstructions 296 were then used to force two BIOME4 simulations. The climate anomaly method 297 allows us to correct for known errors in the climates of HadCM3 and FAMOUS and 298 produce more accurate results from BIOME4, although the method assumes that the 299 pre-industrial errors in each model are systematically present, unchanged over ice-free 300 regions, throughout the whole glacial cycle. We chose to use the actual climate model 301 grids for the BIOME4 simulations, rather than interpolating onto the higher-resolution 302 observational climatology grid, to avoid concealing the significant impact that the 303 climate model resolution has on the vegetation simulation, and to highlight the 304 differences between the physical representation of the climate between the two 305 different models. Because of its lower resolution, FAMOUS cannot represent 306 geographic variation at the same scale as HadCM3, which not only affects the areal 307 extent of individual biomes, but also how altitude is represented in the model, which 308 can have a significant effect on the local climate and resulting biome affinity. The 309 frequency of data available from the FAMOUS run also limits the accuracy of the 310 minimum surface air temperature it can force BIOME4 with, as only monthly average 311 temperatures were available. This results in some aspects of the FAMOUS-forced BIOME4 simulation seeing a less extreme climate than it should, and artificiallyfavours more temperate vegetation in some locations.

314 Soil properties on exposed shelves were extrapolated from the nearest pre-315 industrial land points. There is no special correction for the input climate anomalies 316 over this exposed land, which results in a slightly subdued seasonal cycle at these 317 points (due to smaller inter-seasonal variation of ocean temperatures). The version of 318 the observational climatology distributed with BIOME4 includes climate values for 319 these areas. The BIOME4 runs used the time-varying CO₂ records that were used to 320 force the corresponding climate models, as described in sections 2.2.1 and 2.2.2. As 321 well as affecting productivity, the lower CO₂ concentrations found during the last 322 glacial favour the growth of plants that use the C₄ photosynthetic pathway (Ehleringer 323 et al., 1997), which can affect the distribution of biomes as well. All other BIOME4 324 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.

328 **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. 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).

335 **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.

338 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. 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 subdivision 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. The Arctic Baffin Island sites
(Amarok and Brother of Fog) have highest affinity scores for tundra during the icefree Holocene and last interglacial.

349 At Lake Tulane (Florida) the grassland and dry shrubland biome has the 350 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 351 352 highest scores (Fig. 2a). According to Williams et al. (2000), present day, 6 ka BP, 353 and LGM records of most of Florida and the Southeast of America should be 354 characterized by highest affinity scores for the warm-temperate forest biome 355 (Williams et al., 2000). The discrepancy of our biomization results with those of the 356 regional biomization results of Williams et al. (2000) is due to high percentages of 357 Quercus, Pinus undiff (both are in the grassland and dry shrubland and warm-358 temperate forest biomes), and Cyperaceae and Poaceae that contribute to highest 359 affinity scores of the grassland and shrubland biome. Intestingly, the temperature 360 forest biome has highest affinity scores in a short interval (~15 ka BP) during the 361 deglacation (Fig. 2a). In Jiminéz-Morene et al. (2010) Pinus does not feature in the 362 grassland and dry shrubland biome, but comprises a major component of the 363 southeastern pine forest; hence their biomized Lake Tulane records fluctuates 364 between the 'grassland and dry shrubland' biome and 'southeastern pine forest biome'.

365 In Northwest America pollen data from San Felipe (16 to 47 ka), Potato Lake 366 (last 35 ka), and Bear Lake (last 150 kyr) all show highest scores for the grassland 367 and dry shrubland biome. Potato Lake is currently situated within a forest (Anderson, 368 1993). In our biomizations *Pinus* pollen equally contribute to scores of *boreal forest*, 369 temperate forest, warm-temperate forest and the grassland and dry shrubland biomes. 370 In addition, high contributions of Poaceae occur so that the grassland and dry 371 shrubland biome has highest affinity scores throughout the last 35 kyr. Again, in the 372 Jiminéz-Morene et al. (2010) biomizations Pinus does not feature in the grassland and 373 dry shrubland biome, hence the forest biomes have highest affinity scores in their 374 biomizations. At Carp Lake the Holocene is characterized by alternating highest 375 affinity scores between the temperate forest and grassland and dry shrubland biomes 376 whereas during the glacial the grassland and dry shrubland biome attains highest 377 affinity scores. The age model of Carp Lake suggests this record goes back to the 378 Eemian, and if so, then last interglacial climate was lacking the alternation between

379 the temperate forest and grassland and dry shrubland biomes as was the case during 380 the late Holocene. Modern biomizations at Carp Lake and Bear Lake are similar to 381 modern and those of the LGM also compare well (Thompson and Anderson, 2000). 382 Biomizations for Carp Lake between 10 and 80 ka BP by Jiminéz-Morene et al. 383 (2010) generally look similar to ours, apart from 36, 57-70 and 72-80 ka BP where the 384 temperate forest biome shows highest affinity scores because Pinus undiff. is treated 385 as insignificant in their biomization. Biomizations of Bear Lake between 10 and 80 ka 386 BP are similar to Jiminéz-Morene et al. (2010).

387 3.1.2 Latin America

388 The regional biomization scheme of Marchant et al. (2009) was used for Latin 389 American locations. Hessler et al. (2010) discuss the effects of millennial climate 390 variability on the vegetation of tropical Latin America and Africa between 23N and 391 23S, using similar biomization schemes. In our studyeleven sites from Central and South America are considered covering a latitudinal gradient of 49° (from 20 to -29°) 392 393 and an elevation range of 3900 m (from 110-4010 m asl [above sea level]) (Table 2). 394 Five of the sites are from relatively low elevations (<1500 m asl), from north to south 395 these are: Lago Quexil and Petén-Itzá in Guatamala and Salitre, and Colonia and 396 Cambara in South East Brazil. The high elevation records (>1500 m asl), with the 397 exception of the most northerly site in Mexico (Lake Patzcuaro), are distributed along 398 the Andean chain: Ciudad Universitaria X (Colombia), Laguna Junin (Peru), Lake 399 Titicaca (Bolivia/Peru) and Salar de Uyuni (Bolivia).

400 The five lowland sites indicate the persistence of forest biomes for much of 401 the last 130 kyr (Fig. 2bi). In Central American the Lago Quexil record stretches back 402 to 36 ka BP and has highest affinity scores for the warm-temperate forest biome 403 during the early Holocene. During glacial times the temperate forest biome 404 dominates, intercalated with mainly the grassland and dry shrubland and desert 405 biomes during the LGM and last deglaciation. At Lago Petén-Itzá (also Guatamala) 406 highest affinity scores for the warm-temperate forest biome are recorded for the last 407 86 kyr. The Salitre and Colonia records are the only Latin American sites that fall 408 within the *tropical forest* biome today. The majority of the Salitre record shows high 409 affinities for tropical forest from ~64 ka BP to modern; apart from an interval 410 coinciding with the Younger Dryas which displays highest affinity scores for the 411 warm-temperate forest biome. The southern-most Brazilian record, at Colonia, has 412 highest affinity scores for tropical forest for the last 40 kyr, except between 28 and 21

413 ka BP (~coincident with the LGM) when scores were highest for the warm-temperate 414 forest biome. Between 120 and 40 ka BP highest affinity scores alternate between the 415 tropical forest and warm-temperate forest biome at Colonia. The biomized Colonia 416 record of Hessler et al. (2010) generally shows the same features, apart from an 417 increase in affinity scores fo the dryer biomes between 10 and 18 ka BP. To the south, 418 at Cambara (Brazil), highest affinity scores are found for warm-temperate forest 419 during the Holocene and between 38 and 29 ka BP, whilst during the interval in 420 between they alternate between warm temperate forest and grassland and dry 421 shrubland.

422 Apart from Laguna Junin, higher elevation sites (>1500 m: Lake Patzcuaro, 423 Titicaca, Uyuni, and CUX) do not show a strong glacial-interglacial cycling in their 424 affinity scores; Mexican site Lake Patzcuaro (2240 m) and Colombian site CUX 425 (2560 m) have highest affinity scores mainly for warm-temperate forest over the last 426 35 kyr, although they alternate between *warm- temperate forest* and *temperate forest* 427 during the Holocene and at CUX also during the LGM (Fig. 2bii). Lake Patzcuaro and 428 CUX biomization results for the Holocene, 6 ka BP and LGM compare well with 429 those derived by Marchant et al. (2009). At Uyuni (3643 m) highest affinity scores are 430 for temperate forest and grassland and dry shrubland between 108 and 18 ka BP. At 431 Titicaca (3810 m) high affinity scores are found for *temperate forest* over the last 130 432 kyr, apart from during the previous interglacial (Eemian) when highest affinity scores 433 for the *desert* biome occur. Finally at Lago junin highest affinity scores alternate 434 between warm-temperate forest and temperate forest during the Holocene and 435 temperate forest and grassland and dry shrubland during the glacial.

436 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.).

443 At the mountain site Kashiru swamp in Burundi the Holocene is characterized 444 by an alternation of highest affinity scores for *tropical forest*, *warm temperate forest* 445 and the *grassland and dry shrubland* biomes. During most of the glacial, scores are 446 highest for the *grassland and dry shrubland* biome, preceded by an interval where 447 warm temperate forest showed highest scores (Fig. 2c). Our results are similar to 448 those obtained by Hessler et al. (2010). Highest affinity scores for tropical forest and 449 warm forest were found during the Holocene at the Rusaka Burundi mountain site, 450 whereas those of the last glacial again had highest scores for grassland and dry 451 shrubland biome. At the Rwanda Kamiranzovy Site the grassland and dry shrubland 452 biome displayed highest scores during the last glacial (from ~30 ka BP) and 453 deglaciation, occasionally alternating with the warm temperate forest biome. In 454 Uganda at the low mountain site Albert F (619 m) the Holocene and potentially 455 Bølling Allerød is dominated by highest affinity scores for tropical forest, whereas 456 the Younger Dryas and last glacial show highest affinity scores for the grassland and 457 dry shrubland biome (Fig. 2c). In the higher-elevation Ugandan mountain site 458 Mubwindi swamp (2150 m), the Holocene pollen record shows alternating highest 459 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 460 461 scores for the grassland and dry shrubland biome). In South Africa, the Mfabeni 462 Swamp record shows highest affinity scores for the grassland and dry shrubland 463 biome for the last 46 kyr years occasionally, alternated with the savanna and dry 464 woodland biome, and tropical forest during the late Holocene. At the Deva Deva 465 Swamp in the Uluguru Mountains highest affinity scores are for grassland and dry 466 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 467 468 Tritrivakely (Madagascar) the grassland and dry shrubland biome dominates, apart 469 from between 3 and 0.6 ka BP when the tropical forest biome dominates (Fig. 2c). 470 Our results compare well with those of Elenga et al. (2004) who show a LGM 471 reduction in tropical rainforest and lowering of mountain vegetation zones in major 472 parts of Africa.

473 **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 480 scheme to discuss millennial climate in European vegetation records between 10 and481 80 ka BP.

482 In Southern Europe at the four Italian sites (Monticchio, Lago di Vico, 483 Lagaccione and Valle di Castiglione) the Holocene and last interglacial show highest 484 affinity scores for warm temperate forest and temperate forest. During most of the 485 glacial and also cold interglacial substages the grassland and dry shrubland biome has highest affinity scores, whereas during warmer interstadial intervals of the last 486 487 glacial the temperate forest biome had highest affinity scores again (Fig. 2di). At 488 Tenaghi Phillipon and Ioannina a similar biome sequence may be observed, with 489 highest affinity scores for temperate forest and warm temperate forest during 490 interglacials. During the last glacial and last interglacial cool substages the grassland 491 and dry shrubland biome showed highest affinity scores at Tenaghi Philippon. At 492 Ioannina the LGM and last glacial cool stadial intervals have highest affinity scores 493 for grassland and dry shrubland, whereas affinity scores of glacial interstadial 494 periods are highest for temperate forest (Fig. 2di). Our biomization results for 495 Southern European sites agree well with those of Elenga et al. (2004) who also found 496 a shift to dryer grassland and dry shrubland biomes during glacial times. Instead of a 497 desert and tundra biome Fletcher et al. (2010) define a xyrophytic steppe and 498 eurythermic conifer biome in their biomizations, giving subtle differences in the 499 biomization records, with the Fletcher et al. (2010) biomized records showing an important contribution of affinity scores to the xerophytic steppe biome. 500 501 Characteristic species for the xerophytica shrub biome include artemisia, 502 chenopodiaceae and ephedra, which in the Southern Europe biomization scheme of 503 Elenga et al. (2000) feature in the dessert biome and grassland and dry shrubland 504 biome (only ephedra).

505 All four alpine sites are from altitudes between 570 and 670 m and for all four 506 sites the last interglacial period was characterized by having highest scores for the 507 temperate forest biome (Fig. 2dii). At Füramoos the last glacial showed highest 508 affinity scores for the *tundra* biome, whilst during the Holocene the *temperate forest* 509 biome shows highest affinity scores (Fig. 2dii). In the Fletcher scheme characteristic 510 pollen for the eurythermic conifer biome include pinus and juniperus. In our 511 biomization pinus and juniperus contributes to all biomes except for the desert and 512 tundra biome.

513 Most Northern European sites are mainly represented for the last interglacial 514 period, apart from Horoszki Duze in Poland. At most sites the temperate forest biome 515 and *boreal forest* biome show highest affinity scores during the last interglacial 516 (Eemian), whereas cool substages and early glacial (Butovka, Horoszki Duze) show 517 high affinity scores for the grass and dry shrubland biome These results compare well 518 with Prentice et al. (2000), who suggest a southward displacement of the Northern 519 hemisphere forest biomes and more extensive tundra and steppe like vegetation 520 during the LGM.

521 3.1.5 Asia

522 For the higher latitude site Lake Baikal the biomization scheme of Tarasov et 523 al. (2000) was used. For the two Japanese pollen sites we used the biomization 524 scheme of Takahara et al. (1999). At Lake Baikal, during the Eemian the highest 525 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 526 527 Northern European Sites. Pollen taxa such as Carpinus, Pterocarya, Tilia cordata and 528 Quercus have probably been redeposited or transported over a large distance; 529 however they all make up less than 1% of the pollen spectrum and therefore did not 530 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 *warmtemperate 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).

538 **3.1.6 East Asia/Australasia**

539 For East Asian and Australasian sites the scheme of Pickett et al. (2004) was 540 used. In Thailand the Khorat Plateau site shows highest affinity scores for the *tropical* 541 forest biome over the last ~40 kyr. At New Caledonia's Xero Wapa, the warm-542 temperate forest and tropical forest biomes show highest affinity scores over the last 543 127 kyr. In Australia's Caledonian Fen interglacial times (Holocene and previous 544 interglacial) the savanna and dry woodland biome has highest affinity scores. During 545 the glacial the grassland and dry shrubland biome generally shows highest affinity 546 scores, occasionally alternated with highest scores for the savanna and dry woodland 547 biome during the early part of Marine Isotope Stage (MIS) 3 and what would be MIS 548 5a (ca. 80-85 ka BP). Over most of the last glacial –interglacial cycle highest affinity 549 scores at Lynch's Crater are for the *tropical forest* and *warm temperate forest* biomes 550 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 551 552 increased biomass burning (human activities) causing the replacement of dry 553 rainforest by savannah. In addition, the significance of what is considered to be tundra 554 from MIS 4 is due to an increase in Cyperaceae with the expansion of swamp 555 vegetation over what was previously a lake. At Okarito (New Zealand), the temperate 556 forest biome has highest affinity scores throughout (occasionally alternated with 557 warm-temperate forest), apart from during the LGM and deglaciation (~25to 14ka 558 BP), where those of savanna and dry woodland, and grassland and dry shrubland 559 show highest affinity scores. Biomization results for the Australian mainland and 560 Thailand agree well with those obtained by Pickett et al. (2004) for the Holocene and 561 LGM.

562 3.2 HadCM3/FAMOUS model comparison

563 Although the source codes of HadCM3 and FAMOUS are very similar, 564 differences in the resolution of the models and the setup of their simulations results in 565 a number of differences in both the climates they produce and the vegetation patterns 566 seen in B4H and B4F over the last glacial cycle. Specific regions and times where 567 they disagree on the dominant biome type will be discussed later, but there are a 568 number of features that apply throughout the simulations.

569 Both B4H and B4F keep the underlying soil types constant as for the pre-570 industrial throughout the glacial cycle. In terms of the global land carbon budget, the 571 largest difference between the simulations comes from whether sea-level changes are 572 included or not. The HadCM3 snapshot simulations allowed for the exposure of 573 coastal shelves as sea-level changed through the glacial cycle, with reconstructions based on Peltier and Fairbanks (2006) who used the SPECMAP δ^{18} O record 574 575 (Martinson et al., 1987) to constrain ice volume/sea level change from the last 576 interglacial to the LGM. FAMOUS, on the other hand, kept global mean sea level as 577 for the present day throughout the whole transient simulation. As a consequence the 578 area of land available to vegetation expands and contracts with falling and rising sea 579 level in B4H but remains unchanged in 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.

583 Full details of the climates produced by FAMOUS and HadCM3 in these 584 simulations can be found in Smith and Gregory (2012) and Singarayer and Valdes 585 (2010). In general, land surface temperature anomalies in the HadCM3 simulations 586 are a degree or so colder than in FAMOUS. This difference in temperature, present in 587 some degree/we throughout most of the simulation is attributed mainly to differences 588 in surface height and ice-sheet ice extent. FAMOUS model results are also, on 589 average, slightly drier compared with those of HadCM3. This is related to the model 590 resolution, with HadCM3 showing much more regional variation (some areas become 591 wetter and some drier), whilst FAMOUS produces a more spatially uniform drying as 592 the climate cools. A notable exception to this general difference is in north-western 593 Europe, where FAMOUS more closely reproduces the temperatures reconstructed 594 from Greenland ice-cores (Masson-Delmotte et al., 2005), compared to which the 595 HadCM3 simulations used here have a significant warm bias at the LGM. Millennial 596 scale cooling events and effects of ice-rafting are not features of our model runs, 597 which present a relatively temporally smoothed simulation of the last glacial cycle.

598 **3.3 Data-model comparison**.

We present here an overview of the vegetation reconstructions for the last glacial-interglacial cycle simulated in B4H and B4F. We compare the simulated biomes in B4H and B4F with each other and with the dominant megabiome derived from the pollen-based biomizations, restricting our description of the results to major areas of agreement and disagreement. Maps of the dominant megabiomes produced by B4H and B4F for these periods can be seen in Figure 3.

605 We focus on a few specific periods, detailed below, since reviewing every 606 detail present in this comparison is unfeasible. The pre-industrial period serves as a 607 test-bed to identify biases inherent in our model setup, before climate anomalies have 608 been added. The 6 ka BP mid-Holocene period represents an orbital and ice-sheet 609 configuration favouring generally warm northern hemisphere climate (Berger and 610 Loutre, 1991). The LGM simulation at 21 ka BP is at the height of the last glacial 611 cycle, when ice-sheets were at their fullest extent, orbital insolation seasonality was 612 similar to present and CO₂ was at its lowest concentration (~185 ppm), and the 613 resulting climate was cold and dry in most regions. These three time periods form the

614 basis of the standard PMIP2 simulations and were used in the BIOME 6000 project. 615 We thus additionally compare our simulations with the BIOME 6000 results for these 616 time periods. The 54 ka BP interval is representative of peak warm conditions during 617 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., 618 2002), associated with temporarily higher levels of greenhouse gases, an orbital 619 620 configuration that favours warmer northern-hemisphere summers, and northern 621 hemisphere ice sheet volume roughly half that of the LGM. The time slice 64 ka BP 622 represents MIS 4, both greenhouse gases and northern-hemisphere insolation were 623 lower, and northern hemisphere ice volume was two-thirds higher than at 54 ka BP, 624 resulting in significantly cooler global climate. 84 ka BP is representative of stadial 625 conditions of the early part of the glacial (at the end of MIS 5), after both global 626 temperatures and atmospheric concentrations of CO_2 have fallen significantly and the 627 Laurentide ice-sheet has expanded to a significant size but before the Fennoscandian 628 ice-sheet can have a major influence on climate. The 84 ka BP period can be 629 compared with the Eemian (120 ka BP, the earliest climate simulation used here), 630 which represents the end of the last interglacial warmth (MIS 5e), before glacial 631 inception. The Eemian period (120 ka BP) differs from the pre-industrial mainly in 632 insolation. The earlier parts of the Eemian (e.g. 125 ka BP) are often studied due to 633 their 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 634 635 HadCM3 climates were available.

636 3.3.1 Pre-industrial

637 Our BIOME4 simulations were forced using anomalies from the pre-industrial 638 climates produced by HadCM3 and FAMOUS. Differences between B4H and B4F 639 for this period thus only arise from the way the pre-industrial climate forcing has been 640 interpolated onto the two different model grids we used. Differences between B4H 641 and B4F and the pollen-based reconstructions for this period highlight biases that are 642 not directly derived from climates of HadCM3 and FAMOUS, but are inherent to 643 BIOME4, the pollen-based reconstruction method, or simply the limitations of the 644 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

648 include the sites synthesised here amongst many others) and Marchant et al. (2009) 649 show that they are generally representative of the regionally dominant biome. The 650 biomized records of Carp Lake and Lake Tulane in North America are exceptions, 651 showing dry grassland conditions rather than the forests (conifer and warm-mixed, 652 respectively) that are more typical of their regions (Williams et al., 2000).

653 There is generally very good agreement between B4H and B4F for this period 654 and the high-resolution BIOME6000 and Marchant et al. (2009) studies. A notable 655 exception, common to both B4H and B4F, can be seen in the south-west US being 656 misclassified compared to the regional biomization of Thompson and Anderson 657 (2000). The open conifer woodland they assign to sites in this region appears to be 658 sparsely distributed (their figure 2) amongst larger areas likely to favour grassland 659 and desert, and thus may be unrepresentative of areas on the scale of the climate 660 model gridboxes. The limitations of HadCM3 and FAMOUS's spatial resolution 661 appear most evident in South America, where the topographically-influenced mix of 662 forest and grassland biomes found by Marchant et al. (2009) cannot be correctly 663 reproduced, with disagreement at the grid-box scale between B4F and B4H. Eurasia is 664 generally well reproduced, although the Asian boreal forest does not extend far 665 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 666 667 continental areas also shows the influence of the coarse model resolutions, with B4F more accurately reproducing the southern woodlands but neither simulation 668 669 reproducing the full extent of the desert interior. Both Australian records are from the 670 eastern coastal ranges; there are no long continuous records in the interior because of 671 the very dry conditions. Overall, our comparison with the full BIOME6000 dataset 672 gives reasonable support to our working hypothesis that BIOME4, operating on the 673 relatively coarse climate model grids we use here, is capable of producing a realistic 674 reconstruction of global biomes.

675 **3.3.2 6 ka BP mid-Holocene**

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 result seen in B4H and B4F. An increase in vegetation 682 on the northern boundary of the central Africa vegetation band is the most notable 683 difference compared to the pre-industrial in the regional biomizations (Jolly et al., 684 1998), which is also suggested by the long central African pollen records synthesised 685 here. Both climate model-based reconstructions show grassland on the borders of pre-686 industrial desert areas in North Africa, although the additional amount of rainfall in 687 both models is too low, and the model resolution-too low to represent any significant 688 "greening" of the desert. B4F shows a smaller change in tropical forest area in central 689 Africa than B4H does, agreeing better with the regional biome reconstructions. Both 690 HadCM3 and FAMOUS predict similar patterns and changes in precipitation for this 691 period, but the magnitude of the rainfall anomaly in FAMOUS is slightly lower. The 692 reduction in forest biomes at the tip of South Africa in B4F has some support from 693 Jolly et al. (1998), although B4F initially overestimates forest in this area.

694 B4H and B4F show limited changes elsewhere too. In North America, 695 FAMOUS's increase in rainfall anomalies produce more woodland in the west in B4F 696 compared to the pre-industrial, which is not seen in B4H. This is not a widespread 697 difference shown in the regional biomization, although individual sites do change. 698 Marchant et al. (2009) suggest drier biomes than the pre-industrial for some northern 699 sites in Latin America, agreeing with B4F but not B4H. For Eurasia and into China, 700 Prentice (1996), Tarasov et al. (2000) and Yu et al. (2000) all suggest greater areas of 701 warmer forest biomes to the north and west across the whole continent, with less 702 tundra in the north. Neither BIOME4 simulation shows these differences, however, 703 with some additional grassland at the expense of forest on the southern boundary in 704 B4H, and B4F predicting more tundra in the north. Although both FAMOUS and 705 HadCM3 produce warmer summers for this period, in line with the increased seasonal 706 insolation from the obliquity of the Earth's orbit at this time, the colder winters they 707 also predict for Eurasia skew annual average temperatures to a mild cooling which 708 appears to prevent the additional forest growth to the north and west seen in the 709 pollen-based reconstructions.

710

3.3.3 21 ka BP (Last Glacial Maximum)

For the LGM, both 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 716 spatial coverage to fully describe these differences, showing only smaller areas of 717 forest biomes in southern Europe, central Africa and Australia, but there is again good 718 general agreement between our two BIOME4 simulations and the regional 719 biomizations of the BIOME6000 project.

720 The FAMOUS and HadCM3 grids do not seem to have sufficient resolution to 721 reproduce much of the band of tundra directly around the Laurentide ice-sheet in 722 either B4H or B4F, but the forest biomes the simulations show for North America are 723 largely supported by Williams et al. (2000). However, Thompson and Anderson 724 (2000) suggest larger areas of the open-conifer biome in the southwestern US than in 725 the Holocene that the BIOME4 simulations again do not show. Both B4H and B4F 726 predict a smaller Amazon rainforest area. Marchant et al. (2009) suggest that the 727 Holocene rainforest was preceded by cooler forest biomes, whereas both HadCM3 728 and FAMOUS simulate climates that favours grasslands. Marchant et al. (2009) also 729 provide evidence for cool, dry grasslands in the south of the continent; FAMOUS 730 follows this climatic trend but B4F suggests desert or tundra conditions, whilst B4H 731 shows a smaller area of the desert biome. For Africa, Elenga et al. (2000) show 732 widespread grassland areas where the Holocene has forest, with which the simulations 733 agree, and dry woodland in the southeast, with neither B4H or B4F show; HadCM3 734 and FAMOUS appear to be too cold for BIOME4 to retain this biome. Elenga et al. 735 (2000) also shows increased grassland area in southern Europe, which is not strongly 736 indicated by either B4H or B4F, which have some degree of forest cover here.

737 The large areas of tundra shown by Tarasov et al. (2000) in northern Eurasia 738 to the east of the Fennoscandian ice-sheet are well reproduced by the BIOME4 739 simulations, although HadCM3's slightly wetter conditions produce more of the 740 boreal forest in the centre of the continent in B4H. The generally smaller amounts of 741 forest cover in Europe in B4F agree with the distribution of tree populations in 742 Europe at the LGM proposed by Tzedakis et al (2013) better than those from B4H, 743 possibly due to HadCM3's warm bias at the glacial maximum. Both B4H and B4F 744 agree with the smaller areas of tropical forest in China and southeast Asia 745 reconstructed by Yu et al. (2000) and Pickett et al. (2004) compared to the Holocene, 746 but have too much forest area in China compared to the biomization of Yu et al. 747 (2000). Neither BIOME4 simulation reproduces the reconstructed areas of xerophytic 748 biomes in south Australia, or the tropical forest in the north (Pickett et al., 2004).

749 **3.3.4 54 ka BP (Marine Isotope Stage 3)**

750 There are fewer published biomization results for periods before the LGM, so 751 our model-data comparison is restricted to the pollen-based biomization results at 752 sites synthesised in this paper. Of these sites, only two sites show a different 753 megabiome affiliation when compared to the LGM: in South America Uyuni shows 754 highest affinity scores for the forest biome, and in Australia, Caledonian Fen shows 755 highest affinity scores for the dry woodland biome (both sites show highest affinity 756 score for grassland during the LGM). Overall, the few sites where data are available 757 show little differences compared with the LGM. This is perhaps a surprise given the 758 evidence that this was relatively warm interval in the glacial, in Europe at least 759 (Voelker et al., 2002). These mostly unchanged biome assignments derived from our 760 pollen data records are supported by our BIOME4 simulations in that, although both 761 FAMOUS and HadCM3 do produce relatively warm anomalies compared to the 762 LGM, both B4H and B4F simulations at 54 ka BP are similar to the LGM local to the 763 pollen sites in the Americas, most of southern Europe (apart from Ioannina where the 764 data show highest affinity scores for temperate forest) and east Africa.

765 In other parts of the world, the biomes simulated at 54 ka BP in B4H and B4F 766 do differ significantly from those of the LGM. Both BIOME4 simulations show 767 increased vegetation in Europe and central Eurasia due to the climate influenced by 768 the smaller Fennoscandian ice-sheet, as well as reduced desert areas in North Africa 769 and Australia, generally reflecting a warmer and wetter climate under higher CO₂ 770 availability than at the LGM. However our simulations disagree on both the climate 771 anomalies and the likely impact on the vegetation in several areas in this period. 772 These include differences, both local and far-field, related to prescribed ice-sheets, 773 particularly in North America where the ice-sheet configuration in FAMOUS shows 774 largely separate Cordilleran and Laurentide ice-sheets compared to the more uniform 775 ice coverage of the continent in HadCM3. Further afield, B4H has significantly more 776 tropical rainforest, especially in Latin America, and predicts widespread boreal forest 777 cover right across Eurasia. B4F however, reproduces a more limited forest extent, 778 with more grassland in central Eurasia. The differences in the tropics appear to be 779 linked to a-larger rainfall anomalies in HadCM3 than FAMOUS, possibly due to a 780 stronger response to precessional forcing, whilst the west and interior of northern 781 Eurasia is cooler in FAMOUS than HadCM3, with a greater influence from the 782 Fennoscandian ice-sheet.

783 **3.3.5 64 ka BP (Marine Isotope Stage 4)**

784 There are only a few differences between biomized records at the LGM, 54 ka 785 BP, and 64 ka BP (Figure 3). Apart from one southern European site (Ioannina), 786 which has a highest affiliation with grassland (compared with temperate forest during 787 the LGM), the pollen biome affiliations are much the same as at the LGM for the sites 788 presented here. The two sites in northern Australasia show a highest affiliation with 789 the warm-temperate forest biome during this period, compared with tropical forest at 790 54 ka BP, however affinity scores between the two types are close, so this is unlikely 791 to be related to different climates. The BIOME 4 simulations support this as they also 792 do not show major differences at the pollen sites.

793 Both B4H and B4F are, in general, similar for 64 and 54ka BP. The 64ka BP 794 climate in HadCM3 is cooler and drier than for 54ka BP, with B4H producing larger 795 areas of tundra in north and east Eurasia and patchy tropical forests. There is less 796 difference between 64ka BP and 54ka BP in the FAMOUS reconstructions, which simulates a cooler climate at 54ka BP compared to HadCM3, so B4F and B4H agree 797 798 better in this earlier period than at 54ka BP. North American vegetation distributions 799 primarly differ between B4H and B4F in this period due to the different 800 configurations of the Laurentide ice-sheet imposed on the climate models.

801

3.3.6 84 ka BP (Marine Isotope Stage 5b)

The pollen-based biomization for 84 ka 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 those at 64 ka BP timeslice, although there are not many sites and it is less clear whether they reflect widespread climatic conditions.

808 The BIOME4 simulations reflect the warmer European climate resulting from 809 the smaller Fennoscandian ice-sheet at 84ka BP than 64ka BP, with B4F showing 810 some European forest cover, and B4H extending Eurasian vegetation up to the Arctic 811 coast. B4H shows more of this vegetation to be grassland rather than forest however, 812 probably a result of a slightly cooler climate in HadCM3. Around the southern 813 European pollen sites themselves, however, B4H shows little difference and B4F 814 predicts dry woodlands, perhaps a result of poorly modelled Mediterranean storm-815 tracks that would bring moisture inland.

816 Although there are differences in the configuration of the Laurentide ice-sheet 817 between the HadCM3 and FAMOUS, both B4H and B4F reproduce dry vegetation types in Midwest America and significant boreal forest further north at 84 ka BP. Both 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. Because of increased rainfall in Australia, B4H shows a smaller desert compared with 54 ka BP.

824

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

825 This time-slice represents the previous interglacial, and would be expected to 826 have the smallest anomalies from the pre-industrial control climate of the climate 827 models. The pollen-based biomization shows widespread forest cover for Eurasia, 828 with the only other difference from both the 84 ka BP period and the pre-industrial 829 control being Lake Titicaca, which has the highest affinity toward desert for this 830 period. The affinity scores for temperate forest are almost as high for this site, and neither HadCM3 nor FAMOUS has the resolution to reproduce the local climate for 831 832 this altitude well (Bush et al., 2010), although both do reflect dry conditions near the 833 coast-here.

834 The models do indeed produce relatively small climate anomalies and 835 vegetation similar to the pre-industrial control and each other. Both models produce 836 widespread forest cover north of 40N, much as for the pre-industrial climate, although 837 FAMOUS is slightly too wet over North America for B4F to produce mid-west 838 grasslands as seen in B4H. Both B4H and B4F increase the extent of their tropical 839 forests, although FAMOUS has a relative dry anomaly over central Africa, and B4F 840 has less tropical forest than for the pre-industrial or B4H, which once again appears to 841 have a stronger response to precessional forcing.

- 842
- 843

4 Global terrestrial vegetation changes

844 There is good general agreement between our BIOME 4 simulations and 845 pollen-synthesis, from both this paper and BIOME 6000. Below we calculate 846 quantitative changes in the global terrestrial biosphere and carbon cycle, keeping in 847 mind that these calculations carry some uncertainties relating to several mismatches. 848 As is discussed in section 3.1 there are several occasions where the modern biomized 849 pollen data do not agree with actual biome presence; for example Potato Lake and 850 Lake Tulane in North America. In both cases high contributions of Pinus and some 851 other taxa skewed the affinity scores towards drier biomes (grassland and dry

852 woodland). For the past, not knowing whether a pollen distribution is representative 853 for an area puts restrictions on the biomization method. It is however noted that in 854 most cases the biomized pre-industrial pollen agree well pre-industrial biomes. The 855 climate models produce some differences in climate forcing due to 1) difference in 856 resolution, affecting the biome areal extent and altitude and 2) ice-sheet extent, 857 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) 858 859 there are some biases that can be attributed to biases in BIOME4, some to the 860 biomization method, and some to the models' limiting geographical resolution.

4.1 Biome areas

862 Whilst there is general agreement between B4H and B4F, there are also areas 863 and periods with significant regional differences. A clearer picture of the effect on the 864 global biosphere can be seen by using the global total areas of each megabiome for 865 the two simulations (Figure 4). Cooler temperatures, reduced moisture, and lower levels of CO₂ through the glacial result in a general reduction of forest biomes and 866 867 increases in grassland, desert, and tundra. Lower levels of atmospheric CO₂ also 868 preferentially favour plants using the C4 photosynthetic pathway (Ehleringer et al., 869 1997), contributing to the expansion of the grassland and desert biomes during the 870 glacial. The changes in atmospheric CO_2 levels through the glacial cycle are common 871 to all the BIOME4 simulations, so CO_2 fertilisation effects and C3/C4 competition are 872 not responsible for differences in vegetation response between B4F and B4H. B4F 873 predicts consistently lower areas of warm-temperate and boreal forest than B4H, and 874 higher amounts of grassland and desert. FAMOUS also neglects the additional area of 875 land that HadCM3 sees as continental shelves are exposed, reducing the area of land 876 available to the biosphere, although some of this additional land is occupied by the 877 northern hemisphere ice-sheets in HadCM3. The global total areas of biomes 878 highlights a significant oscillation in the areas of the different megabiomes of ~20 kyr 879 in length – this is particularly notable between 60 and 120 ka BP in the grassland 880 megabiome and results from the 23 kyr cycle in the precession of the Earth's orbit. 881 The precession cycle exerts a significant influence on the seasonality of the climate, 882 as noted in tropical precipitation records (e.g. the East Asian monsoon; Wang et al., 883 2008). Such variations are not explicitly evident in the dominant megabiome types at 884 any of the pollen sites, but the precession oscillation does appear in the individual

biome affinity scores of several sites (Fig. 2), lending support to this feature of themodel reconstructions.

887 4.2 Net Primary Productivity

888 Net Primary Productivity (NPP) is the net flux of carbon into green plants (in 889 this case terrestrial plants) due to photosynthesis, after accounting for plant respiration. Global NPP derived from our BIOME4 simulations for the PI is 74 PgC 890 year⁻¹ for B4H and 78 PgC year⁻¹ for B4F. These values are somewhat higher than 891 previously estimated present-day range of 46-62 PgC year⁻¹ (Tinker and Ineson, 1990; 892 Nemani et al., 2003). Recent estimates using eddy covariance flux data estimate 893 global NPP as ~62 PgC year⁻¹ (assuming 50% carbon use efficiency to convert from 894 895 GPP to NPP; Beer et al. 2010).

896 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 897 898 observational climate dataset for the pre-industrial due to the anomaly approach used 899 to reduce the impact of climate model biases (see methods section 2.1.3). Therefore, 900 any overestimate in NPP is not a result of the climate model forcing but possibly due 901 to biases in the vegetation model, and/or biases in the observational climatology used 902 to drive the model, and the spatial resolution used. For example, the lower resolution 903 topography does not represent mountainous regions such as the Andes well nor its 904 topographically-induced variation in vegetation (see section 3.3.1), which may 905 positively skew NPP values. The model may also overestimate NPP compared to 906 observationally based techniques for the modern or pre-industrial partly because it 907 does not contain any representation of non-climatically induced changes, e.g. 908 cultivation or land degradation.

The LGM BIOME4 simulations show a global NPP decline to ~42 PgC year⁻¹ 909 910 in B4F and 48 PgC year⁻¹ in B4H. While these are also higher than some other modelbased estimates of 28-40 PgC year⁻¹ (e.g. François et al., 1999; 2002), the relative 911 912 decrease in the LGM in our simulations to approximately two-thirds of PI is 913 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⁻¹ 914 915 (Ciais et al., 2012); with LGM primary productivity approximately 50% lower than 916 their PI estimate.

917 The PI-LGM difference is greater in B4F than in B4H (Fig. 5a) primarily due 918 to the fact that HadCM3's glacial land area increases as sea-level lowers, enabling 919 additional NPP on continental shelf regions, whereas FAMOUS land area remains the 920 same. This is demonstrated by recalculating global NPP for B4H neglecting exposed 921 shelf regions (B4H NS), which then matches the values from B4F (Fig. 5a, green 922 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 923 924 LGM is 40% for B4H_NS and 35% for B4H compared to the PI. The impact of large 925 continental ice-sheets reducing the land surface area available for primary production 926 has a negligible effect on NPP compared to reduced CO₂ and glacial climate change. 927 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, 928 global NPP only decreases by a maximum of $\sim 5 \text{ PgC yr}^{-1}$. In addition, sensitivity tests 929 with B4H, with and without CO_2 , variation suggests that CO_2 fertilization, rather than 930 931 climate, is the primary driver of lower glacial NPP (accounting for around 85% of the 932 reduction in global NPP at the LGM).

933 Some differences in the timing of some multi-millennial peaks/troughs in NPP 934 between B4H and B4F are apparent, especially in the earlier half of the simulation. 935 These differences, all of the order of a few thousand years, can largely be ascribed to 936 the different CO₂ forcings used for B4H and B4F as well as the multiple snap-shot 937 setup of the HadCM3 run, which only produces simulations at 2 or 4 ka intervals, 938 compared to the 1 ka resolution of B4F. Differences in the forcing provided by the 939 ice-sheet reconstructions used in the models, as well as in the strength of their 940 responses to orbital forcing in the early part of the glacial (see Figure 4) may also play 941 a role.

Both BIOME4 simulations predict slightly lower NPP during the previous 942 interglacial, the Eemian (3-5 PgC yr⁻¹ lower) compared with pre-industrial times. The 943 944 first large-scale decrease in NPP occurs during the initial glaciation following the 945 Eemian, between 120 ka BP and 110 ka BP (in both simulations). There is then a second large drop of -10 PgC yr⁻¹ (HadCM3_S) to -20 PgC yr⁻¹ (B4H_NS, B4F) 946 947 between 75 ka BP and 60 ka BP, associated with MIS 4. NPP then increases during MIS 3, followed by the final reduction $(-10 \text{ PgC year}^{-1})$ to lowest values during the 948 LGM (Figure 6). We note here that the details of the magnitude and timing of the 949 950 NPP variations will be highly dependent on the prescribed CO_2 curve given that CO_2 951 fertilization is the predominant factor driving the changes. A recent composite CO₂ 952 curve derived from several ice core records (Bereiter et al., 2013) has CO₂ that is 520ppm higher during MIS4 than either Vostok or EDC records. Further sensitivity
tests with B4F forced with higher CO₂ levels suggest that NPP could be up to 8
PgC/yr higher at certain time slices (see supplementary Figure 1).

956

957 **4.3 Terrestrial carbon storage**

958 Early modelling studies and data-based reconstructions produced a range of 959 270-1100 PgC decrease in terrestrial carbon storage during the LGM compared with 960 pre-industrial time (see summary table 1 in Kohler and Fischer, 2004). These 961 estimates were based on various techniques including isotopic mass balance based on known marine and atmospheric δ^{13} C values (Bird et al., 1994), and either data-based 962 or simple model-based reconstructions where constant carbon storage per unit area of 963 964 each biome was assumed (e.g. Prentice et al., 1993; Crowley, 1995). These early 965 estimates were unreliable, however, because (a) they do not account for variation in 966 carbon storage within biomes and (b) they neglect the substantial influence of 967 atmospheric CO₂ concentration on carbon storage (see Prentice and Harrison, 2009, 968 for a fuller discussion). More recent studies have narrowed the range of LGM 969 terrestrial carbon storage decreases to 300-700 PgC. Prentice et al. (2011) estimated a 970 550-694 PgC decrease at the LGM using the LPX dynamic vegetation model forced 971 by four Palaeoclimate Modelling Intercomparison Project Phase II climate model runs 972 for the LGM. Using isotopic and modelling methods Ciais et al. (2012) suggested that 973 only 330 PgC less carbon was stored in the terrestrial biosphere at the LGM than PI 974 Holocene. While this is of the same order as other estimates it represents a reduction 975 of only 10% from PI. Ciais et al. (2012) also included a large inert carbon pool to 976 represent permafrost and peatland carbon storage (which are not included in most 977 dynamic vegetation models). Their optimization procedure suggested that this inert 978 carbon pool was larger by 700 PgC at the LGM than PI, meaning the reduction in 979 their active terrestrial biosphere was therefore larger than most other studies have 980 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 that are characteristic of the soil and vegetation. Although the heterogeneity of soil organic matter means that some 987 soil carbon varies on millennial timescales, the soil response to changes in climate 988 tends to be dominated by the more labile carbon pools, with effective residence times 989 for soil carbon being measured in decades rather than centuries (Carvalhais et al., 990 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 991 992 unlikely to introduce major inaccuracy.

993

We estimate total terrestrial carbon storage as the sum of vegetation carbon, 994 C_{veg} , and soil carbon, C_{soil} derived using equations 1 and 2 below:

995
$$C_{veg} = \sum_{biome} NPP_{biome} \cdot \tau_{biome}^{v}$$
[1]

996
$$C_{soil} = \sum_{biome} NPP_{biome} \cdot \tau^{s}_{biome} \cdot \exp\left[-k\left(T - T_{ref}\right)\right]$$
[2]

where $\tau^{\nu}_{\textit{biome}}$ is the turnover time of vegetation carbon, which is assumed to depend 997 998 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_{biame}^{s} is 999 modified by the multiplier $\exp\left[-k(T-T_{ref})\right]$, where T is the surface temperature at 1000 1001 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_{biome}^{v} and τ_{biome}^{s} were 1002 1003 estimated separately for the B4F and B4H by dividing modern carbon storage by the 1004 model's reconstructed pre-industrial NPP, using carbon storage values for each 1005 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. 1006

1007 The small differences in pre-industrial NPP by biome between B4H and B4F (related to both model setup and resolution differences between HadCM3 and 1008 FAMOUS) result in differences in τ_{biome}^{v} and τ_{biome}^{s} values used to calculate carbon 1009 1010 storage, and hence different sensitivities to changes in NPP. The assumption of 1011 equilibrium between carbon storage and simulated NPP inherent to this method means 1012 that the calculation of these time constants, and the resultant estimates of terrestrial 1013 carbon storage, are rather sensitive to small differences in the setups of the models 1014 and the choice of modern carbon storage data used for comparison. This leads to an 1015 additional uncertainty of around 10% on the terrestrial carbon storage numbers thus 1016 derived.

1017 During the interglacials B4F and B4H estimate high terrestrial carbon storage: 1018 2100 PgC during the pre-industrial period and 2000 PgC during the last interglacial 1019 (Fig. 5b). However, entering the glacial, B4F predicts larger carbon storage decreases 1020 than B4H. During the LGM, the terrestrial carbon reduction of 800 PgC is nearly 1021 twice as large in B4F compared with B4H (470 PgC). Roughly one third of the 1022 difference between B4F and B4H can be accounted for by the increase in continental 1023 shelf area in HadCM3 that are not included in FAMOUS. The rest comes partly from 1024 the wetter and warmer climate in glacial HadCM3 than FAMOUS, which enables a 1025 greater retention of forest biome areas into the glacial in B4H (Figures 2 and 3), and 1026 partly from differences in the carbon turnover times derived for each model. In 1027 particular the timescales derived for B4F likely give an upper bound on the change in 1028 terrestrial carbon that might be expected from the FAMOUS glacial climate 1029 anomalies.

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

1036 Closer examination of the trends during the last glacial cycle reveals that modelled terrestrial carbon storage (Fig. 5b) displays variation at the ~23 kyr time-1037 1038 scale that is not evident for NPP (Fig. 5a), in both B4F and B4H for the early glacial. 1039 The prevalence of a ~23 kyr cycle relates to the precession of the Earth's orbit, 1040 changing the seasonality of climate. This periodicity is particularly notable between 1041 60 and 120 ka BP (when eccentricity modulation of precession is largest) in the 1042 grassland and temperate forest megabiome areas (Fig. 4). The largest contributor to 1043 this multi-millennial variability in carbon storage is the extent to which northern 1044 hemisphere mid-latitudes are forested (temperate forest vs. grassland). This variation 1045 at 23-kyr periodicity is more evident in B4F than B4H, even though both models 1046 drive similar sized periodical changes in megabiome coverage. In B4H, slightly 1047 wetter glacial conditions result in greater overall forested areas; a decline in temperate 1048 and tropical forest is compensated for by an increase in warm-temperate and boreal 1049 forest (Fig. 4). B4F, on the other hand, shows declines in all forest types through the

1050 glacial. This drives a greater glacial decline in B4F carbon storage, as well as slightly1051 larger precessional variation in carbon storage.

1052 The first large-scale reduction in terrestrial carbon storage occurs shortly after 1053 the previous interglacial, where both models (including B4H) show a 500 PgC 1054 decrease (Figure 6). Predicted sizes of the terrestrial biosphere then vary around a 1055 1800 PgC mean by about ± 100 PgC for B4H and B4H_NS, whereas B4F shows 1056 another large decrease at ~ 65 ka BP by another 500 PgC, providing terrestrial carbon 1057 storage estimates in MIS 4 that are similar to the LGM.

1058

1059 **4.4 Implications for ocean carbon**

1060 Changes in ocean carbon storage have been calculated here by combining the 1061 modelled changes in terrestrial biosphere carbon storage with changes in atmospheric 1062 carbon dioxide recorded in ice cores. The difference in atmospheric carbon between 1063 the PI and LGM is approximately 180 PgC (Barnola et al., 1987) which when added 1064 to the decrease in terrestrial carbon storage, equates to an increase in total ocean 1065 carbon storage of 1050 PgC for B4F and 650 PgC for B4H.

1066 Globally decreased LGM deep ocean stable carbon isotope ratios (δ^{13} C), as recorded by benthic foraminifera at -0.3 to -0.4‰, suggests that global LGM 1067 terrestrial carbon storage was decreased by 500 to 700 Pg compared with the PI 1068 (assuming vegetation and soil δ^{13} C of -25‰) (e.g. Broecker and Peng, 1993; 1069 Duplessy et al., 1988, Bird et al, 1996; Kaplan et al., 2002; Beerling et al, 1999). A 1070 1071 more recent estimate derived from a compilation of 133 ocean cores is $-0.34 \pm 0.13\%$ 1072 (Ciais et al., 2012). An ensemble of ocean circulation model simulations suggests a 1073 similar decrease of $-0.31 \pm 0.2\%$ (Tagliabue et al., 2009).

1074 Using our modelled glacial-interglacial terrestrial carbon storage changes the 1075 above approach may be inverted to estimate global ocean δ^{13} C changes over the same 1076 time period. The mass balance approach of Bird et al. (1996) was followed to estimate ocean δ^{13} C at any point from 120 ka BP to the PI. Using the modelled terrestrial 1077 1078 biosphere carbon mass and that of the atmosphere (from the ice core record), 1079 contributions to global ocean mass changes were estimated. First, changes in total terrestrial biosphere δ^{13} C were estimated by multiplying the terrestrial carbon storage 1080 1081 calculated at each grid point (described above in section 3.4.3) by the model output δ^{13} C for each grid cell from BIOME4 (the model outputs discrimination, which is 1082

1083	then subtracted from the atmospheric δ^{13} C). These were then averaged to produce a
1084	global terrestrial biosphere δ^{13} C (Fig. 6a). Ice core records suggests variations in
1085	atmospheric δ^{13} between -6.4 to -7‰ but the time periods covered only extends
1086	from the LGM through the deglaciation (Leuenberger et al., 1992; Lourantou et al.,
1087	2010; Schmitt et al., 2012) and the penultimate deglaciation (Schneider et al, 2013),
1088	but does not cover the last glacial period. Comparison of the two time periods shows
1089	that the LGM was around 0.4‰ heavier than the penultimate glacial maximum,
1090	suggestive of a long-term trend (Schneider et al., 2013). We use the values from the
1091	ice core records for the available time periods and interpolate between 22 and 105 kyr
1092	BP to echo the long-term trend. Sensitivity tests (not shown) demonstrated that the
1093	calculated $\delta^{13}C$ ocean changes would not be significantly different whether constant
1094	modern (-6.5‰) or varying atmospheric $\delta^{13}C$ was used. Differences in calculated
1095	ocean δ^{13} C were generally less than 4% (0.02‰) and were a maximum of 15% during
1096	the Younger Dryas (~12-11 kyr BP) from either prescribing a modern -6.5‰ or
1097	measured -7% . In other words, global ocean $\delta^{13}C$ is not particularly sensitive to
1098	atmospheric δ^{13} C. Calculated terrestrial and atmospheric δ^{13} C were combined and,
1099	assuming total isotopic mass balance over time, total ocean $\delta^{13}C$ anomalies from pre-
1100	industrial were calculated for the last 120 kyr (Fig. 6b).

The modelled terrestrial biosphere δ^{13} C (Fig. 6a) displays the largest increase 1101 during the LGM when atmospheric CO₂ was at its lowest concentrations, due to 1102 changes in C_4 vegetation input (C_4 vegetation discriminates against ¹³C less than C_3 1103 vegetation when carbon is incorporated by photosynthesis). Consequently, $\delta^{13}C$ 1104 increases (becomes less negative) when C4 vegetation is more prevalent. The 1105 differences in biome area between B4F and B4H (Fig. 4), in particular warm 1106 temperate and boreal forest coverage, do not result in large differences in terrestrial 1107 biosphere δ^{13} C. The extent of C₄ type vegetation is similar between the models and 1108 differences in other biomes have little impact on overall isotopic signature. 1109

1110 The reconstructed total ocean δ^{13} C of the two models mimics the trends in 1111 total terrestrial carbon storage; when carbon storage is reduced, ocean δ^{13} C decreases 1112 and when carbon storage is increased, ocean δ^{13} C increases (Figure 6, 7). Changes to 1113 terrestrial biosphere δ^{13} C are of secondary importance compared to the size of the 1114 terrestrial carbon pool. The total ocean LGM to PI change in δ^{13} C as estimated using 1115 this method is -0.34‰ for B4H and -0.65‰ for B4F (Fig. 6b). The additional 1116 exposed continental shelf areas available in HadCM3 account for less than half of the 1117 difference between the two (compare B4H and B4H_NS in Fig. 6b). Even though 1118 B4F and B4H display similar trends in terrestrial biosphere δ^{13} C, the larger decrease 1119 in terrestrial carbon from B4F results in almost double the change in ocean δ^{13} C, 1120 although as noted above this is likely at the extreme end of the uncertainty range of 1121 the consequences of the FAMOUS climate anomalies.

The predicted PI to LGM decrease in total ocean δ^{13} C from B4H is similar to 1122 that inferred e.g. by Ciais et al. (2012) and Tagliabue et al. (2009) whereas B4F seems 1123 1124 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 1125 modelled ocean δ^{13} C over the entire glacial cycle (Fig. 6b and c). The absolute 1126 1127 magnitude of glacial-interglacial variation in B4H is closer to that in the 1128 reconstructions, whereas B4F variation is nearly twice the amplitude. However, the 1129 temporal variation in B4F has some features that are more similar to the data 1130 compilation, such as lighter values in MIS4 that are similar to the LGM values (Fig. 6b and c). The δ^{13} C excursion of deep Pacific δ^{13} C stack ~ 64 ka BP (coincident with 1131 1132 Marine Isotope Stage 4 or the early Wisconsin glacial advance) is as large as, or 1133 larger than that of the LGM (Oliver et al., 2010), and is not notable in the B4H-1134 derived estimates (Fig. 6). The very low deep Pacific values might not be completely 1135 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, 1136 Bereiter et al., 2012). Most longer benthic foraminiferal δ^{13} C records show even lower 1137 values during the penultimate glaciation, as part of a longer timescale trend in 1138 increasing ocean δ^{13} C since ca. 250 ka BP (Hoogakker et al., 2006; Piotrowski et al., 1139 1140 2009; Oliver et al., 2010), which is not captured here. This may be related to longer-1141 term in-carbon reservoirs changes that may be linked to changes in ocean ventilation 1142 and/or productivity (Wang et al., 2001; Hoogakker et al., 2006; Rickaby et al., 2007), 1143 not represented in our modelling approach.

1144 Our model estimates assume a constant inert terrestrial carbon pool 1145 (permafrost and peatlands). As described in section 4.3, Ciais et al (2012) infer that 1146 this carbon pool was larger by around 700GtC at the LGM compared with the pre-1147 industrial. We have estimated the impact on ocean δ^{13} C of including this estimate and 1148 its uncertainty (700GtC ± 600 GtC; Ciais et al, 2012), assuming that the inert 1149 terrestrial carbon pool was the same size at the last interglacial as the PI with an 1150 average δ^{13} C of -27‰, linearly interpolating to the LGM estimate. While there are 1151 large uncertainties on the inert terrestrial pool, in general its inclusion improves the 1152 B4F comparison to data (Supplementary Figure 2) and results in poorer simulated 1153 changes from B4H. Including uncertainties in the size of the inert terrestrial carbon 1154 store, atmospheric CO2, atmospheric δ^{13} C, and discrimination in permafrost, the PI to 1155 LGM decline in global ocean δ^{13} C from the B4F model is -0.4 ± 0.2‰, and -0.1 ± 1156 0.2‰ for B4H.

1157 While the distribution of δ^{13} C in oceans is affected by several factors such as 1158 reorganisation of water masses (especially in the North Atlantic), ocean productivity 1159 and export (Brovkin et al., 2002; Kohfeld and Ridgwell, 2009) and nutrient 1160 utilisation, the modelled results presented here suggest that the large-scale trends in 1161 ocean δ^{13} C may be dominated by terrestrial carbon storage variation, as Shackleton 1162 (1977) first proposed.

1163

1164 **5. Conclusions**

1165 We have used a new global synthesis and biomization of long pollen records 1166 in conjunction with model simulations to analyse the sensitivity of the global 1167 terrestrial biosphere to climate change over the last glacial-interglacial cycle. Model 1168 output and biomized pollen data generally agree, lending confidence to our global-1169 scale analysis of the carbon cycle derived from the model simulations. We used the 1170 models to estimate changes in global terrestrial net primary production and carbon 1171 storage. Carbon storage variations have a strong 23-kyr (precessional) cycle in the 1172 first half of the glacial cycle in particular. Estimates of global carbon storage by a 1173 BIOME4 simulation forced by HadCM3 climate at the LGM are ~470 PgC below 1174 modern levels, taking the contribution of exposed continental shelves and their 1175 colonisation are taken into account. Other intervals of significant reductions in 1176 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 δ^{13} C, 1177 using output of B4H, B4H_NC and B4F, and compiled palaeo-archives of ocean δ^{13} C 1178 suggest an important role of terrestrial carbon storage changes in driving ocean $\delta^{13}C$ 1179 changes. Modelled ocean δ^{13} C changes derived with B4F are larger because of larger 1180 1181 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 1182

ice-sheet prescription (Fig. 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 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.

1192

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.

1197

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1789 Table 1. Details of the various biomization schemes applied for the different regions.

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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)

1797 Table 2: Details of the locations of pollen-data records synthesised in this study.

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	Core	Latitude	Longitu de	A.S. L. (m)	Age ~ / (ka BP)	Reference	Biomization 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 <i>et al.</i> 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	L -1 D - 11	52.05	109.0		114 - 120		
Japan	Lake Baikai	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

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

1805 Table 3: values for τ_{biome}^{ν} and τ_{biome}^{s} (years) by megabiome derived for B4F and B4H 1806

1808 TrF: tropical forest; WTeF: warm-temperate forest; TeF: temperate forest; BoF:
1809 boreal forest; SDW; savannah and dry woodland; GDS: grass and dry shrubland;
1810 De: desert; Tn: tundra

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

1815 Figure 2: Biome affinity scores for the various regions. (ai) For Northeast America, 1816 using the Williams et al. (2000) biomization scheme, (aii) For North and Northwest 1817 America using the Thompson and Anderson (2000) biomization scheme. (2b) For 1818 Latin America using the Marchant et al. (2009) biomization scheme. (2c) For Africa 1819 using the Elenga et al. (2004) biomization scheme. (2di) For Southern Europe using 1820 the Elenga et al. (2004) biomization scheme, (2dii) Alps using the Prentice et al. 1821 (1996) biomization scheme, and (2diii) northern Europe using the Tarasov et al. 1822 (2000) biomization scheme. (2e) Lake Baikal using the Tarasov et al. (2000) biomization scheme, (2fi) Japan using the Takahara et al. (2000) biomization scheme. 1823 1824 (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. S
indicates the inclusion of potentially-vegetated continental shelves after sea level
lowering, NS indicates no vegetated continental shelves following sea level lowering.

Figure 5: Net Primary Production and carbon storage throughout the last glacial cycle
derived from the model-based biome reconstructions. B4H includes the additional
influence of land exposed by sea-level changes, B4H_NS and B4F do not.

1837 1838 Figure 6: (a) modelled δ^{13} C for terrestrial biosphere; (b) change in modelled total 1839 ocean δ^{13} C (c) benthic foraminifera deep ocean δ^{13} C compiled by Oliver et al (2010).









desert





— desert

















(2fii)







