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Title: **Precessional forcing of tropical vegetation carbon storage**

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Running header: **Precessional forcing of tropical vegetation carbon storage**

ABSTRACT: Since the Mid-Pleistocene Revolution, which occurred about one million years ago, global temperatures have fluctuated with a quasi-periodicity of ~100 thousand years (kyr). The pattern of past change in the extent of woodlands, and therefore by inference vegetation carbon storage, has been demonstrated to have a strong positive link with this global temperature change at high and mid latitudes. However, understanding of climate systems and ecosystem function indicates that the pattern of woodland change at low latitudes may follow a fundamentally different pattern. We present output from the intermediate complexity model GENIE-1, comprising a single transient simulation over the last 800 kyr and a 174-member ensemble of 130 kyr transient simulations over the last glacial cycle. These simulations suggest that whilst vegetation carbon storage in mid-high northern latitudes robustly follows the characteristic ~100 kyr cycle, this signal is not a robust feature of tropical vegetation which is subject to stronger direct forcing by the precessional (21 kyr) orbital cycle (albeit with a highly uncertain response). We conclude that the correlation of palaeoenvironmental records from low latitudes with global temperature change must be done with caution.

Key words: **Carbon storage, Earth System modelling, GENIE, orbital forcing, seasonality**

Orbital forcing and vegetation

The record of the waxing and waning of ice sheets as determined by oxygen isotope records has long been regarded as the framework for past global climate change (Emilliani, 1955; Martinson *et al.*, 1987; Lisiecki & Raymo, 2005). Temperature change determined from these records is widely accepted as the major driver of past environmental change (Siddall *et al.*, 2010) and underpins efforts to understand the likely effects of ongoing global climate change, e.g. IPCC 2007.

On geological time scales, variations in the orbital configuration of the Earth have been generally accepted as a major driver of global climate change following Milankovitch (1948). Through the Quaternary record (the last ~2.6 million years), orbital cycles can be broken down into three major components that vary with different characteristic periodicities: eccentricity (~400 and ~100 thousand years [kyr]), obliquity (~41 kyr) and precession (~21 kyr) (Berger and Loutre, 1991). Although a complete explanation for glacial cycles, generally accepted to be the result of a complex interplay between these orbital cycles, remains elusive (Crucifix and Rougier, 2009), global change has exhibited a quasi-periodicity of ~100 kyr throughout the last one million years (Shackleton, 2000, Lisiecki and Raymo, 2005) with, considering more regional scales, an increasing influence of precession closer to the equator (Clement *et al.*, 2004; Berger *et al.*, 2006). The precessional cycle is also important for tropical climate because it controls the position of the Inter-Tropical Convergence Zone (ITCZ), which modulates the pattern of rainfall (Clement *et al.*, 2004). In turn, the ITCZ position also impacts other important low latitude climate phenomena, e.g. Monsoons (Braconnot *et al.*, 2008) and El Niño Southern Oscillation (ENSO) (Clement, 1999; Koutavas *et al.*, 2006).

The link between woodland extent and warmer global climates has been established through comparison of fossil pollen records from mid-latitudes with the δ^{18}O SPECMAP stack (Tzedakis *et al.*, 1997). Comparison with the SPECMAP stack has become a standard tool to provide chronologies for tropical paleoecological data where radiocarbon dating cannot be used or needs to be supplemented, e.g. Sabana de Bogata, Colombia (Hooghiemstra, 1984), Gulf of Guinea (Frédoux, 1994) or Lynch's crater, Australia (Kershaw *et al.*, 2007). From these extended chronologies, a general relationship of maximum woodland extent and warm intervals has been observed in the montane tropics. Data from the lowlands are far more ambiguous, with increasing evidence of forest cover being retained during glacial episodes (Bush *et al.*, 2011), though probably being lushest, i.e. most carbon stored in plant matter, during warm, wet events.

The ~100 kyr cycle of climate and vegetation change through the Quaternary at high latitudes is well established (Shackleton, 1969; Tzedakis *et al.*, 1997). However, recent low-latitude palaeoenvironmental records, not dated through pollen correlation, have suggested that the pattern of vegetation change does not conform to that seen at high latitude (Scholz *et al.*, 2007; Bush *et al.*, 2010; Gosling *et al.*, 2009). These low latitude palaeoenvironmental records suggest that the precessional and eccentricity cycles are both of major importance for vegetation at low latitudes and the combination of the two cycles determines the large scale pattern of the vegetation response. Independent observations of Quaternary mega-droughts in tropical African lakes (Scholz *et al.*, 2007) and South American vegetation change (Bush *et al.*, 2009) have been linked to variation in precessional forcing. Bush *et al.* (2009) suggest that an increase in intensification of the dry season would likely have the greatest influence upon vegetation. Modelling studies have also implicated a likely role for the precessional forcing of vegetation (Claussen *et al.* 2006), with particular importance in the tropics (Tjallingi *et al.* 2008). Improving understanding of the pattern of vegetation response to global climate change across the latitudes has major implications for understanding: i) past patterns of carbon storage, and ii) ecosystems response to predicted future climate change (e.g. Malhi *et al.* 2008).

GENIE-1 simulations of terrestrial carbon storage

We have performed a transient simulation of global climate over the last 800 kyr with the intermediate complexity model GENIE-1 (Lenton *et al.*, 2006), which incorporates a simple model of vegetation and soil carbon storage (Williamson *et al.*, 2006). Aspects of this simulation, including details of the model set-up and transient boundary conditions (prescribed ice sheets, CO_2 and orbital forcing), has been detailed previously in Holden *et al.* (2010a). The simulated temporal variation in soil and vegetative carbon for the global average (Fig. 1a) and five latitudinal bands (defined by grid cell boundaries at ~23° and ~51° in both hemispheres) (Fig. 1b-f) are plotted. The projected carbon storage within each latitude band reflects both land area (greatest at high and mid northern latitudes) and carbon density. Vegetation carbon density is generally highest in the tropics, due to increased productivity, whilst soil carbon density is generally highest at high-latitudes, due to decreased respiration rates. In this simulation, preindustrial global storage of 537 Gt (gigatonnes; x10^9 tons) of vegetative carbon and 1,840 GT of soil carbon compares to a (highly uncertain) range of model and data estimates of, respectively, 450 to 650 Gt and 850 to 2,400 Gt (Bondeau et al, 2007, and references therein). The modelled distributions of preindustrial carbon storage are also reasonable, despite the simple atmospheric model (the dynamics of atmospheric transport in GENIE-1 are crudely represented by diffusive processes). Compared to observations, the over-diffusive atmosphere leads to less distinct deserts whilst boreal forest is too sparse, especially in Eurasia, due to difficulties in transporting moisture to the continental interiors (Lenton et al 2006). However, the patterns of change of carbon storage over time are less easily explained.

Fig. 1 illustrates that the modelled glacial-interglacial variability of terrestrial carbon is highly latitudinally dependent, suggesting that the processes controlling tropical vegetation are quite distinct from those at mid-high northern latitudes. Variability of carbon storage in high northern latitudes (Fig. 1b) is driven primarily by changes in vegetated area in response to the extent of the ice mass. The northern extent of the mid-northern latitude band is set at 51^oN which is coincident with the southern extent of the Laurentide ice sheet. Consequently, this band is not directly influenced by loss of vegetation area due to ice sheet coverage. Simulated changes in both vegetative and soil carbon storage in the mid-northern latitude band are dominated by temperature, exhibiting a high positive correlation with annual-average temperature (R = 0.94 and 0.72 respectively) and displaying the ~100 kyr quasi-periodicity apparent in $\delta^{18}O$ records (Fig. 1c). In the GENIE-1 simulation, moisture availability, especially during glacial periods, is not a limiting factor for vegetation growth at mid latitudes.

At low latitudes, however, the pattern of carbon storage through time is quite different when compared with high- and mid-northern latitudes. At low southern latitudes in particular, (Fig. 1e) there are two fundamentally different relationships: i) vegetative carbon is only weakly (and *negatively*) correlated with annual average temperature (R = -0.24), and ii) soil carbon exhibits a very strong (again negative) correlation with annual average temperature (R = -0.98); where the increased soil carbon during cold periods presumably reflects decreased respiration rates. Increased soil carbon during glacial times facilitates increased storage of soil moisture, favouring the growth of vegetative carbon and likely contributing to the modelled increase of low-latitude vegetation during cold periods. However, in this GENIE-1 parameterisation, the largest changes in tropical vegetation are driven by the precessional cycle, with carbon storage in southern tropical vegetation inversely correlated ($R = -0.69$) with the peak to peak difference in local temperature across the seasonal cycle.

Although this simulation suggests that vegetative changes are likely driven by quite different processes at different latitudes, we cannot assume the detail of the modelled changes in this single parameterisation is a robust result. The parameters driving vegetative changes are very uncertain so that the delicate balance between numerous competing effects cannot be assumed to be correct, especially under very different climate states. Complex vegetation models coupled to high resolution GCMs exhibit considerable uncertainty even when forced by the well-understood modern state (Friedlingstein *et al.*, 2006). In order to address the modelled robustness to uncertain vegetation parameters, we performed a 174 member ensemble of simulations over the last glacial cycle (130 ka ago to present). The parameterisations are a subset of the 480 member 'Last Glacial Maximum plausibility-constrained' (LPC) parameter set (Holden *et al.*, 2010b) which all exhibit plausible preindustrial and Last Glacial Maximum (LGM) climates and vegetation states, filtered (here to assist tractability) by the constraint that they exhibit a collapse of Atlantic Meridional Overturning during glacial terminations (Holden *et al.*, 2010a). Ensemble-averaged preindustrial terrestrial carbon storage is 440±70 Gt (vegetation) and 1,250±170 Gt (soil carbon). Uncertainties are represented throughout by the ensemble standard deviations (1σ).

In order to evaluate the robustness of the temporal variability displayed in Fig.1, we consider the ensemble-averaged correlation with respect to the single 800 kyr simulation. The Net Primary Productivity (NPP) in the mid-northern latitude band (Fig 2a) exhibits an ensemble averaged correlation of $R=0.92 \pm 0.10$ with the 800 kyr simulation, indicating that the response plotted in Fig 1c is a highly robust result of GENIE-1. However, the ensemble-averaged correlation of low southern latitude NPP (Fig 2b) is $R=0.34 \pm 0.24$, and includes 16 ensemble members which are (albeit weakly) negatively correlated with the single simulation, suggesting that tropical vegetation responds to a range of (highly uncertain) competing processes. Notably, and unsurprisingly, the nature of the response of tropical vegetation to glacial cycles is sensitive to the parameterisation of CO_2 fertilization - the sensitivity of vegetation to uncertain CO_2 fertilization is well known (e.g. Lapola *et al*, 2008). Sixty-two ensemble members have a CO_2 fertilization parameter (Williamson *et al*, 2006) $k14 > 432$

ppm (which equates to an increase of >50% in the photosynthesis rate in response to a doubling of preindustrial CO_2). In these 62 simulations southern tropical vegetation exhibits an average correlation of R=0.80 ±0.28 with atmospheric CO_2 concentration (compared to R=0.46 ±0.61 in the 112 remaining simulations). However, 16 ensemble members are strongly *negatively* correlated ($R < -0.5$) with atmospheric CO_2, suggesting that the indirect (temperature) effect of CO_2 also plays a significant role in determining tropical vegetation (all of the simulations assume a positive fertilization effect). The disentanglement of the roles played by temperature, CO_2 fertilization and seasonality in the determination of tropical NPP is not straightforward, and likely not a useful exercise here in view of the neglect of important atmospheric circulation dynamics in GENIE-1. Furthermore, as we force the model with prescribed CO_2 and ice sheets, we cannot separate the direct role of orbital variability on vegetation from the indirect role, via its governing influence on these forcing mechanisms (which are, in reality, not forcing mechanisms but earth system feedbacks in their own right). Our ensemble analysis does, however, highlight the substantial uncertainties which exist even in this simple model, and furthermore suggests the possibility that glacial-interglacial changes in tropical vegetation may provide a useful constraint on CO_2 fertilization.

Discussion

For these purposes, the notable weakness of GENIE-1 is the absence of a fully dynamic atmosphere. Orbitally-driven variability in monsoon systems is potentially key to variability in the tropics (Braconnot *et al.*, 2008), but GENIE-1 can only crudely model such changes through diffusive transport. However, cognizant of this constraint, the broad pattern of large scale changes in the temporal variability of carbon storage simulated in GENIE-1, reflecting the decreasing influence of ice sheets and the increased direct influence of precessional forcing at tropical latitudes, is likely to be robust. An improved understanding will require the application of transient 3D dynamical atmosphere modelling together with an investigation of the uncertainty in the modelling of vegetation itself (as has been addressed here). Such an evaluation of the coupled climate-vegetation uncertainty is very challenging given the current constraints on computing power, although models with a reduced complexity dynamical atmosphere such as CLIMBER-2 (Petoukhov *et al.*, 2000) or GENIE-2 (Lenton *et al.*, 2007) are sufficiently efficient to facilitate such an analysis.

The GENIE-1 simulations presented here thus support the inferences from fossil pollen records that precession is a relatively more important driver of vegetation change at low latitudes than at high and mid latitudes (Bush *et al.*, 2009; Gosling *et al.*, 2009). The increasing influence of a precessional signal away from the northern ice sheets indicates that the correlation of low latitude pollen records with global climate should be performed with extreme caution; and strongly suggests that wherever possible independent radiometric dating should be sought. However, the pattern of vegetation carbon change shown in the model supports the use of correlation of vegetation records to temperature (SPECMAP) at mid and high latitudes (following Tzedakis *et al.*, 1997). The challenge now is to develop robust ecological and palaeoecological datasets that test the precessional model for vegetation change at low latitudes, particularly in lowland regions.

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Figure caption2

Figure 1. Modelled variation in global terrestrial carbon storage and climate over the last 800 ka for five latitudinal bands: (a) global average; (b) high northern latitudes; (c) mid northern latitudes; d) low northern latitudes; (e) low southern latitudes; (f) mid southern latitudes. The latitude bands are defined by grid cell boundaries at ~23^o and ~51^o in both hemispheres. Annual average temperatures, vegetative carbon, soil carbon and peak-to-peak differences in temperature across the seasonal cycle are shown in the 1st, 2nd, 3rd and 4th traces (top to bottom) in each panel, respectively (red, green, brown and blue, respectively when viewed in colour online at wileyonlinelibrary.com). Note the seasonality axis is reversed. Temperatures are expressed as sea-level equivalent surface air temperatures, averaged over land.

Figure 2. 174-member GENIE-1 ensemble of simulations over the last 130 kyr. Net Primary Productivity (NPP) expressed relative to preindustrial, spatially averaged over a) mid northern latitudes (~23ºN to 51ºN) and b) low southern latitudes (~0ºS to 23ºS).

Figure 1

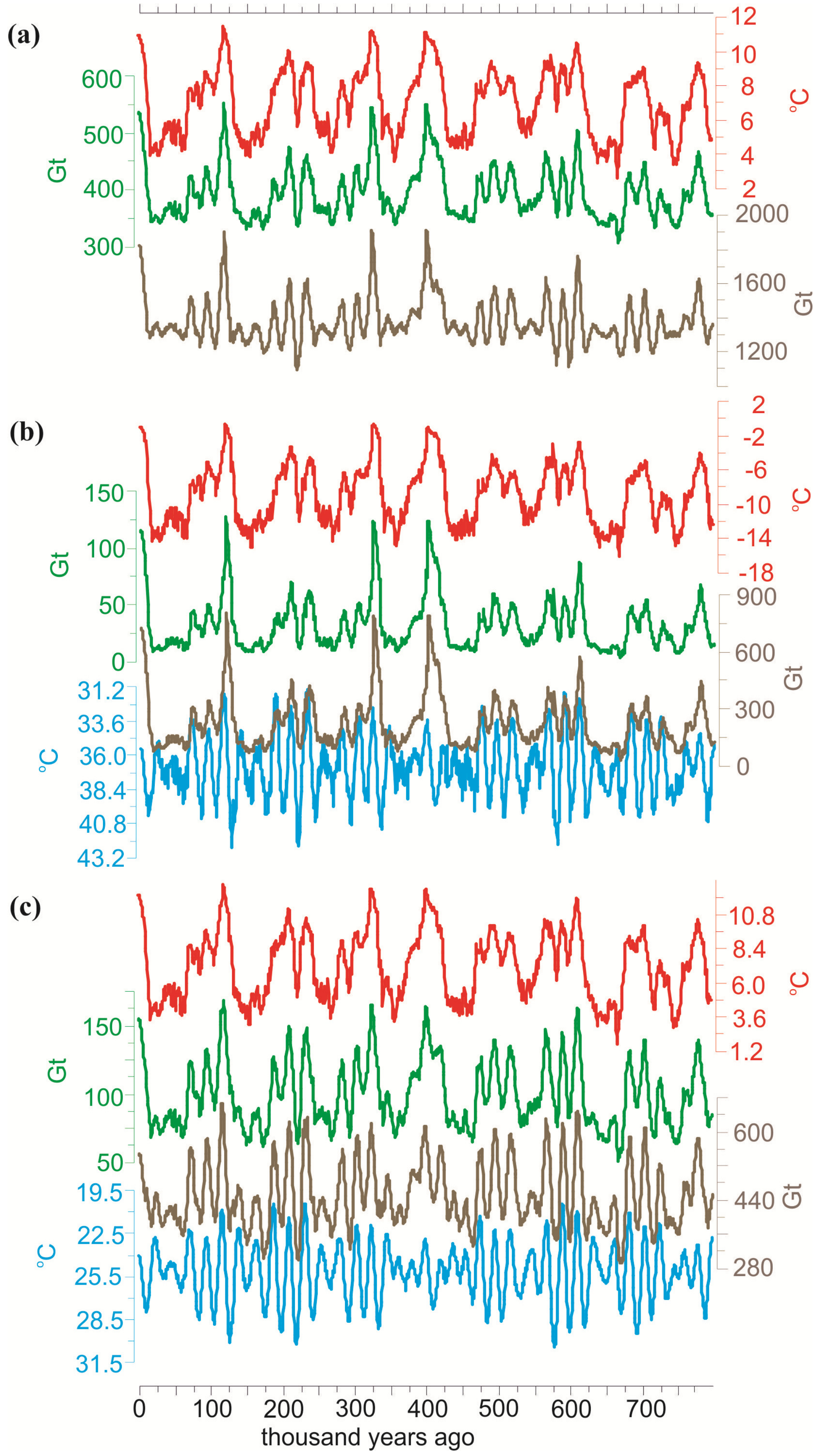
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Figure 1 (continued)

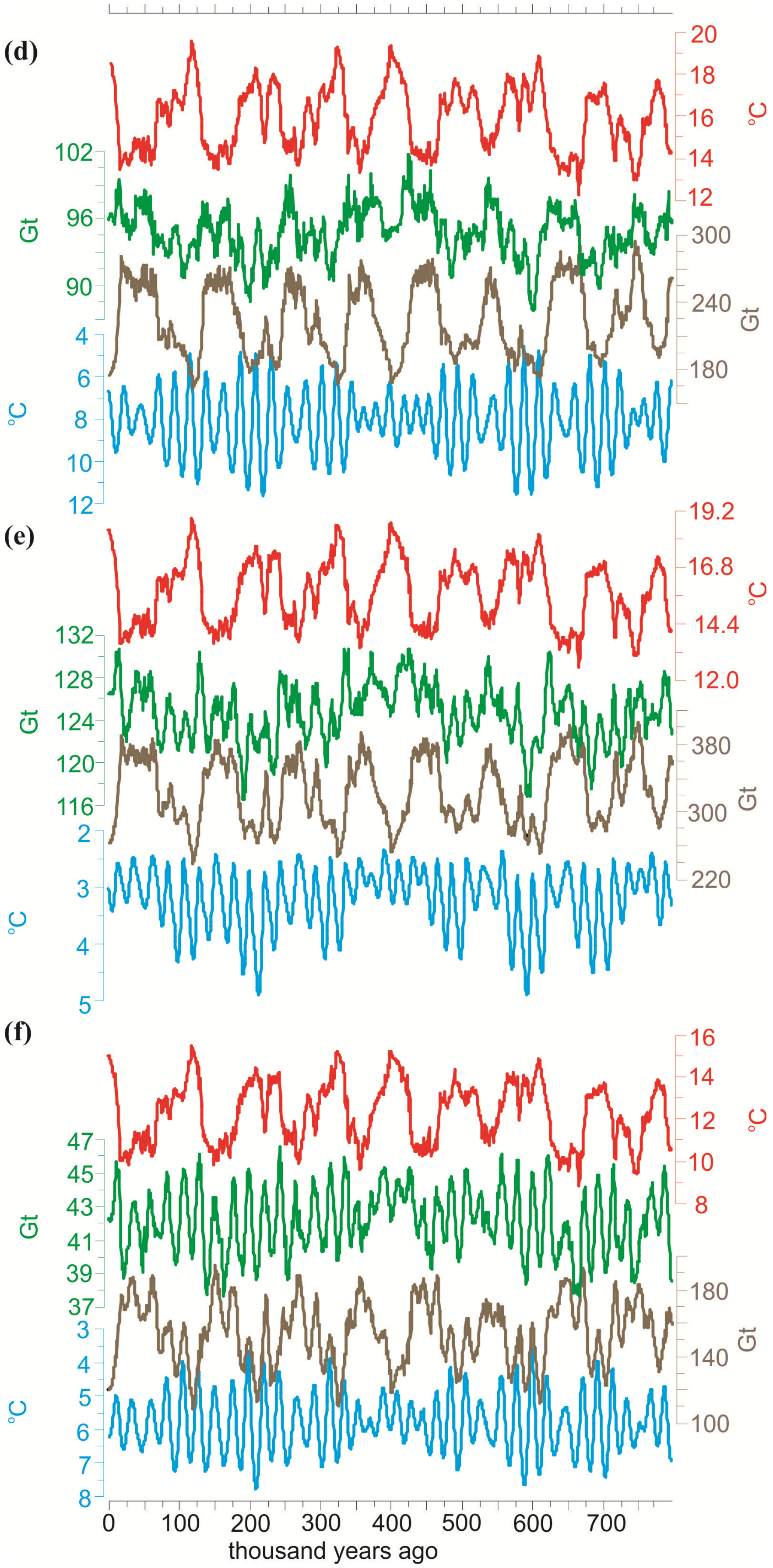
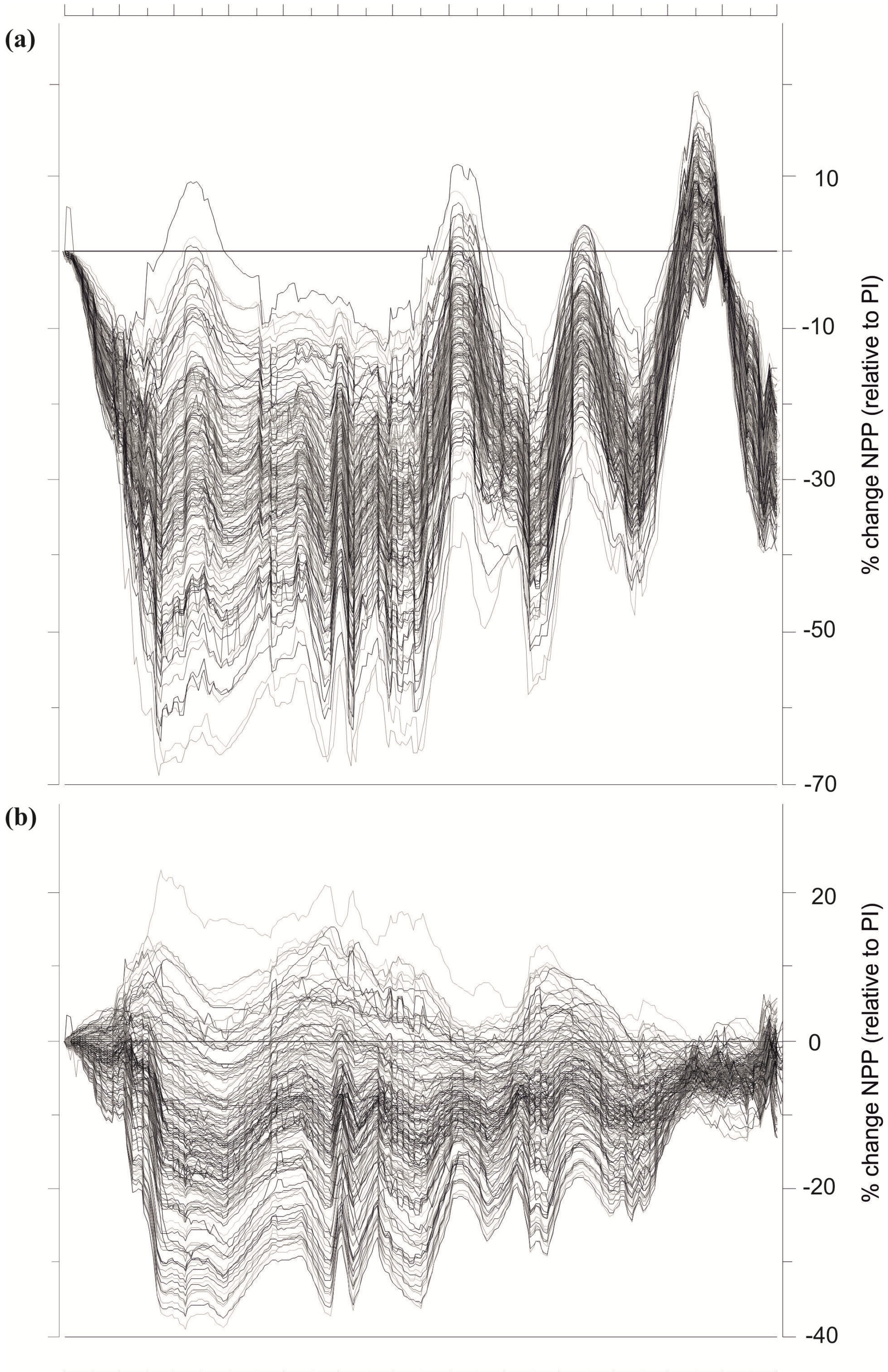


Figure 2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