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## Long-term sensitivity of soil carbon turnover to warming

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The sensitivity of soil carbon to warming is a major uncertainty in projections of carbon dioxide concentration and climate<sup>1</sup>. Experimental studies overwhelmingly indicate increased soil organic carbon (SOC) decomposition<sup>2–8</sup> at higher temperatures, resulting in increased carbon dioxide emissions from soils. However, recent findings have been cited as evidence against increased soil carbon emissions in a warmer world<sup>9,10</sup>. In soil warming experiments, the initially increased carbon dioxide efflux returns to pre-warming rates within one to three years<sup>10–14</sup>, and apparent carbon pool turnover times are insensitive to temperature<sup>15</sup>. It has already been suggested that the apparent lack of temperature dependence could be an artefact due to neglecting the extreme heterogeneity of soil carbon<sup>16</sup>, but no explicit model has yet been presented that can reconcile all the above findings. Here we present a simple three-pool model that partitions SOC into components with different intrinsic turnover rates. Using this model, we show that the results of all the soil-warming experiments are compatible with long-term temperature sensitivity of SOC turnover: they can be explained by

rapid depletion of labile SOC combined with the negligible response of non-labile SOC on experimental timescales. Furthermore, we present evidence that non-labile SOC is more sensitive to temperature than labile SOC, implying that the long-term positive feedback of soil decomposition in a warming world may be even stronger than predicted by global models<sup>1,17–20</sup>.

The short-term temperature dependence of decomposition and heterotrophic respiration in soils is well established experimentally (see, for example, refs 2–8), and is modelled either by a constant  $Q_{10}$  value of  $\sim 2$  ( $Q_{10}$  is the proportional increase in reaction rate for a 10 K warming) or more accurately by the Arrhenius equation or slight modifications thereof<sup>3,5</sup>. This short-term response conceals enormous heterogeneity in SOC: soils include compounds with intrinsic turnover times (that is, turnover times at a reference temperature) ranging from  $<1$  yr to  $>6 \times 10^3$  yr (refs 4, 16, 21). Geographical patterns generally show younger SOC <sup>14</sup>C ages in warmer climates<sup>4,16,21,22</sup>, consistent with the hypothesis that climatic warming should reduce global SOC by reducing residence times.

It is well established that a one-pool representation of SOC dynamics is insufficient to explain experimental findings from warming and incubation experiments<sup>5,16</sup>. But no model has yet been presented that is able to reconcile the above observations with refs 10–15. To this end, we used experimental data from ref. 6 to fit simple illustrative models of SOC decomposition. The data were derived from temperature-controlled incubations of an undisturbed soil from a tropical rain forest site with a mean annual temperature of 27 °C. Carbon dioxide (CO<sub>2</sub>) efflux was measured at ten intervals through a 24-week period (see Methods). The soil was taken to consist of  $n$  pools of carbon content  $c_i$ , each decaying at a temperature-dependent rate  $k_i$  over time  $t$ :

$$dc_i(t)/dt = -k_i c_i(t) \quad (1)$$

We considered Arrhenius models with a single reference decay rate  $A$  for all pools, and  $n$  activation energy values  $E_i$ :

$$k_i(T_k) = A \exp(-E_i/RT_k) \quad (2)$$

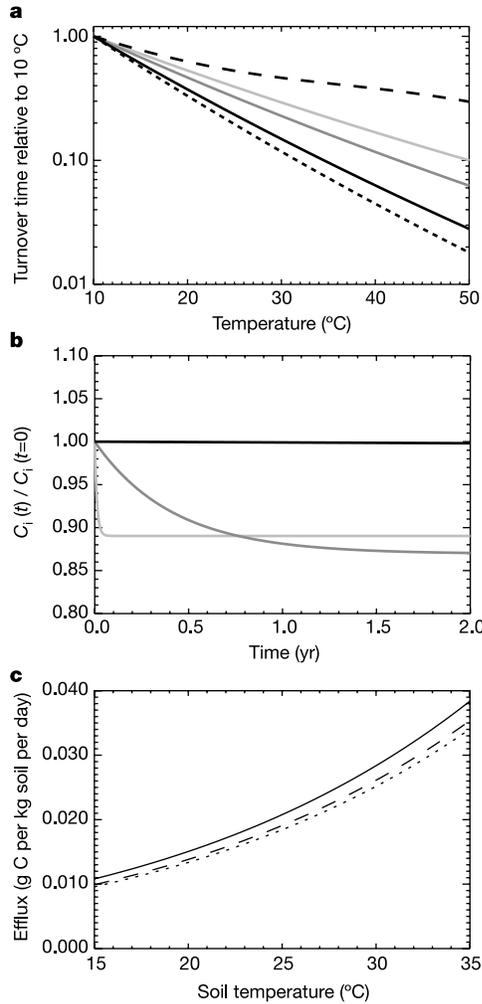
where  $T_k$  is soil temperature in kelvin and  $A$  the theoretical decay rate at  $E_i = 0$ ;  $R$  is the universal gas constant.

We started by fitting a model with  $n = 1$ , then increased  $n$  until no significant improvement of a  $\chi^2$  criterion was obtained (see Methods). This procedure selected a model with  $n = 2$  (Table 1a). The time-course of CO<sub>2</sub> efflux during the 24-week observation period is thus appropriately modelled by the decay of two SOC pools following Arrhenius kinetics but differing in activation energy. But the total soil carbon content implied by the two-pool decay models (Table 1) is far less than the measured initial carbon content of 29.4 g C per kg soil. We therefore added a third pool, effectively inert over the timescale of the experiment, which accounts for  $\sim 95\%$  of SOC. The fitted turnover time for this pool is arbitrarily large. A lower limit for its activation energy (see Methods) is 68,000 J mol<sup>-1</sup>, implying a turnover time of 260 yr at 25 °C.

Adopting the three-pool Arrhenius model with  $E_3 = 68,000$  J mol<sup>-1</sup>, we first reconsider the analysis of incubation experiments in ref. 15. A one-pool model based on equation (1) was used there to analyse the fractional decay of SOC after incubation for 1 yr. Inverting the solution to equation (1) for a single SOC pool gives an apparent turnover time,  $\tau$ :

$$\tau = -t_1 / \ln[c(t_1)/c(0)] \quad (3)$$

where  $t_1$  is the time at the end of the incubation<sup>15</sup>. Applying this definition to modelled total soil carbon content  $c(t_1)$ , with  $t_1 = 1$  yr, markedly reduces the apparent sensitivity of turnover time to temperature despite the built-in temperature dependence of all the rate constants (Fig. 1a). This paradox arises because total soil carbon  $c(t)$  is dominated by the slowest pool; over a year, the two faster pools have largely decayed. The apparent turnover time is then closely approximated by  $c_3(0)/c(0)$ . This ratio contains no



**Figure 1** Temperature responses of the three-pool Arrhenius model. **a**, Turnover times of the three pools as a function of temperature (solid lines): fast (light grey), intermediate (medium grey) and slow (black). The dotted black line uses the best-fit value for activation energy (Table 1b), the solid line  $68,000 \text{ J mol}^{-1}$  as a lower bound. The uppermost line shows turnover times calculated with the method of ref. 24. **b**, Modelled response of the pool sizes to a  $2^\circ\text{C}$  warming (grey shades as **a**). **c**, Modelled temperature response of  $\text{CO}_2$  efflux after warming the soil by  $2^\circ\text{C}$  for 1 month (dashed line) or 1 yr (dotted line), compared to the temperature response without warming (solid line).

information about the temperature sensitivity of the carbon pools.

Responses of the three carbon pools in an idealized soil warming experiment (a step change of  $+2^\circ\text{C}$  maintained over two years: see Methods) were then simulated, assuming the soil was initially in equilibrium at  $27^\circ\text{C}$  (Fig. 1b). The first pool is close to a new equilibrium after 1 month and the second pool after 2 yr.  $\text{CO}_2$  efflux from the soil is dominated by the first two pools and returns to equilibrium within  $\sim 2$  yr. The observed equilibration of the faster SOC components has been attributed to a process called ‘acclimation’<sup>12,13</sup>. Acclimation (or acclimatization) implies a gradual adaptation of living organisms or assemblages to changing environmental conditions: in this case, a change in the temperature sensitivity of soil microbial metabolism. Figure 1c shows the theoretically derived temperature dependence of the SOC decomposition rate before and immediately after warming the soil for different periods. The effect of the warming treatment is to lower the rate at any given temperature. This adjustment is to be expected as a simple result of fast labile SOC depletion relative to the bulk of more stable SOC. No biological adaptation, as suggested by the term ‘acclimation’<sup>12,13</sup>, is needed to explain it.

Equation (2) implies that the more slowly decaying fractions of SOC should respond more steeply to temperature change than the labile components (Fig. 1a, equation (4), and ref. 23). To test this hypothesis, we used results from ref. 5 where a two-pool Arrhenius model was fitted to data from a wide range of incubation experiments with varying temperature from different climates and soil types. We selected those 13 experiments that lasted at least 100 days (range: 104–720 days). The model of ref. 5 defines only one activation energy,  $E$ , for both pools. However, there is a highly significant negative correlation between values of  $E$  (in units of  $\text{J mol}^{-1}$ ) estimated in ref. 5 and the initial fraction of the fast pool:  $E = 60,578 - [35,556 c_1(0)/c(0)]$ ,  $r = -0.70$ ,  $P = 0.996$ . We also computed the total SOC turnover time, defined as  $c(0)/[-dc(0)/dt]$ , at a reference temperature of  $15^\circ\text{C}$ . A clear trend, with higher  $E$  for soils with a higher turnover time, is shown—consistent with predictions of our three-pool model (Fig. 2). Both analyses indicate that soils containing less labile material have a higher sensitivity of decomposition to temperature.

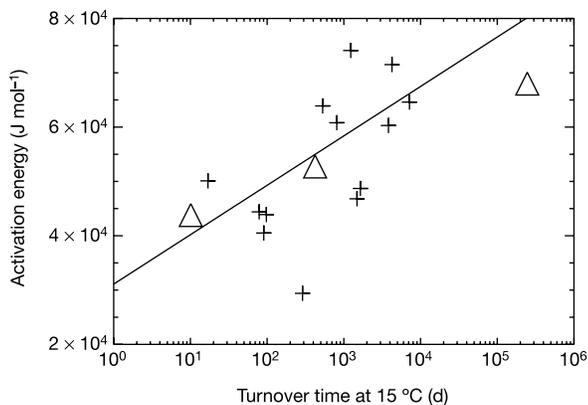
Models of SOC decay in a warming climate are based on experimental temperature responses<sup>1,17–20</sup>. Experiments lasting months to years measure only the response of the faster decaying components. But most of the Earth’s SOC is in slowly decaying components<sup>21</sup>. Our results suggest that even stronger temperature responses, and a greater magnitude of the positive SOC feedback, are to be expected in response to warming over decades to centuries.

In contrast with earlier studies<sup>24,25</sup>, ref. 26 showed little change in total SOC along a high-latitude temperature gradient. But the trend in net primary production along this gradient is probably similar to that in SOC turnover, leading to approximately constant SOC (see

Table 1 Results of model optimization

a Arrhenius model					
Model version	Number of parameters	Initial concentration (g C per kg soil)	Turnover time at $25^\circ\text{C}$ (d)	Activation energy ( $\text{J mol}^{-1}$ )	$\chi^2$
One-pool	3	1.07	80.3	44,259	3.49
Two-pool	5	0.08	5.5	43,960	1.18
		1.4	203.8	52,920	
b Arrhenius model with total soil carbon					
Model version	Number of parameters	Initial concentration (g C per kg soil)	Turnover time at $25^\circ\text{C}$ (d)	Activation energy ( $\text{J mol}^{-1}$ )	$\chi^2$
Two-pool	5	0.33	25	48,092	2.95
		29.07	17,232	64,334	
Three-pool	7	0.08	5.5	43,805	1.18
		1.39	201.7	52,744	
		27.93	$2.77 \times 10^6$	76,359	

Optimal parameter and reduced  $\chi^2$  values for models fitted to  $\text{CO}_2$  efflux data obtained by incubating fractions of the same soil sample at temperatures ranging from 15 to  $45^\circ\text{C}$ . **a**, Arrhenius models; **b**, the same with initial soil carbon content as an additional constraint.



**Figure 2** Activation energy and turnover time. Crosses, estimated activation energy for 13 soils from ref. 5 based on incubation experiments and a two-pool Arrhenius model, plotted against inferred turnover time at 15 °C. There is a strong trend for the more slowly cycling pools to have a higher activation energy, implying a steeper temperature response to warming (linear regression: activation energy ( $\text{J mol}^{-1}$ ) =  $26,829 + [4,259 \ln(\text{turnover time (d)})]$ ,  $r = 0.59$ ,  $P = 0.98$ , solid line). Triangles, comparable values based on the three-pool model of this study.

ref. 27 for a further critique). Total ecosystem respiration shows no pronounced temperature dependence across Europe<sup>28</sup> but more closely matches gross primary production, as would be theoretically expected<sup>1</sup>: geographical trends in total respiration, unlike <sup>14</sup>C ages, convey no information about the temperature dependence of SOC decomposition rates.

That models used to interpret SOC decomposition measurements should account for SOC heterogeneity has been pointed out before<sup>5,16,29</sup>. Simple models as used here assume that the Arrhenius equation is appropriate to describe any given SOC ‘pool’, although the pools themselves may be heterogeneous. This simplification is necessary given the limited available experimental data. Using a more complex theoretical model allowing continuous variation in SOC quality, Ågren and Bosatta<sup>30</sup> suggested that decomposition rates should vary less when analysed across environments with different ‘native’ temperatures than when a soil is perturbed away from its native temperature. Our model makes the opposite prediction (see Methods). Both remain to be tested.

Our simple model can account for the apparent lack of temperature dependence presented in ref. 15 as well as the apparent acclimation of total respiration in soil warming experiments<sup>10–14</sup>. We conclude that the hypothesis of a positive feedback from SOC decay to global warming is fully consistent with the available evidence. Furthermore, the response of soil carbon loss over century timescales is likely to be stronger than is suggested by fixed- $Q_{10}$  models<sup>17–20</sup>, including coupled climate–carbon-cycle models<sup>20</sup>. □

**Methods**

**Data**

Holland *et al.*<sup>6</sup> incubated four replicate homogeneous samples to 10 cm depth of the same soil from an undisturbed forest site in eastern Amazonia (Fazenda Victoria, near Paragominas, State of Pará, Brazil, 2° 59' S, 47° 31' E) at 15 °C, 25 °C, 35 °C, 45 °C and 55 °C for 24 weeks. All samples were kept at field capacity to avoid variations due to soil moisture content. Soil CO<sub>2</sub> efflux was determined through measurement of accumulated CO<sub>2</sub> concentrations in the sampling jars and ventilation before and after the sampling period, which was 1 h during the first week, and 24 h thereafter. Measurements were made during the first day after pre-incubating overnight at the experimental temperature, and then 3 days, 1, 2, 4, 7, 10, 13, 17 and 24 weeks after the pre-incubation. The sample frequency followed the pattern of soil heterotrophic respiration, being more frequent at the beginning when respiration rates were high and less so as respiration declined. During the first day, the linear increase of CO<sub>2</sub> concentrations in the sampling jar was tested by measurements at 1, 3, 5 and 24 h after pre-incubation.

**Model fitting**

Model parameters were fitted using the downhill simplex method. We computed the reduced  $\chi^2$  value to quantify agreement between modelled and measured CO<sub>2</sub> fluxes

assuming a constant measurement error of 0.1  $\mu\text{g C per g soil per h}$ , based on data given by ref. 6, Fig. 3e. The error bars shown there were computed from the different measured fluxes of four soil samples, and represent both instrumental errors and differences between samples. In order to account only for approximately constant instrument errors, we took a value close to the smallest recorded error bars at the lowest temperature and lowest flux. Incubation data for 55 °C were excluded from the model fitting because they showed evidence of thermal inhibition. The starting time of the model,  $t = 0$ , was taken to be 12 h before the end of the pre-incubation period, such that the efflux at  $t = 1, 3, \text{ or } 7$  days corresponds to the measured daily average flux during day 1, 3, or 7 of the incubation. Adding more pools than shown in Table 1 produced no significant improvement in  $\chi^2$ . When total soil carbon before incubation was used as an additional constraint (Table 1b), a three-pool model was required, but the activation energy of the slowest pool ( $E_3$ ) was highly uncertain. Therefore, the parameter  $E_3$  was not counted when computing degrees of freedom to derive the reduced  $\chi^2$  value. We varied  $E_3$  while holding all other parameters at their optimized values, and obtained reduced  $\chi^2$  values of 1.24 at 70,000, 1.36 at 68,000, and 1.94 at 66,000  $\text{J mol}^{-1}$ , respectively.  $E_3 = 68,000 \text{ J mol}^{-1}$  was adopted as a practical lower bound.

**Model application**

To mimic soil warming experiments, we assumed that initial concentrations,  $c_i(0)$ ,  $i = 1, \dots, n$ , were equal to the equilibrium concentrations at the mean annual temperature,  $T_0$ . This assumption implies constant input rates  $k_i(T_0)c_i(0)$ . When the soil is warmed by an amount  $\Delta T$  over a time  $t_1$ , with no change in inputs, the sizes of the carbon pools become:

$$c_i(t_1) = c_i(0) \left\{ e^{-k_i(T_0 + \Delta T)t_1} + \frac{k_i(T_0)}{k_i(T_0 + \Delta T)} (1 - e^{-k_i(T_0 + \Delta T)t_1}) \right\} \quad (4)$$

Immediately after the treatment, total CO<sub>2</sub> efflux at any temperature  $T$  is computed as  $F_{\text{tot}}^{\text{treated}} = \Sigma k_i(T)c_i(t_1)$ , which differs from the initial temperature response  $F_{\text{tot}} = \Sigma k_i(T)c_i(0)$ . Because  $c_3(0) \gg c_2(0)$  and  $c_3(0) \gg c_1(0)$ , the response of the soil on long timescales as seen in total SOC pool changes can be approximated by the ratio of initial to warmed decay rates (or warmed to initial turnover times) of the slow pool:  $\Sigma c_i(t_1) / \Sigma c_i(0) \approx c_3(t_1) / c_3(0) \approx k_3(T_0) / k_3(T_0 + \Delta T)$ . Conversely, because  $k_3 \ll k_1$  and  $k_3 \ll k_2$ , over short timescales total SOC hardly changes, while the flux response is dominated by changes in the fast pools. If we define an average decomposition rate  $k = [\Sigma k_i c_i(t_1)] / \Sigma c_i(t_1)$ , the inverse of the average turnover time, the variation in  $k$  over short timescales is dominated by changes in total efflux,  $\Sigma k_i c_i(t_1)$ , while changes over long timescales are determined by changes in total SOC,  $\Sigma c_i(t_1)$ . Since total SOC is dominated by the slow pool, and total efflux by the fast pools, and  $E_3 > E_2 > E_1$ , we predict a steeper temperature response of  $k$  for different soils at varying native temperatures (long-term response), than when the same soils are perturbed away from their native temperatures (short-term response).

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## Early Pliocene hominids from Gona, Ethiopia

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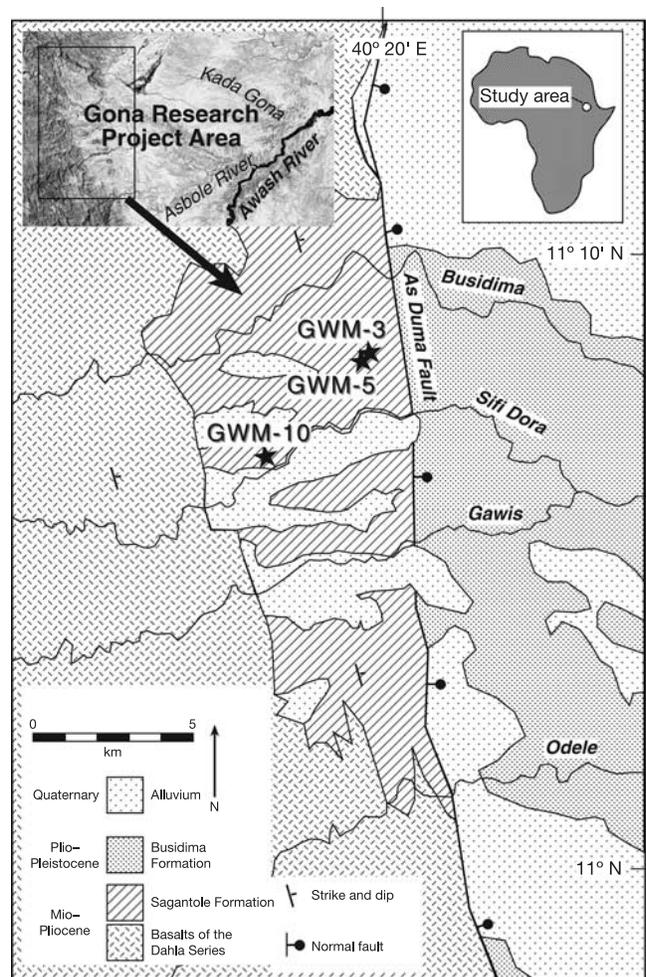
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Comparative biomolecular studies suggest that the last common ancestor of humans and chimpanzees, our closest living relatives, lived during the Late Miocene–Early Pliocene<sup>1,2</sup>. Fossil evidence of Late Miocene–Early Pliocene hominid evolution is rare and limited to a few sites in Ethiopia<sup>3,4,5</sup>, Kenya<sup>6</sup> and Chad<sup>7</sup>. Here we report new Early Pliocene hominid discoveries and their palaeoenvironmental context from the fossiliferous deposits of As Duma, Gona Western Margin (GWM), Afar, Ethiopia. The hominid dental anatomy (occlusal enamel thickness, absolute and relative size of the first and second lower molar crowns, and premolar crown and radicular anatomy) indicates attribution to *Ardipithecus ramidus*. The combined radioisotopic and palaeomagnetic data suggest an age of between 4.51 and 4.32 million

years for the hominid finds at As Duma. Diverse sources of data (sedimentology, faunal composition, ecomorphological variables and stable carbon isotopic evidence from the palaeosols and fossil tooth enamel) indicate that the Early Pliocene As Duma sediments sample a moderate rainfall woodland and woodland/grassland.

The Early Pliocene fossiliferous sediments at As Duma in the Gona Palaeoanthropological Research Project (GPRP) area are located in the Busidima and Gawis drainages at the base of the Gona western escarpment in the Afar portion of the Ethiopian rift (Fig. 1). During four field seasons between 1999 and 2003, over 1,500 fossils have been recovered from 40 palaeontological sites, seven of which included hominid remains (Table 1 and Supplementary Table 1). These fossil-rich deposits are divided from the younger Hadar and Busidima Formations (3.4 million years (Myr) ago to <0.5 Myr ago) to the east by a major normal fault (Fig. 1). Most of the As Duma sites are distributed across two distinct fault blocks separated by an apparently minor normal fault. The west-dipping orientation of the minor fault implies that all of the GWM-3 block (containing sites GWM-3/3w, and -16) is stratigraphically lower than the GWM-5 block (sites GWM-1, -5m, -5sw and -9), although the lack of stratigraphic repetition between blocks makes the time separation between sites and blocks unclear. Given their many sedimentologic similarities, we interpret these blocks as a part of a single depositional sequence. Similarities



**Figure 1** A geological map and thematic mapper (TM) image insert depicting the location of the hominid sites at As Duma in the Gona Western Margin, GPRP study area, Afar, Ethiopia. The north–south trending As Duma fault offsets the younger ( $\leq 3.4$  Myr ago) Hadar and Busidima Formations against the newly identified Early Pliocene deposits of the Sagantole Formation.