

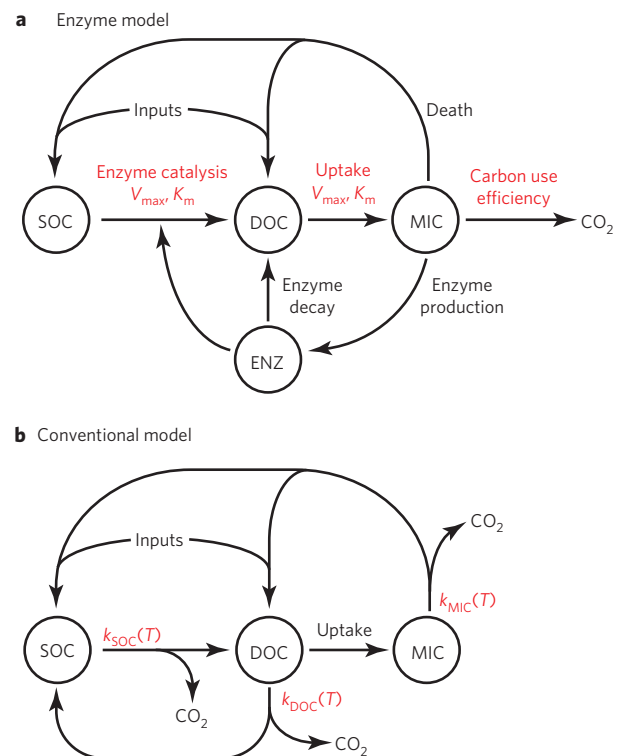
# Soil-carbon response to warming dependent on microbial physiology

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Most ecosystem models predict that climate warming will stimulate microbial decomposition of soil carbon, producing a positive feedback to rising global temperatures<sup>1,2</sup>. Although field experiments document an initial increase in the loss of CO<sub>2</sub> from soils in response to warming, in line with these predictions, the carbon dioxide loss from soils tends to decline to control levels within a few years<sup>3–5</sup>. This attenuation response could result from changes in microbial physiological properties with increasing temperature, such as a decline in the fraction of assimilated carbon that is allocated to growth, termed carbon-use efficiency<sup>6</sup>. Here we explore these mechanisms using a microbial-enzyme model to simulate the responses of soil carbon to warming by 5 °C. We find that declines in microbial biomass and degradative enzymes can explain the observed attenuation of soil-carbon emissions in response to warming. Specifically, reduced carbon-use efficiency limits the biomass of microbial decomposers and mitigates the loss of soil carbon. However, microbial adaptation or a change in microbial communities could lead to an upward adjustment of the efficiency of carbon use, counteracting the decline in microbial biomass and accelerating soil-carbon loss. We conclude that the soil-carbon response to climate warming depends on the efficiency of soil microbes in using carbon.

Existing models of soil carbon (C) response to warming are based on first-order decay of soil organic C (SOC) with the role of microbes as decomposers implicit in the decay constants<sup>7–9</sup>. However, new models are emerging that couple soil C turnover directly to microbial biomass and physiology<sup>10,11</sup>. In these models, microbial biomass and extracellular enzymes catalyse the conversion of polymeric SOC to dissolved organic carbon (DOC), which is assumed to be the rate-limiting step in SOC decomposition. Microbial-enzyme models could prove powerful tools for investigating feedbacks between warming and SOC, because temperature directly affects enzyme activity and microbial physiology<sup>6,12–14</sup>.

We incorporated temperature sensitivity into a microbial-enzyme model (Fig. 1a) to explore mechanisms underlying the ephemeral increase in soil respiration with sustained warming. These mechanisms include depletion of SOC (refs 4,7–9), thermal acclimation of microbial physiology<sup>3,14</sup> and altered plant C inputs<sup>15</sup>. On the basis of positive empirical relationships between enzyme activities and microbial biomass<sup>16</sup>, we assume that enzyme production is directly proportional to microbial biomass in our model. We represent the temperature sensitivity of enzyme activity according to the Arrhenius relationship and established biochemical theory<sup>12</sup>. Our model also incorporates temperature sensitivity of microbial carbon-use efficiency (CUE). CUE may decline with temperature if respiration responds more positively to temperature than biomass production, thereby



**Figure 1 | Diagram of soil C models.** Structure of the microbial-enzyme (a) and conventional (b) models of soil C decomposition under warming. Temperature-sensitive parameters are shown in red. The distinguishing feature of the enzyme model is that microbial biomass (MIC) affects the conversion of SOC to DOC through the production of extracellular enzymes (ENZ). In the conventional model, microbial processes are not explicitly coupled to soil C turnover, so changes in microbial biomass and enzyme production cannot feed back on decomposition.

reducing allocation of assimilated C to growth<sup>17</sup>. Empirical studies in soils suggest that microbial CUE declines by at least 0.009 °C<sup>–1</sup> (ref. 6), but in aquatic systems the magnitude of the decline is uncertain<sup>17</sup> (see Supplementary Information for a literature review). Therefore, we conducted model runs with and without temperature-sensitive CUE.

Soil-warming models should not only reproduce the ephemeral increase in soil respiration, but also generate plausible changes in SOC, microbial biomass and enzyme pools. For example, empirical studies suggest that microbial biomass and enzyme activity may decline with warming<sup>14,18,19</sup>. The SOC response is less clear, but dramatic changes in SOC pools have not yet been reported, except in

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03 arctic systems<sup>20</sup>. We therefore focused on parameter combinations that could generate these patterns. We also conducted preliminary runs to verify that model behaviours were consistent with theory and other empirical observations (Supplementary Discussion). For example, our model predicts that the temperature sensitivity ( $Q_{10}$ ) of respiration declines at higher temperatures and at lower substrate availabilities<sup>12</sup>.

Our initial simulations enabled CUE to decline with temperature and examined the effects of 5 °C warming on soil respiration, SOC, DOC, microbial biomass and enzymes. The model predicted an initial increase in soil respiration due to the temperature sensitivity of enzyme activity (Fig. 2a: blue dotted lines). However, warming reduced CUE from 0.31 to 0.23, which reduced the amount of assimilated C that was allocated to microbial growth. Consequently, microbial biomass declined and soil respiration returned to control levels within a few years as the model approached steady state. As enzyme production is linked to biomass, the decline in CUE ultimately limited the enzyme catalyst for SOC decomposition. At this level of temperature sensitivity for CUE, the SOC pool increased slightly after 30 yr of warming (Table 1; Fig. 2a: blue dotted lines). This increase contrasts with the depletion of SOC substrates predicted by models lacking an explicit coupling of microbial processes and SOC turnover<sup>7–9</sup>.

As some studies find that CUE is invariant with temperature<sup>17</sup>, we also investigated warming effects with CUE held constant at 0.31. As with the temperature-sensitive CUE scenario, warming increased enzyme activity, but the CO<sub>2</sub> pulse and SOC losses were much greater (Fig. 2a: red dashed lines). Because inputs must equal outputs at steady state, soil respiration ultimately returned to control values, but only after the SOC pool declined by more than 30%. These patterns were observed because enzymatic conversion of SOC to DOC initially stimulated microbial growth. Increased biomass led to more enzyme production, which fed back positively to SOC decomposition and respiration. With CUE held constant, SOC depletion ultimately constrained respiration because enzymes ran short of substrate. Notably, microbial biomass under warming consistently exceeded control values, which contradicts evidence from field and laboratory experiments<sup>14,18,21</sup>.

Thermal acclimation has also been proposed to explain the ephemeral increase in soil respiration with warming<sup>3,14</sup>. We therefore examined the impact of acclimation on carbon cycling responses to warming to see if they were consistent with empirical observations. We define acclimation broadly to include evolutionary adaptation, community shifts and physiological changes. We first simulated acclimation by reducing the temperature sensitivity of CUE. Relative to the variable-CUE scenario, microbial biomass and enzyme pools increased (owing to greater allocation of assimilated C to production), thereby stimulating SOC decomposition and CO<sub>2</sub> release (Fig. 2a: green dot-dashed lines).

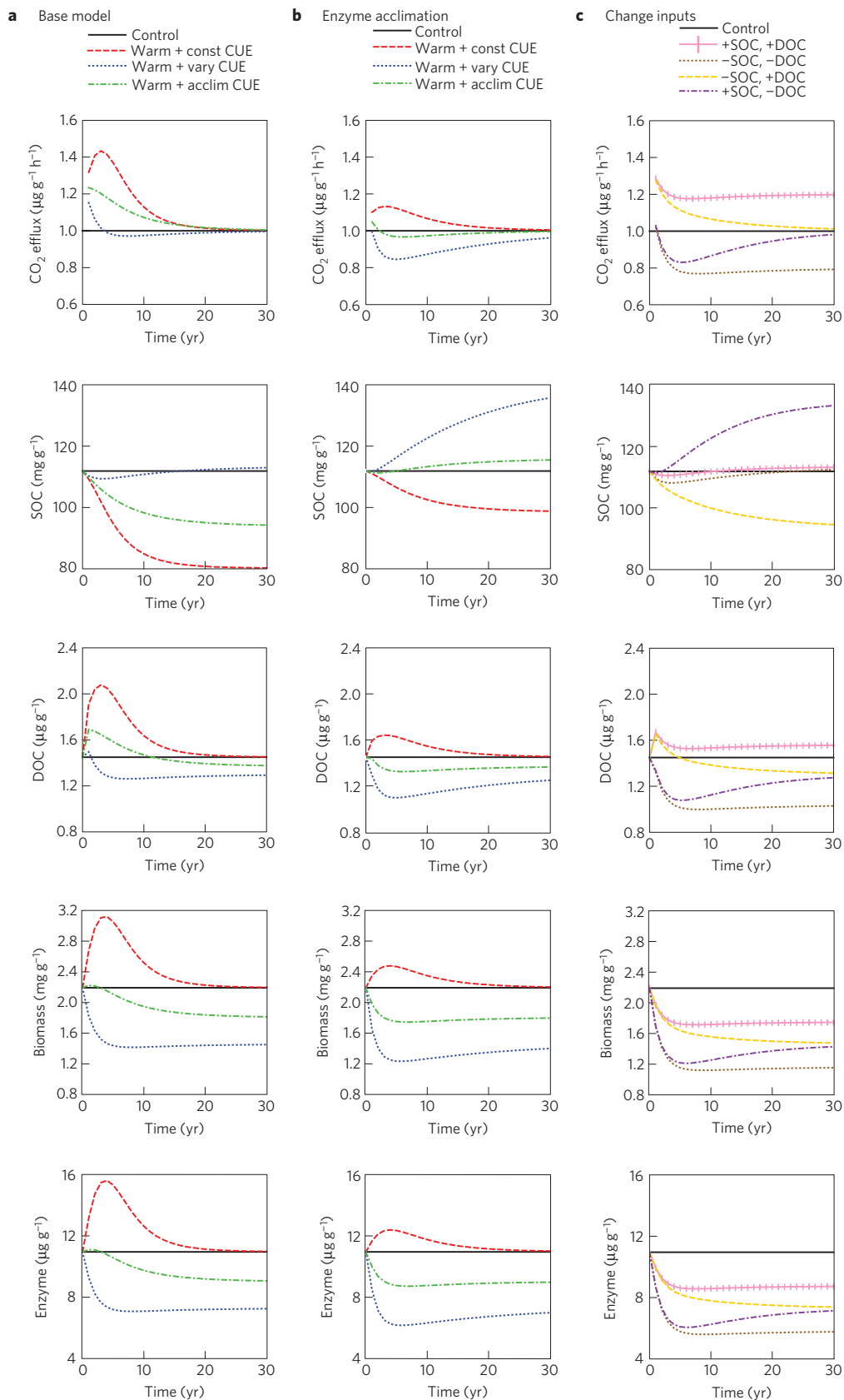
Ecological and evolutionary processes in the microbial community could also reduce the temperature sensitivity of enzymes through reductions in maximal activity ( $V_{\max}$ ; ref. 13) and increases in the half-saturation constant ( $K_m$ ), consistent with thermal adaptation of respiratory enzymes<sup>22</sup>. Therefore, we invoked acclimation through a 50% reduction in the temperature sensitivity of  $V_{\max}$  and a 50% increase for  $K_m$ . Enzyme acclimation reduced CO<sub>2</sub> losses, regardless of the CUE–temperature relationship, with peak soil respiration declining by 14–21% (Fig. 2b). SOC conversion to DOC was slower under these conditions, which constrained microbial biomass and resulted in SOC pools that were 20–23% greater after 30 yr relative to the no enzyme acclimation scenario. Notably, the enzyme-acclimation scenario with acclimated CUE (Fig. 2b: green dot-dashed lines) was consistent with empirical patterns, showing an ephemeral increase in soil respiration<sup>3–5</sup> and a decline in microbial biomass<sup>14,18,21</sup>.

Some studies suggest that climate warming may alter plant C inputs<sup>15,23</sup>, so we asked whether this mechanism could contribute to an ephemeral response of soil respiration. In these simulations, microbial CUE was temperature sensitive, and we varied SOC and DOC inputs by  $\pm 20\%$ . Altering total SOC + DOC inputs changed the equilibrium CO<sub>2</sub> efflux proportionately, but had relatively little effect on SOC pool size (Fig. 2c: pink hatched and brown dotted lines). However, holding total input constant while decreasing the DOC:SOC ratio decreased the availability of labile C, which caused a reduction in microbial biomass and an accumulation of SOC (Fig. 2c: purple dot-dashed lines; compare to base model in Fig. 2a: blue dotted lines). Increasing DOC relative to SOC inputs had the opposite effect—microbial growth and enzyme production increased relative to the base model, resulting in a more than 15% decline in the SOC pool (Fig. 2c: yellow dashed lines). The DOC addition partly offset the decline in microbial biomass derived from reduced CUE under warming. This simulation is consistent with an ephemeral increase in soil respiration<sup>3–5</sup> and a reduction in microbial biomass<sup>14,18,21</sup> under warming, although the SOC losses are greater than in the base model scenario, where inputs are constant.

Several of our simulations show an attenuation of the soil-respiration response to warming (Fig. 2), which is expected because CO<sub>2</sub> losses must ultimately equal C inputs in a steady-state model. However, the defining feature of our enzyme model is that microbial processes affect the integral under the soil-respiration curve, resulting in a range of predictions for soil C storage (Table 1). For instance, enabling CUE to decline with temperature while increasing the DOC:SOC input ratio releases more than 15% of SOC. If we assume no change in C inputs but a lower (acclimated) temperature sensitivity for CUE, we observe a similar SOC loss (Fig. 2a). In contrast, higher temperature sensitivities for CUE cause little change in the SOC pool (Fig. 2a). For the scenarios predicting large SOC losses with warming, the soil-respiration curves imply large and sustained CO<sub>2</sub> losses and a slow return to control respiration values, which would be inconsistent with empirical data<sup>3–5</sup>. However, we need additional studies of microbial biomass, enzyme activity and CUE responses to warming to test our model scenarios and accurately predict the timescale and magnitude of SOC change.

Last, we tested whether conventional soil C models<sup>7–9,24</sup> could reproduce the observed ephemeral increase in respiration<sup>3–5</sup> with a decline in microbial biomass<sup>14,18,21</sup>. As conventional model structures vary and do not always include a microbial biomass pool, we constructed a second model with a biomass pool and a structure representative of many conventional models (Fig. 1b). Even though microbial processes were not explicitly coupled with soil C turnover, our conventional model predicted an ephemeral increase in respiration under warming accompanied by decreases in microbial biomass and DOC, whether we simulated a fixed or declining CUE (Fig. 3, Supplementary Discussion). Yet, in contrast to our enzyme model with temperature-sensitive CUE, warming caused a large net loss of SOC over 30 yr. Therefore, conventional models without direct coupling between microbes and soil C turnover cannot simulate negative feedbacks on decomposition caused by reductions in microbial biomass and enzyme production.

Our enzyme-model simulations demonstrate that soil microbial biomass and enzyme activities may control feedbacks between climate warming and SOC loss. In our model, increases in microbial biomass stimulate SOC release. We hypothesize that studies detecting large losses of SOC in response to environmental drivers should also find increased decomposer biomass. For example, permafrost melting alleviates diffusion constraints on enzyme activity and probably enables microbial biomass to increase, generating large SOC losses<sup>20</sup>. Similarly, relieving nutrient

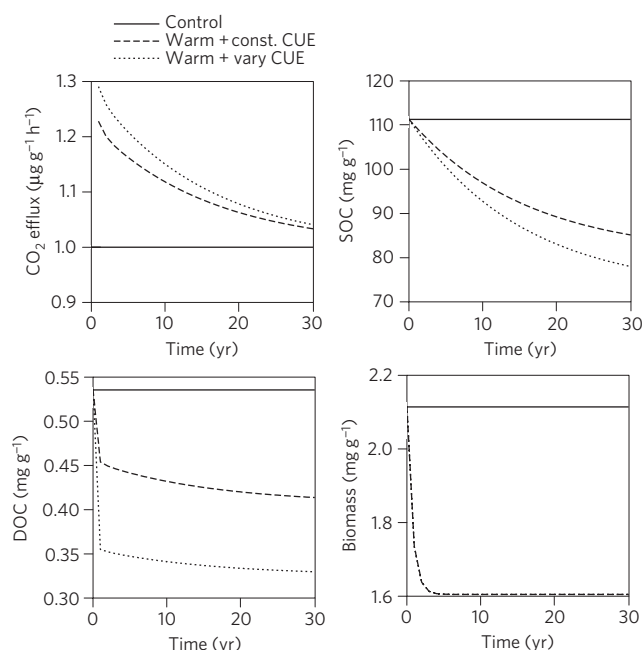


**Figure 2 | Modelled soil CO<sub>2</sub> and carbon-pool responses to 5 °C warming in the enzyme-driven model. a,** CUE was held constant, varied or acclimated to vary with a 50% reduction in temperature sensitivity. **b,** The same as **a** but with acclimation of enzyme and kinetic parameters simulated as a 50% increase in the temperature sensitivity of  $K_m$  and a 50% decline in the sensitivity of  $V_{max}$ . **c,** C inputs altered by  $\pm 20\%$  with CUE varying. Panels show predicted CO<sub>2</sub> efflux rates from the soil surface and pool sizes of SOC, DOC, microbial biomass and extracellular enzyme concentration.

**Table 1 | Modelled changes in SOC pool size.**

Scenario*	30 yr change in SOC pool size (%)
Control	0
CUE varies	+1
CUE acclimates	-16
CUE acclimates + enzyme acclimation	+3
Low SOC, high DOC inputs + CUE varies	-15
LH inputs + CUE varies + enzyme acclimation	+2
LH inputs + CUE acclimates	-29
LH inputs + CUE acclimates + enzyme acclimation	-13

\*Control run and model scenarios predicting an ephemeral rise in soil respiration and reduced microbial biomass in response to 5 °C warming, consistent with empirical observations<sup>3–5,14</sup>. LH inputs = Low SOC, high DOC inputs.



**Figure 3 | Modelled soil CO<sub>2</sub> and carbon-pool responses to 5 °C warming in the conventional model.** A reduction in CUE was represented by a 50% reduction in transfer efficiency between carbon pools shown in Fig. 1b. Panels show predicted CO<sub>2</sub> efflux rates from the soil surface and pool sizes of SOC, DOC and microbial biomass. Lines overlap in the bottom right panel owing to identical microbial biomass values.

constraints on microbes may result in greater biomass, enzyme production and SOC loss<sup>10,25</sup>. Conversely, in ecosystems where low temperature does not strongly constrain microbial biomass, C feedbacks may be weak or negative. For example, in ecosystems without permafrost, reductions in microbial CUE and soil moisture resulting from warming can reduce microbial biomass and generate a negative feedback to soil C losses<sup>19,26</sup>. Overall, our model simulations and sensitivity analyses (Supplementary Table S1) suggest that empirical studies could advance understanding of carbon–climate feedbacks by focusing on the temperature sensitivity of microbial CUE and extracellular enzyme activity.

Our enzyme model provides a simple framework for representing interactions between microbial processes and environmental change. However, present model structures could reveal other mechanisms consistent with empirical studies. CUE and enzyme activities need not be the only factors that control soil C responses

to warming, though we note that researchers can readily measure the importance of these parameters. Furthermore, our framework could be extended to incorporate other factors that influence environmental feedbacks through microbial communities. For example, the original model that we adapted from ref. 10 couples C cycling to N, a linkage that may alter the magnitude and direction of carbon–climate feedbacks in global models<sup>27</sup>. Accounting for C quality might also refine our model predictions, because the temperature sensitivity of enzymatic degradation may increase as substrate quality declines<sup>9,12,28</sup>. This relationship could be important over decades to centuries if microbial decomposition causes large SOC losses, because residual C may be lower in quality. Warming-induced changes in microbial community composition could also influence substrate quality through microbial turnover and SOC formation<sup>29</sup>. Furthermore, our model parameters represent community composition only implicitly, yet community shifts could affect biomass and enzyme production directly. A new generation of coupled models that account for these microbial properties should improve estimates of soil C change and the magnitude of feedbacks in the carbon–climate system.

## Methods

Initial pool sizes were derived from a spin-up model run at 20 °C (Supplementary Tables S2, S3). Inputs of SOC and DOC each represent an annual flux of ~44 g C m<sup>-2</sup> to the top 1 cm of soil surface. Other rate parameters were selected to produce reasonable pool sizes at equilibrium. We chose a microbial turnover rate of 0.0002 h<sup>-1</sup>, corresponding to a biomass mean residence time of ~200 d. Half of the dead biomass enters the DOC pool whereas the remainder becomes SOC. Enzyme-loss rates corresponded to a mean residence time of ~42 d. Microbes were assumed to allocate 0.012% of their biomass to enzyme production per day. We assumed that microbial CUE declined linearly (CUE = 0.63–0.016 T) with increasing temperature between 0 and 25 °C (Supplementary Methods).

For enzyme kinetic parameters, we made the simplifying assumption that one enzyme degrades the entire SOC pool. We also assumed that SOC substrate would not saturate enzyme reactions, and therefore chose a  $K_m$  value of 600 mg cm<sup>-3</sup>, which is larger than our target SOC pool size of ~112 mg cm<sup>-3</sup>. Our temperature sensitivity function is linear and positive for  $K_m$ . We selected the pre-exponential term in the Arrhenius relationship to produce  $V_{max}$  values that generated stable biomass and SOC at 20 °C. We followed a similar procedure for uptake kinetic parameters, but the pools were insensitive to these parameter choices because enzymatic decomposition is the rate-limiting step in our model. Activation energy for SOC decomposition was set at 47 kJ mol<sup>-1</sup>, similar to values found empirically for the degradation of complex organic material<sup>30</sup>.

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## Author contributions

M.A.B. and M.D.W. conceived the project, and S.D.A. built the model. S.D.A. and M.A.B. conducted model runs. All authors contributed to writing the paper.

## Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on [www.nature.com/naturegeoscience](http://www.nature.com/naturegeoscience). Reprints and permissions information is available online at <http://npg.nature.com/reprintsandpermissions>. Correspondence and requests for materials should be addressed to S.D.A.

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