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Warming-related increases in soil CO_2 efflux are explained by increased below-ground carbon flux

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The universally observed exponential increase in soil-surface CO_2 efflux ('soil respiration'; F_S) with increasing temperature has led to speculation that global warming will accelerate soil-organic-carbon (SOC) decomposition[1], reduce SOC storage, and drive a positive feedback to future warming[2]. However, interpreting temperature–F_S relationships, and so modelling terrestrial carbon balance in a warmer world, is complicated by the many sources of respired carbon that contribute to F_S (ref. 3) and a poor understanding of how temperature influences SOC decomposition rates[4]. Here we quantified F_S, litterfall, bulk SOC and SOC fraction size and turnover, and total below-ground carbon flux (TBCF) across a highly constrained 5.2 °C mean annual temperature (MAT) gradient in tropical montane wet forest[5]. From these, we determined that: increases in TBCF and litterfall explain >90% of the increase in F_S with MAT; bulk SOC and SOC fraction size and turnover rate do not vary with MAT; and increases in TBCF and litterfall do not influence SOC storage or turnover on century to millennial timescales. This gradient study shows that for tropical montane wet forest, long-term and whole-ecosystem warming accelerates below-ground carbon processes with no apparent impact on SOC storage.

Soils of the Earth annually release ~60 Gt of carbon (C) to the atmosphere through soil-surface CO_2 efflux (F_S; 'soil respiration'), dwarfing CO_2 emissions from fossil fuel combustion by a factor of seven[6]. This large C flux is approximately balanced by the flux of C entering soils through TBCF (the sum of C flux to below ground to support root production and respiration, root exudates, herbivory and symbionts) and litterfall[7]. Given the importance of SOC in the global C cycle, the effects of warming on the balance of inputs and losses will have a large impact on the net sink strength of the terrestrial biosphere[2]. Efforts to quantify underlying processes, however, have been inadequate for projecting the effects of warming on terrestrial C balance[4]. For example, warming seems to be increasing global F_S (ref. 1), but how much, if any, of this increase is derived from accelerated SOC decomposition remains poorly quantified. Although many studies have documented short-term (annual to decadal) increases in SOC decomposition with warming, these responses often are ephemeral[8], in part because of various acclimation processes including reduced substrate supply, microbial adjustments at cellular and community levels, and changes in litter and soil-C quality[4,8]. Extrapolating short-term results to long-term (centennial to millennial) responses is further complicated by observations that gross and net primary production also increase with warming[9–11], with a corresponding increase in the amount of C sent below ground by plants[11]. Finally, SOC studies have failed to show changes in stock size with warming, with precipitation seeming to exert a much stronger influence on SOC storage than temperature[12].

To address these critical knowledge gaps, we tested two hypotheses on the potential response of SOC storage to long-term, whole-ecosystem warming. The first posits that warming increases the turnover rate for SOC, which drives the often-observed increase in F_S. This implies that the current capacity of the world's forests to retain SOC will decline with warming if increased inputs do not keep pace with accelerated decomposition of SOC. Further, increased detrital production could stimulate SOC decomposition[13–15] and accelerate net SOC loss. Our second hypothesis posits that warming-related increases in primary production drive higher F_S through elevated above-ground and below-ground carbon inputs[11], and their subsequent conversion to CO_2. With our second hypothesis, there need not be warming-driven increase in the turnover of older SOC as decomposition of the increased inputs can explain increased F_S. And although increased C inputs can stimulate SOC decomposition, thereby reducing storage, warmer temperatures can also accelerate processes of SOC formation[16], with one potential outcome being no net change in SOC storage. These two hypotheses are conceptually straightforward, but tests have been lacking because of the logistical and technical difficulties associated with whole-stand warming and the tracking of below-ground C inputs. So far, results from artificial warming experiments, MAT gradient studies and *ex situ* incubation studies have been conflicting[4,17].

We directly tested our hypotheses about the response of SOC storage to warming by using a whole-ecosystem study in tropical montane wet forest arrayed across a highly constrained 5.2 °C MAT gradient[5]. This MAT gradient represents a critical advance over previous gradient studies because the various factors that can affect ecosystem processes other than temperature are held constant[5], including: soils (all Acrudoxic Hydrudands in four closely related soil series); parent material (all tephra-derived substrate of similar type and age); moisture (constant plant available soil moisture); vegetation (>85% of stand basal area across the MAT gradient is composed of one canopy and one mid-storey species); and long-term disturbance history (late-stage aggrading forests). To further constrain this gradient and minimize disturbance effects, we selected plots that represent maximum biomass for a given MAT (ref. 5).

We previously reported that F_S increased linearly and positively with MAT along this gradient[5]. Here we report that both TBCF and litterfall, representing most detrital C inputs to soil, also increase linearly and positively with MAT (Fig. 1), in line with cross-site global analyses of the response of TBCF to rising temperature[11]. We then combined quantification of SOC stocks by depth (0–10 cm, 10–30 cm, 30–50 cm and 50–91.5 cm) with radiocarbon-based

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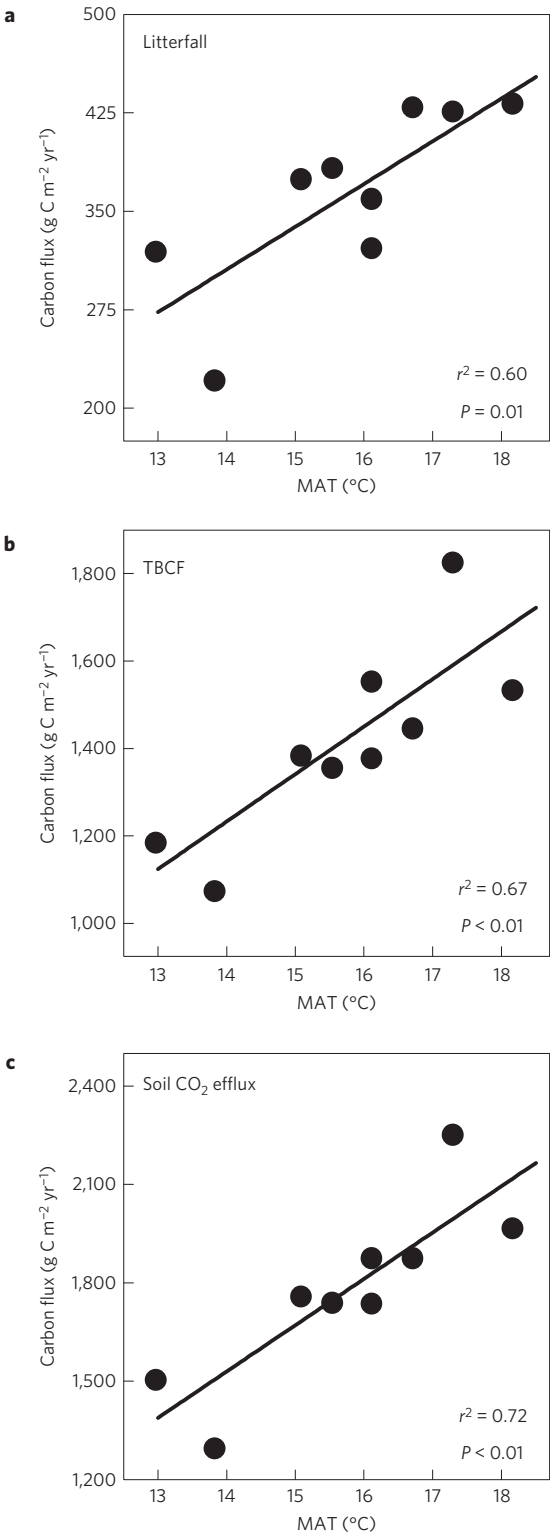

Figure 1 | The effects of mean annual temperature (MAT) on the components of total below-ground carbon flux (TBCF). a–c, Annual flux rates for: litterfall (**a**), TBCF (**b**) and soil-surface CO_2 efflux (**c**) in tropical montane wet forest in Hawaii all showed strong linear increases with rising MAT ($n=9$).

mean residence time (MRT) estimates for bulk SOC across the MAT gradient. Strikingly, radiocarbon-based estimates of MRT revealed no relationship between SOC MRT and MAT for any depth (Fig. 2a–d). Similarly, MAT had no effect on radiocarbon-based estimates of turnover for four SOC fractions (soluble, light, intermediate and heavy) in 0–10 cm depth soils, those soils most likely to show a response to MAT (Supplementary Information and Supplementary Figs A1 and A2). In addition, neither SOC stocks at any depth (Fig. 2e–h) nor SOC fraction size for surface soils (Supplementary Information and Supplementary Figs A1 and A2) varied with MAT. As radiocarbon-based turnover rate for bulk SOC is a strong predictor of the turnover rate for acid-insoluble SOC (Supplementary Information and Supplementary Fig. A3), we conclude that across our gradient, temperature has little detectable influence on turnover of bulk SOC, on the size and turnover of even labile SOC fractions with high MRT, or on the size and turnover of the most stable C fractions in mineral soil. Lending further support for our second hypothesis, SOC turnover estimated from stock and MRT measurements for bulk SOC represents <5% of F_S, or ~0.39 Mg C ha^{-1} yr^{-1}. These numbers may underestimate the actual contribution of SOC decomposition to F_S because bulk SOC MRT may not accurately capture the dynamics of the more rapidly cycling SOC pools. Relying on fraction size and MRT for SOC in 0–10 cm soils, we calculated a total flux of 0.40 Mg C ha^{-1} yr^{-1}. As this depth contributes >75% of SOC-derived F_S for the bulk SOC calculations, even a doubling of our estimated SOC flux translates to <10% of F_S being derived from decomposition of SOC that is older than 1 yr, in line with independent estimates for aggrading tropical forests[18].

Our results provide compelling evidence that, alone (for example, not accompanied by changes in vegetation or moisture) and in the long-term (that is, centuries to millennia), warming will have little effect on SOC storage in tropical montane wet forest. Critically, the lack of change in SOC stocks across this MAT gradient cannot be interpreted as faster SOC decomposition being offset by faster SOC formation rates due to increased inputs of detrital C and temperature effects on decomposition and formation processes[16,18]. This combination of balancing processes would necessarily drive down the age, and hence MRT of SOC and associated fractions, which we did not observe. As above-ground litterfall and TBCF increased with MAT (Fig. 1), but MAT had no effect on SOC storage and turnover, we conclude that the additional C entering soils at warmer sites is being rapidly decomposed and released as CO_2 from the rhizosphere or on the soil surface. Further, the lack of a MAT effect on SOC storage and MRT indicates that the increase in C inputs with warming is not driving an increase in SOC turnover[13–15].

The current perspective on SOC stabilization and decomposition is that physical protection mechanisms, including organo-mineral associations and protection within soil aggregates, exert a primary control on SOC decomposition[19]. Organo-mineral associations are particularly strong for soils containing short-range-order (SRO), or other poorly crystalline phases of Al such as allophane, imogolite and organo-complexed Al (ref. 20). Although the soils of our MAT gradient exhibit some oxic properties typical of the Ultisols and Oxisols that dominate the lowland tropics[5], they are relatively young (~20,000 yr) and of volcanic ash origin, and so some level of amorphous mineralogy is expected along with a strong positive influence on C stabilization[20]. The primary objective of mineralogical analyses here was to rule out the possibility that temperature-mediated changes to soil mineralogy are driving the absence of SOC storage or MRT responses to warming. If increasing SRO mineral content were to result in more effective physical protection of SOC from decomposition at warmer temperatures, our results would be confounded and difficult to interpret. Consistent with previous research[20], we found clear evidence of mineral control on SOC MRT (Fig. 3). However, SRO patterns were opposite in direction from those that would confound our results—cooler soils were associated with higher SRO content, which is to be expected given that soils weather more slowly at cooler temperatures. Specifically, we found significant relationships between SRO content and SOC MRT for soils at the two middle depths. For surface soils

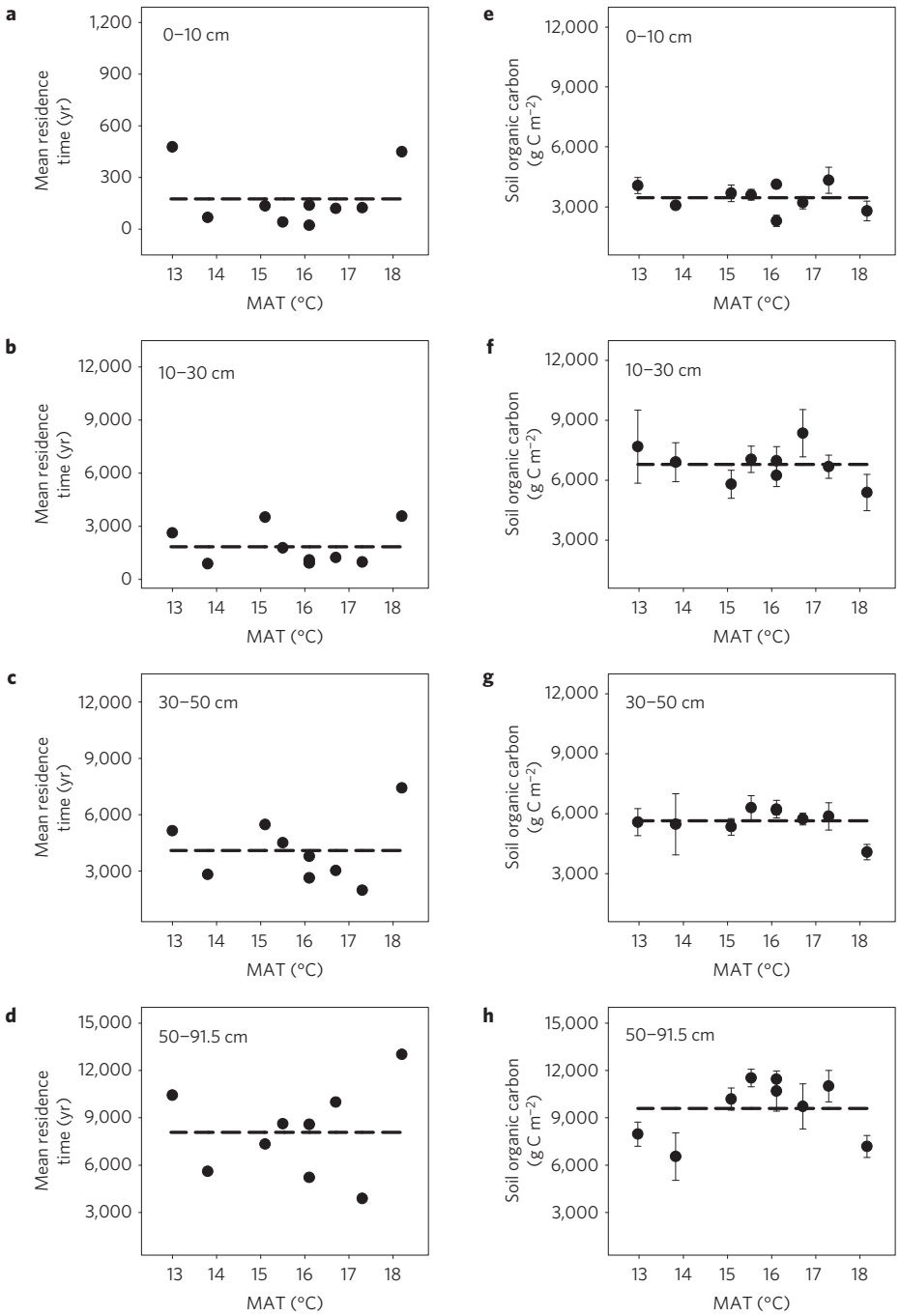

Figure 2 | Mean residence time (MRT) and soil organic carbon (SOC) storage do not vary with mean annual temperature (MAT). a–h, Effects of MAT on SOC MRT (**a–d**; means; *y*-axis scale varies) and SOC stocks (**e–h**; means ±1 s.e.m.; *y*-axis scale varies) for 0–10, 10–30, 30–50 and 50–91.5 cm soil depths in tropical montane forest in Hawaii. No error bars are provided for radiocarbon analyses as they were performed on one composite sample per site and depth. Regression analyses revealed that none of the relationships was significant, and so dashed lines represent means across all plots along the MAT gradient ($n=9$).

that were all low in SRO Al, bulk SOC MRTs are short—of the order of a century indicating rapid turnover, as has been previously documented in Hawaii[20] and elsewhere in the tropics[4]. Yet SOC MRT for this depth is unrelated to MAT, indicating that controls on turnover in surface soils include some combination of low substrate availability[2,8] and perhaps longer-term microbial adjustments to changes in MAT (refs 4,8,21). These findings are confirmed by analyses of fractionated 0–10 cm depth soils, which showed no discernible effect of MAT on the size or MRT of individual SOC fractions (Supplementary Information). For the two mid-depth soil layers where SRO minerals were abundant, soil mineralogy exerts a substantial influence on SOC MRT, but there is no apparent effect of MAT. Given the very long MRTs for SOC in the deepest soils (>10,000 yr), stabilization may be caused by a combination of high concentration of SRO minerals, but also additional factors such as primary organo-complexed Al, or concretions into micro-aggregates of crystalline Fe oxides that render C unavailable for microbial processing[20].

These results show that temperature can influence below-ground processes through geological timescale effects on soil mineralogy

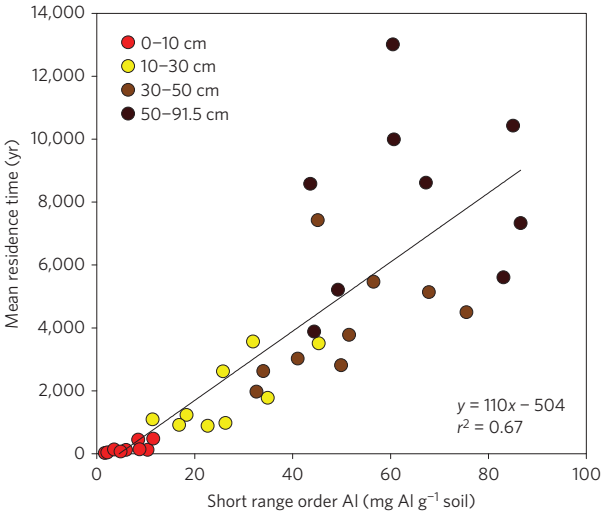

Figure 3 | The relationship between short-range order (SRO) aluminium (Al) and the mean residence time (MRT) for soil organic carbon (SOC) for the four sampled depths in tropical montane wet forest in Hawaii. Across-depth and mean annual temperature (MAT) SRO Al content explains >66% of the variation in SOC MRT. If the deepest soils, where the largest variability was found, are excluded then 75% of the variation in MRT is explained by SRO Al. For the surface 10 cm of soil, SRO Al content was very low and there was no relationship with MAT. However, for 30–15 and 50–91.5 cm depth soils, SRO Al content was high and decreased linearly with increasing temperature ($r^2 = 0.35$ and 0.54 for 30–50 and 50–91.5 cm depth soils, respectively; $n = 9$). The SRO Al content of 10–30 cm depth soil was intermediate, but there was no pattern with MAT.

(Fig. 3) as well as physiological timescale effects on productivity (Fig. 4), which highlights the need for SOC studies to examine both the direct biochemical effects of temperature on SOC turnover, and any indirect geological or physiological effects of temperature on SOC turnover. Critically, the data presented here provide no evidence for hypothesis one that warmer temperatures exert a direct effect on SOC storage through accelerated decomposition. Conversely, our work shows a limited capacity of soils to retain the additional inputs from warming-related increases in primary production and below-ground C inputs—either because increased inputs decompose more rapidly with warming or soils have a maximum capacity to protect and store organic C (ref. 22), with unprotected C being quickly mineralized. Notably, a 50% increase in detrital C inputs across MAT had little effect on SOC MRT or stock[14,15]. In contrast, nitrogen (N) has been implicated in the stabilization of detrital C through suppression of lignin-degrading enzymes and formation of recalcitrant compounds[23], and we observed warming-related increases in the cycling and availability of soil N (unpublished data). Conversely, increases in rhizosphere carbon flux in free-air CO_2 enrichment experiments have been shown to increase soil-organic-N cycling through enhanced microbial and enzymatic activity with no effect on total SOC storage[24].

The various lines of evidence presented here strongly support our second hypothesis: TBCF and litterfall increase with MAT, which drives higher F_S, but neither elevated temperature nor increased detrital inputs affect storage or turnover of most SOC (Fig. 4). This conclusion aligns with recent evidence from free-air CO_2 enrichment experiments showing that root exudation increased with exposure to elevated CO_2, but increases in recent, root-derived C were rapidly respired and returned to the atmosphere[24].

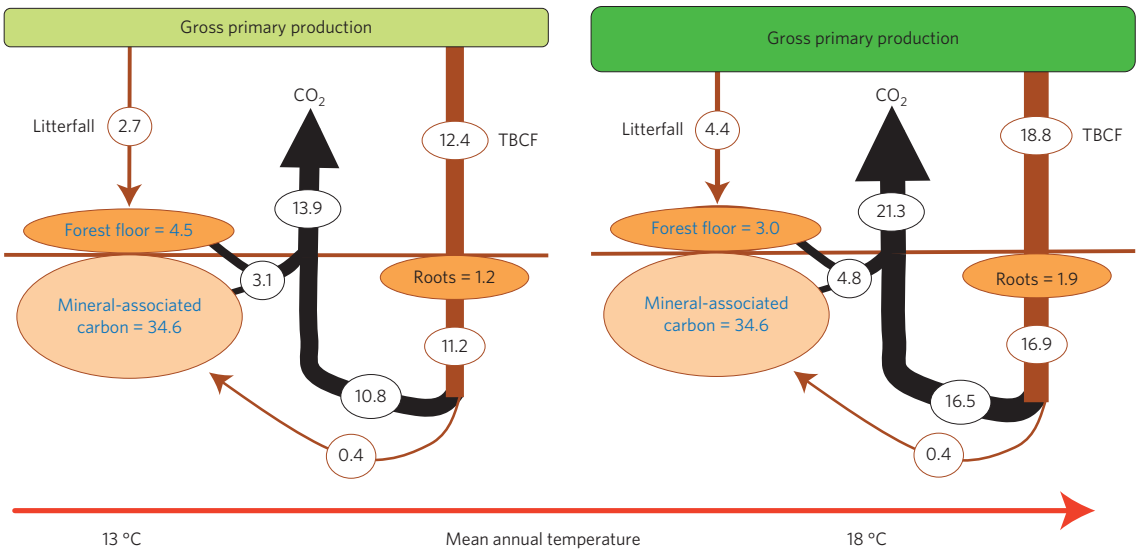

Figure 4 | Our test of ecosystem response to increasing mean annual temperature (MAT) supports the hypothesis that nearly all of the temperature-driven increase in soil-surface CO_2 efflux is derived from increased total below-ground carbon flux (TBCF) and secondarily from increased litterfall both resulting from an anticipated increase in stand-level net primary productivity with warming. Soil organic carbon (SOC) storage and turnover were unrelated to temperature across our 5.2 °C MAT gradient, indicating that long-term, whole-ecosystem warming increases below-ground C cycling with no change in SOC storage. The lack of change in SOC mean residence time (MRT) despite increased below-ground inputs indicates little stimulation of SOC turnover due to higher inputs. Taken together, these findings show that over long periods of time, SOC storage and turnover are not influenced by warming, but rather SOC stock and turnover seem to be controlled by physical, biological and chemical characteristics of soil. Fluxes (Mg C ha^{-1} yr^{-1}) are in black and stocks are in blue (Mg C ha^{-1}). Root increment is estimated to be 10% of TBCF (ref. 18). Litterfall sources contributed between 17 and 22% to efflux, based on mass-balance estimates for our plots and the calculation that litter decomposes within ~1 yr of release from the canopy. Combining stock and bulk SOC MRT estimates, we calculate that decomposing SOC contributes <5% of F_S, with a mean contribution to efflux of 0.39 Mg C ha^{-1} yr^{-1}. At 77–82%, TBCF is estimated to represent most F_S. Forest floor mass for these mature forest plots turns over rapidly, even at the coolest sites, but the forest floor is assumed to be approximately in steady-state for a given site and so across the gradient. Given the very old dates for most SOC across plots and MRT-based estimates of SOC loss, we also assumed that SOC storage is in steady-state. Given steady-state, low rates of SOC loss are balanced by low formation rates of new SOC.

This interpretation is supported by recent evidence from the Arctic, where a two-decade experiment showed warming-induced increases in both microbial activity and mineral soil-C storage[25].

We note that forest floor mass declined linearly with rising MAT (from 450 to 300 g C m^{-2}). Relying on a classic mass-balance approach, we used forest floor mass and litterfall rates to estimate that turnover rates for unprotected fine detritus not associated with mineral soil are 2.3 times faster at the warmest compared with the coolest site (litter turnover = MAT × (−0.17) + 3.77; $r^2 = 0.82$; $Q_{10} \approx 4.5$). These findings are in line with well-established responses of litter decomposition to temperature[2,8]. Further, earlier work from this gradient showed a strong pattern of declining coarse woody debris storage with warming[26]. These findings suggest that when detrital C is not protected, as is the case for fresh fine litter, coarse woody debris, or C newly released into the rhizosphere, substrate supply does not limit reaction rates and decomposition can respond much more strongly to increases in temperature than the substrate-limited decomposition of SOC protected by soil minerals[8]. Such an interpretation is consistent with recent findings showing that the temperature sensitivity of SOC decomposition depends strongly on the availability of labile C (ref. 27). Although our study does not address short-term warming responses, and findings from past studies are clearly mixed[4,18], our findings for tropical montane wet forest point to an intriguing set of conclusions. Long-term warming alone: increases below-ground inputs, which in turn drive warming-related increases in F_S through accelerated cycling of labile, unprotected C; has no effect on the storage of bulk SOC, with neither SOC turnover nor formation responding to rising temperature; and has no effect on the distribution and turnover of SOC in soil C fractions. Overall, however, we caution that there is a strong need for a new generation of large-scale, cross-site studies that systematically address SOC responses to warming in the context of whole-ecosystem process rates.

Methods

Site description. This research took place on the eastern flank of Mauna Kea Volcano, Hawaii Island, within the Hawaii Experimental Tropical Forest and the Hakalau Forest National Wildlife Refuge. Forests are characterized as closed-canopy, *Metrosideros polymorpha*-dominated tropical montane wet forest. Soils are all Acrudoxic Hydrudands and are derived from tephra ash deposits from Mauna Kea volcanism. The underlying Pleistocene-aged flow is dominated by hawaiite and mugearite[5]. The nearly constant and old age (>10,000 yr) of SOC in the deepest soil layer supports a constant substrate age across the MAT gradient.

Plot selection. To minimize disturbance history effects, repeat airborne light detection and ranging (LiDAR) measurements of forest structure were used to select seven sites at each of six target elevations, where each site represents the maximum above-ground biomass present at a given elevation. LiDAR-based information at a 1.12 m resolution was acquired with the Carnegie Airborne Observatory[28] (CAO) to quantify mean tree height across each elevation band specified on a single substrate type and age (Supplementary Information). For the two coolest sites, LiDAR data were not available, and so traditional inventory techniques were used to identify two high-biomass stands across a 4 km^2 area of forest growing on the appropriate geology and soils[5].

Stock and flux measurements. We measured F_S and litterfall in each of the nine 20 × 20 m plots located across a 5.2 °C MAT gradient (ref. 5). We used a mass-balance-based approach to estimate TBCF (ref. 18), which is defined as the annual total of C flux to below ground for the production and maintenance of roots, mycorrhizae and other symbionts, and C released as root exudates, herbivory or biomass turnover. As this C must be respired or stored, TBCF can be estimated as: F_S − litterfall + Δ [$C_S + C_F + C_R$], where C_S represents mineral soil C, C_F represents forest floor C and C_R represents live root C (ref. 18). We measured F_S monthly using previously described methods[5]. We measured litterfall monthly in 8 permanently installed 0.174 m^{-2} collectors per plot, from which litter was collected, oven-dried and weighed using standard methods[18]. Both sets of flux measurements were conducted between April 2009 and March 2010. We assumed that annual change in soil C was negligible on the basis of our radiocarbon analyses and findings for adjacent but more disturbed sites[18]. We also assumed that erosion and leaching losses of C were minor components of TBCF at our sites[18] and so were not measured. On the basis of previous results[18], we assumed that 10% of TBCF was allocated to coarse root growth. Although relevant for TBCF accounting purposes, any errors associated with this assumption would have a minor influence on overall TBCF estimates[18], and no effect on our SOC and F_S estimates because coarse root C is long-lived. From previous work on error distribution in TBCF calculations[18], we anticipate that error propagation in calculating TBCF is negligible. Soil temperature and moisture were recorded at the location and time of measurement using temperature probes and loggers[5]. Detailed repeat measurements across MAT showed no diurnal variation in soil-surface CO_2 efflux, and so were not used to construct annual soil-surface CO_2 efflux budgets[5].

We measured forest floor mass across the gradient to understand litterfall decomposition rates through collections of all recognizable plant material (litter layer C) at eight 0.174 m^{-2} quadrats per plot. These samples were dried to constant weight and analysed for [C] (Costech Elemental Combustion System). Mineral-associated SOC (Mg C ha^{-1}) was estimated across the gradient in three cores per plot (or five cores if coefficient of variation was >25% based on the original 3 cores) to 91.5 cm using a 5.75-cm-diameter soil core with plastic sleeves, from which both C content as above and bulk density were determined[18]. We analysed bulk density and percentage of C from four depth increments (0–10 cm, 10–30 cm, 30–50 cm and 50–91.5 cm) to determine C stocks.

Soil samples were physically separated into soluble, light, intermediate and heavy fractions using a sequential density fractionation method relying on progressively denser solutions of sodium poly-tungstate to isolate soil C fractions[29]. Sub-samples of bulk soil and soil fractions were ground to <150 μm mesh size for elemental and isotope analyses. Radiocarbon analyses of all bulk soils were completed at the Centre for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory and fraction-based radiocarbon analyses were completed at the ^{14}CHRONO Centre for Climate, the Environment, and Chronology at Queen's University Belfast (details provided in Supplementary Information). SRO Al concentration was determined by hydroxylamine hydrochloride hydrochloric acid extraction method combined with 16 h of shaking[30]. Linear regression and diagnostic analyses for data conformance to assumptions were performed in SigmaPlot (Version 11.0).

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Author contributions

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Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to C.P.G.

Competing financial interests

The authors declare no competing financial interests.