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REVIEW

Emerging relationships among microbes, soil carbon storage and climate change

Soil carbon and microbes in the warming tropics

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Abstract

1. Climate warming could destabilise the Earth's largest terrestrial store of reactive carbon (C), by accelerating the decomposition of soil organic matter. A third of that C store resides in the tropics. The potential for tropical soils to sequester C, or to act as an additional source of CO_2, will depend on the balance of C inputs and outputs, mediated by the response of soil microbial communities and their activity to perturbation.
2. We review the impact of warming on microbial communities and C storage in humid tropical forest soils over multiple time-scales.
3. Recent in situ experiments indicate high sensitivity of tropical forest soil C mineralisation to warming in the short term. However, whether this will translate into long-term soil C decline remains unclear. At decadal time-scales, high sensitivity of soil C mineralisation to warming is consistent with the correlation between the inter-annual variation in the tropical land surface temperature and atmospheric CO_2 growth rate, and with simulations using the Carnegie-Ames-Stanford Approach biosphere model. This observed sensitivity may further contribute to climatic change over millennial time-scales, suggested by radiocarbon dating of organic matter in river basins showing a twofold acceleration in tropical soil C release during the late-glacial warming period. However, counter to this evidence, long-term stability of tropical soil C is suggested by observed steady-state soil C turnover across temperature gradients with elevation, and by the presence of C in tropical soils that pre-dates the Holocene Thermal Maximum and late-glacial warming periods.
4. To help reconcile these recent experimental findings and long-term observations, we propose mechanisms to explain tropical soil C and microbial responses to warming across multiple time-scales. Combined in situ experimental and monitoring approaches—large-scale and cross-site—are urgently needed to resolve the interplay of these mechanisms across spatial and temporal scales, to shape a better understanding of the relationship between soil microbes and C storage in tropical soils.

KEYWORDS
CASA model, climate warming, Ratkowsky model, soil microbial community, soil organic matter, tropical forest

1 | INTRODUCTION

There is a widespread concern that the global terrestrial C store is vulnerable to warming, as increased temperatures can stimulate microbial degradation of soil organic matter and release of carbon dioxide (CO_2) to the atmosphere, thereby contributing to further climate warming (IPCC, 2021). The uncertainty attached to this feedback is greatest for the biome that dominates the global C exchange between the atmosphere and terrestrial biosphere, tropical forests (Cavaleri et al., 2015). Tropical forests exchange more C with the atmosphere than any other ecosystem and contain two thirds of global plant biomass C (Pan et al., 2011) and over a quarter of global soil C (Jackson et al., 2017), while the biota that store and cycle this C account for the majority of Earth's biodiversity on land (ter Steege et al., 2013). Tropical soil C stores and our future climate will be strongly influenced by the manner in which the microbes in tropical forest soils will respond to warming, but empirical information is scarce and severely restricts our ability to forecast future climate change (Cavaleri et al., 2015). Data are beginning to emerge from field experiments, but this evidence must be placed in the context of our emerging wider understanding of how microbes govern the terrestrial C cycle.

Over the last decade there have been major advances in our understanding of how soil C storage is underpinned by the action of microbial communities. These advances have arisen thanks to evolving methods to quantify microbial organic C use (Cotrufo et al., 2013; Hagerty et al., 2018; Wang et al., 2021), microbial mineralisation of organic C (Blagodatskaya & Kuzyakov, 2008) and the stabilisation of microbial residues in soils (Liang et al., 2019). Microbes are now understood to drive both soil C accumulation through their anabolism and via the stabilisation of microbial residues (Cotrufo et al., 2013), and C loss through their catabolism and mineralisation of stable organic matter, including via 'priming effects' (i.e. microbial co-metabolism of growth-limiting nutrients and C from organic matter;Blagodatskaya & Kuzyakov, 2008). This revised perspective on the formation and destabilisation of soil C, therefore, places soil microbiota centrally (Figure 1). These microbe-mediated processes appear ultimately to constrain soil and ecosystem C storage. In field experiments, priming effects have been shown to offset C gains from increased NPP under elevated CO_2 (Terrer et al., 2021), and changes in the microbial community and in its C use have been shown to affect long-term C loss under warming (DeAngelis et al., 2015; Melillo et al., 2017). In parallel, models representing microbial processes have projected global soil C emissions this century to be as high as 300 Pg C (Wieder et al., 2013), although the uncertainties are still equally large (Sulman et al., 2018). Better understanding of how a warming climate will affect tropical forest soils requires this microbe-centric perspective of soil C dynamics.

In our analysis, we first consider tropical forest soils, climate, productivity and diversity (Section 2). We focus on humid tropical forest (rainfall >2,000 mm/year), although we briefly consider tropical mountains and wetlands. We review results from experiments (Section 3) and examine their relevance over longer time-scales. Over recent decades, can C release from tropical soils in response to inter-annual variation in land surface temperature explain atmospheric CO_2 growth rates, and further, is there historical evidence for (in)stability of tropical soil C (Section 4)? How are these longer term responses influenced by interactions with plants and changes in other climatic variables? (Section 5). Finally, we propose mechanisms to explain the response of tropical soil microbes and soil C to warming across multiple time-scales and outline new directions for future research (Section 6).

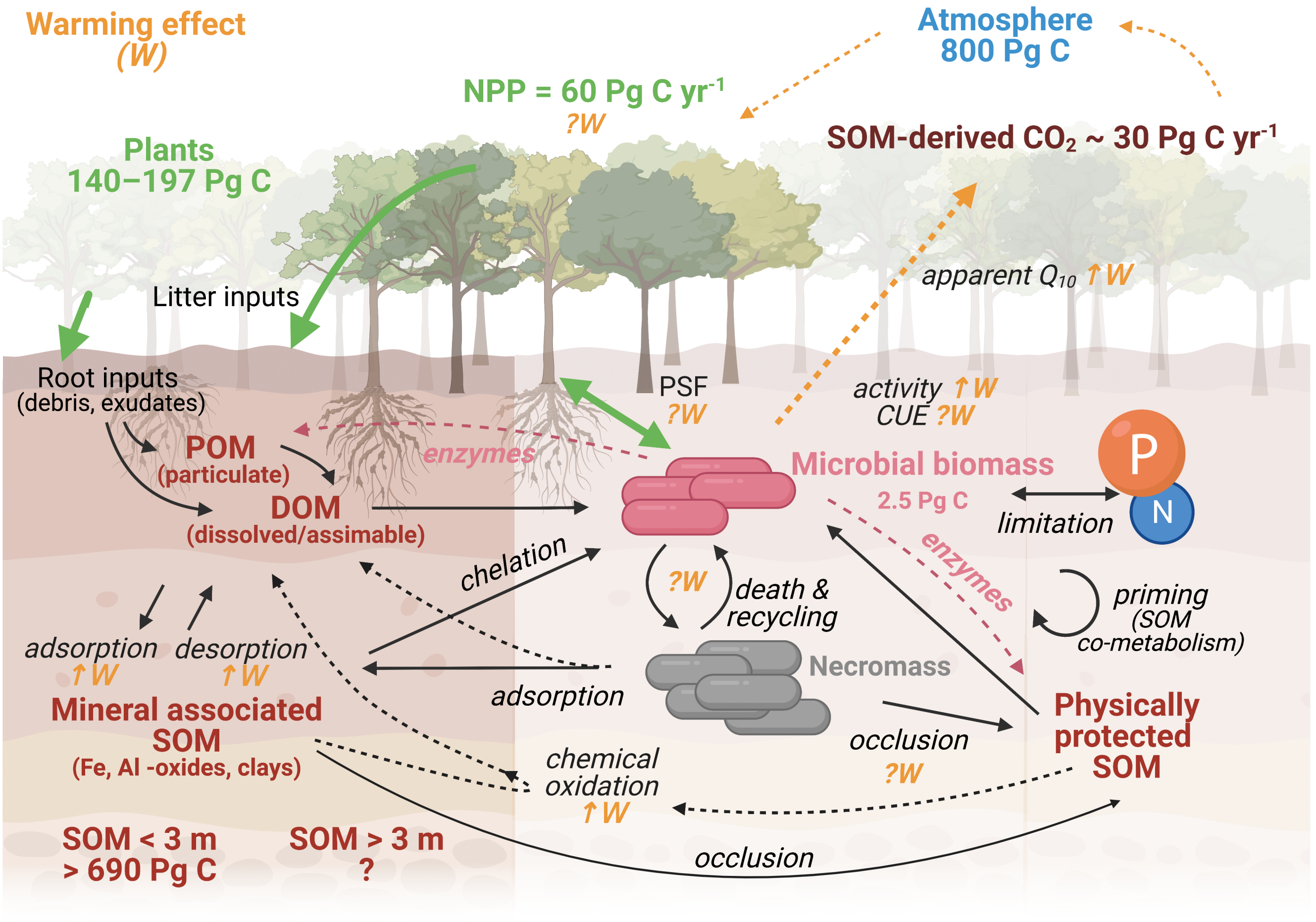
2 | TROPICAL FOREST CHARACTERISTICS AND INFLUENCE ON SOIL MICROBES AND C STORAGE UNDER WARMING

2.1 | Soils

A third of global soil C is held in the tropics and is distributed among a very wide range of parent materials, ages, geomorphology and landforms (Figure 2); (Jackson et al., 2017; Quesada et al., 2010). Tropical soils are, however, often generalised as being strongly weathered, a result of a warm humid climate and because they were largely unaffected by recent glaciation (Sanchez & Logan, 1992). Strongly weathered soils are indeed abundant in the tropics with Oxisols and Ultisols representing about 46% of land cover (Figure 2). Oxisols and Ultisols are clay-rich, moderate to strongly acidic soils, characteristically low in exchangeable rock-derived nutrients and of low cation exchange capacity (Sanchez & Logan, 1992). This generalisation is consistent with broad global patterns of terrestrial nutrient limitation, with increased limitation by P at lower latitudes and elevations (Camenzind et al., 2018; Du et al., 2020), but should be applied with caution: the tropics also contain highly fertile soils (e.g. Alfisols; Figure 2), montane systems (Wagai & Kitayama, 2012) and wetlands (Dargie et al. 2017). Further large stores of C are held in subsoils (>3 m depth) estimated to be in excess of 500 Pg C globally (Jackson et al., 2017), with considerable C stores in tropical subsoils (Trumbore et al., 1995).

2.2 | A changing climate

The tropical land surface is predicted to warm by 3–5°C this century (IPCC, 2021). Although the predicted warming for the tropics



Short-term (<1 yrs.)

- Intrinsic response of ***microbial activity, respiration and growth*** (Ratkowsky model)
- Intrinsic response of ***enzymes*** (Arrhenius kinetics)
- ***Priming effects***, driven by release of low molecular weight C
- Destabilization of weakly-sorbed C

W↑

Medium-term (1-10 yrs.)

- ***Microbial community change***
- ***Adaptation of growth and C-use***

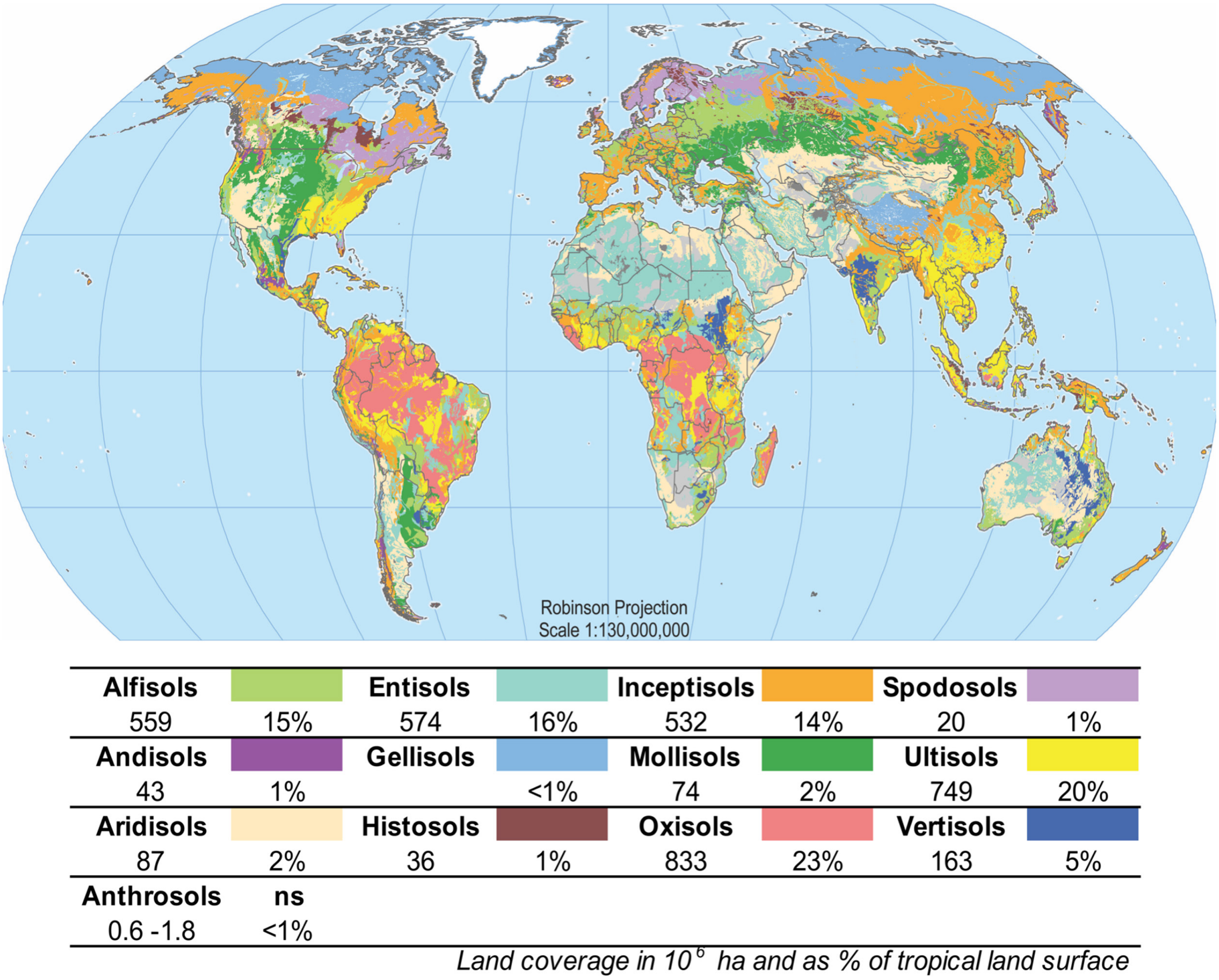
W?

Long-term (> 10 yrs.)

- Inputs to soil, via ***plant community and NPP*** change
- Plant-soil-feedbacks (PSF) via changes in ***plant-microbial associations*** (both pathogenic or mutualistic)
- ***Physico-chemical protection***

W?

FIGURE 1 The tropical forest soil C cycle and its response to a warming climate. The temperature response of soil-derived CO_2 emission (*apparent* Q_{10}) is determined by the combined *intrinsic* responses of specific soil processes. Warming interactions are denoted by '*W*', including the hypothesised direction of response, or a question mark where unknown. Tropical forest C pool sizes are shown for plants (Pan et al., 2011), microbial biomass (Serna-Chavez et al., 2013) and SOM (>3 m depth; Jackson et al., 2017). Further substantial C stores have been found at depths >3 m (e.g. to 8 m; Trumbore et al., 1995) although no comprehensive estimate exists. Tropical forest C fluxes are shown for plants (net primary productivity (NPP; Pan et al., 2011), of which approximately 50% is released as plant-derived respiration (not shown in figure) and the remainder as soil-derived respiration via soil microbial activity. Abbreviations are: DOM, dissolved organic matter; POM, particulate organic matter; PSF, plant-soil feedback (positive interactions between plants and microbial symbionts; negative interactions between plants and pathogens); SOM, soil organic matter. Warming interactions are highlighted by dashed orange lines, including accelerated CO_2 emission from abiotic sources (desorption, chemical oxidation) and biotic sources (microbial activity including enzyme activity and priming), and PSF. For illustrative purposes, priming is shown to affect protected SOM although other SOM pools are also likely affected (Bernard et al., 2022; Blagodatskaya & Kuzyakov, 2008). Created with BioRender.com



Alfisols	🟩	559	15%
Entisols	🟦	574	16%
Inceptisols	🟧	532	14%
Spodosols	🟪	20	1%
Andisols	🟪	43	1%
Gellisols	🟦		<1%
Mollisols	🟩	74	2%
Ultisols	🟨	749	20%
Aridisols	🟨	87	2%
Histosols	🟫	36	1%
Oxisols	🟥	833	23%
Vertisols	🟦	163	5%
Anthrosols	**ns**	0.6 -1.8	<1%

Land coverage in 10^6 ha and as % of tropical land surface

FIGURE 2 Global soils and the land coverage of soil orders found in the tropics. Although often assumed to represent tropical soils, strongly weathered Oxisols and Ultisols represent only 43% of soils in the tropics, which contain all 12 USDA soil orders. Data for the 11 most abundant orders are from Sanchez and Logan (1992). Gelisols are typically associated with high-latitude permafrost regions but are present, albeit scarce, in tropical high-elevation ecosystems (Dudeja, 2011). Anthrosols ('ns': not shown on map) are anthropogenically modified soils, and their coverage is estimated here based on the coverage of historical human settlements in Amazonia and the presence of Amazonian Dark Earth soils (6,000–18,000 km^2; Sombroek et al., 2003). Soil map© (FAO, 2005)

is lower than for higher latitudes, the impact could be severe because for the most part the tropical climate has relatively little seasonal temperature variation. The tropical climate is also predicted to traverse significantly beyond its historical climatic limits before other biomes (Mora et al., 2013), with increased temperature variability and more frequent extreme temperature events (Vogel et al., 2017).

The future tropical climate is likely to be be further transformed by increased drought frequency and land-use change at multiple scales (Brando et al., 2019). Forest conversion reduces the local land surface albedo and decreases evapotranspiration (Cao et al., 2010; Spracklen et al., 2018), which can translate into significant climate impacts at the regional scale (Humphrey et al., 2021), including land surface warming (Cao et al., 2010; Spracklen et al., 2018) and fire risk (Brando et al., 2019). The estimated fraction of forest loss in the Amazon (~17% deforested in addition to ~17% degraded, Gatti et al., 2021) is close to a projected, though uncertain, loss that could lead to a tipping point (20%–40% of forest loss), beyond which the regional climate could shift permanently to warmer and drier conditions that might no longer support tropical rainforest (Nobre et al., 2016; Spracklen et al., 2018). The tropical climate is projected to be further influenced by more frequent and more extreme El Niño Southern Oscillation (ENSO) events (Wang et al., 2019) and other periodic changes of tropical sea surface temperatures. In short, tropical biota, including soil microbes, will be exposed to unprecedented climatic regimes over the coming decades, with poorly understood consequences for their survival, for global biogeochemical cycles and for net emissions of CO_2.

2.3 | Productivity and biogeochemistry of tropical forests

The way microbial activity feeds back on climate warming in tropical soils may differ from higher latitude soils because in the tropics, C turnover is faster (e.g. 17 times faster, 15 years compared to 255 years at high latitudes, Carvalhais et al., 2014) and tropical soils are generally more strongly weathered. The peak in ecosystem C turnover for the tropics (Carvalhais et al., 2014) also corresponds with observations that both net primary production (NPP; Pan et al., 2011) and soil respiration (Hashimoto et al., 2015) are largest at tropical latitudes. This is important considering that soil microbial community growth is primarily limited by C availability and is therefore dependent on NPP and C inputs from aboveground (Hobbie & Hobbie, 2013). Tropical forest soil microbial communities, therefore, exist in an environment of high C inputs and have high metabolic rates, with the outcome that small fractional changes under warming could influence atmospheric CO_2 concentrations relatively rapidly.

The generally strongly weathered nature of tropical soils means that, compared to soils from higher latitudes, microbial C metabolism may be more strongly limited by nutrients that are either wholly or primarily derived from rock weathering, including P. Indeed, several studies reflect this difference, with evidence for P limitation of microbial C metabolism in lowland tropical forests (Camenzind et al., 2018). Despite this, the mechanism by which microbes in tropical soils decompose soil organic matter when stimulated by an energy input (e.g. in the form of easily degradable C; 'priming') appears to occur due to microbial demand for N (Nottingham et al., 2015), as found outside the tropics (Blagodatskaya & Kuzyakov, 2008). A likely explanation for this is that microbes can access inorganic P sources independently to C (e.g. chelation or biochemical mineralisation), whereas N acquisition from soil organic matter is tightly coupled to C release through biological mineralisation. Consequently, under warming, different nutrients may regulate microbial metabolism of different C pools, P (or other rock-derived nutrients) during the decomposition of plant debris or N during the decomposition of older soil organic matter.

The temperature sensitivity of C mineralisation in weathered tropical soils will be further influenced by the high abundance of secondary minerals, especially Fe and Al oxides (Quesada et al., 2010), which have high affinity for (Gu et al., 1995)—and high sorption capacity with (Tipping, 1981)—organic C. By reacting with organic matter, these minerals can form organo-metallic complexes that harbour significant pools of low molecular weight C that are protected from microbial decomposition (Figure 1; Cotrufo et al., 2013). As much as 50% of this mineral-associated C pool is derived from microbial residues (Liang et al., 2019). Although little direct information on the contribution of microbial necromass to the mineral-associated C pool is available for tropical soils, it could be considerable given that, globally, tropical soils contain the highest microbial C biomass (Serna-Chavez et al., 2013) and support the highest rates of C turnover (Carvalhais et al., 2014). The potentially large contribution of mineral-associated organic matter to C storage in tropical soils was demonstrated in an analysis which found that in acidic and moist soils, Fe and Al oxyhydroxides were the best predictors of SOM stabilisation (Rasmussen et al., 2018). The result has been corroborated by studies showing that weathered tropical soils had the greatest capacity to sorb added dissolved organic C (Abramoff et al., 2021); and that the accumulation of mineral-associated C is greater in soils with higher concentrations of Fe oxyhydroxides (Kirsten et al., 2021). However, mineral-associated C, adsorbed to metal complexes, may be sensitive to mineralisation under warming. Because adsorption is an exothermic process while desorption is endothermic, adsorption is expected to decrease with warming, and desorption to increase (ten Hulscher & Cornelissen, 1996). Consistent with this expectation, laboratory warming of Hawaiian soils stimulated the release of mineral-sorbed C (Neupane et al., 2021). The release of mineral-sorbed C under warming may contribute significantly to CO_2 emission to the atmosphere, given that the rapid turnover of low molecular weight C in soils is known to contribute a major portion of the total soil CO_2 efflux (van Hees et al., 2005).

2.4 | Tropical forest diversity

Warming impacts in tropical forests may also differ from other ecosystems due to the high biodiversity found both above and belowground. Global plant diversity peaks in the humid tropics (ter Steege et al., 2013). One possible explanation for this is the energy-diversity theory, where warmer temperatures result in increased energy inputs, evolutionary rates and species diversity (Tilman et al., 2012). Soil microbial diversity has similarly been observed to be higher in warmer tropical climates, also increasing at lower latitudes for fungi (Tedersoo et al., 2014) and bacteria (Zhou et al., 2016) and increasing for both at lower elevations in tropical forest (Nottingham et al., 2018). Temperature, however, is only one of several environmental factors that influence soil microbial diversity, including a dominant influence of pH on soil bacteria for which diversity is strongly constrained in acidic soils (Fierer & Jackson, 2006). The biodiversity of soil arthropods, particularly ants and termites, is also high in tropical forest, which play an important role in the soil C cycle both directly and indirectly by affecting microbial communities through trophic effects (Bardgett & van der Putten, 2014). These diversity patterns occur at landscape scales but are also reflected in responses to experimental warming, with increased microbial diversity widely observed in soil warming experiments in cooler climates (DeAngelis et al., 2015; Zhou et al., 2020). Together, these findings point towards an important question: will warming in the tropics lead to increased soil biotic diversity, or is there a thermal threshold above which certain species will cease to persist (with associated consequences for plants and C storage)?

Warming may also affect tropical diversity and C cycling indirectly through changes in the formation of symbiotic relationships. It is unclear whether the diversity of soil biota is consistently highest in the tropics, but the diversity of interactions between soil microbes and plants is considered highest in tropical forests (Bagchi et al., 2014; Bardgett & van der Putten, 2014; Mangan et al., 2010). Tropical forest plant diversity and community composition are known to be partly maintained via interactions with pathogenic microbes, including endophytic or root- and seed-associated fungi (Bagchi et al., 2014; Mangan et al., 2010). These fungal pathogens are thought to decrease the survival of conspecific, neighbouring plants, explaining the observation of decreased survival of conspecific seedlings in field experiments (Comita et al., 2010). Emerging evidence that warming may change the nature of microbial-plant interactions has been shown for seedlings, where warmer temperatures increased the survival of conspecific seedlings (Bachelot et al., 2020). One potential explanation for this specific result is that warming—and the further interaction with drying—reduced the growth of fungal pathogens that cause negative density-dependent interactions (Bagchi et al., 2014), with the implication that tropical forest diversity might conceivably decline in a warmer world.

Plant species diversity is often reinforced by mutualistic relationships, for example, changes in the activity of mycorrhizal fungi. Mycorrhizal associations may explain the observation of greater plant species diversity in forest dominated by arbuscular mycorrhizal fungi symbionts (Alexander & Lee, 2005), compared to forests dominated by ectomycorrhizal fungi (Corrales et al., 2018). Experimental evidence suggests mycorrhizal fungi are affected by warming, with clear implications for plant performance: a meta-analysis of mycorrhizal fungal responses to experimental warming reported a dominant response (60% of cases) of increased biomass and decreased activity, although tropical forests were not represented (Mohan et al., 2014). In tropical forests, changes in the abundance and activity of arbuscular mycorrhizal fungi will have large consequences for NPP, as they are important in facilitating plant P acquisition in weathered soils (Alexander & Lee, 2005). In contrast, changes in ectomycorrhizal fungal communities under warming may have further consequences for soil C storage because their abundance is positively correlated with soil C storage globally (Averill et al., 2014), a pattern thought to arise because of constraints imposed by the presence of ectomycorrhizal fungal upon the activity of other saprophytic fungi and through the input of their residues. Thus, the influence of warmer temperatures on the performance or even survival of these pathogenic and mutualistic microbial communities may impact plant viability and productivity, and have further implications for soil C storage.

In summary, the response to future warming by microbial communities and, consequently, biogeochemical process rates in tropical soils will be characterised by key conditions that differ from their higher latitude counterparts: warmer temperatures, higher rates of C turnover, higher species diversity (of plants and of some soil biota), greater dependence on symbiotic plant–microbe associations and soils with generally lower P availability and large pools of sorbed, mineral-associated C. The way perturbations of tropical soil microbes will affect soil C stores will depend on how increasing temperatures interact with these conditions (Figure 1).

3 | EMPIRICAL EVIDENCE FOR WARMING IMPACTS ON MICROBES AND SOIL C OVER DIFFERENT TIME-SCALES

3.1 | Intrinsic temperature responses: Incubation experiments, growth and enzyme kinetics

Soil heterotrophic CO_2 emission will increase with warming in the short term when substrate supply is not limiting microbial metabolism, as widely demonstrated in experiments performed outside the tropics (Crowther et al., 2016). The pattern has been supported for tropical soils in laboratory incubation experiments. For example, Holland et al. (2000) demonstrated exponential rises in CO_2 efflux during 14-day incubations of tropical soils, with similar temperature sensitivities observed when substrate was non-limiting, irrespective of soil type.

The short-term increase in the heterotrophic CO_2 flux can be explained by the intrinsic temperature response of enzyme catalytic activity and of microbial metabolism. In this context, 'intrinsic´ refers to the direct effect of temperature on a specific process as measured under controlled laboratory conditions; in contrast to ´apparent´, which is the observed effect as measured in field experiments and influenced by other factors co-varying with temperature (Davidson and Janssens, 2006; Figure 1). Maximum potential enzyme activity (V_{max}) increases exponentially with temperature following Arrhenius theory (following exp(−1/temperature)), modified by substrate availability via Michaelis–Menten kinetics, with an optimum temperature for activity generally well above ambient temperature (Wallenstein et al., 2011). In tropical soils, for example, increases in V_{max} have been measured at temperatures up to 40°C (Nottingham et al., 2016), well beyond the predicted temperatures under climate warming—although this does not necessarily reflect increased metabolic activity of microbes for which the thermal optima of growth is generally lower (see below; Bååth, 2018). The overall effect of increased V_{max} on substrate depolymerisation rates under warming may be reduced by decreases in substrate affinity (Razavi et al., 2015) and by enzyme deactivation (Alvarez et al., 2018), although the responses of these enzymatic traits to warming remain poorly characterised in tropical soils.

The effect of temperature on microbial growth has been characterised by a square root function (Ratkowsky et al., 1983), where the square root of growth increases linearly with temperature to an optimum temperature (T_{opt}) and then declines. Differences in the growth–temperature relationship below T_{opt} is determined by T_{min}, representing a theoretical minimum growth temperature, measured by the *y*-intercept of the square root-growth increase with temperature (Bååth, 2018). Accordingly, T_{min} has been used to represent the sensitivity of microbial community growth to temperature (Bååth, 2018). A tight relationship between mean annual temperature (MAT) and T_{min} of growth has been found in soils globally, across an arctic gradient (Rinnan et al., 2009) and extending to hot deserts (van Gestel et al., 2013), indicating that community growth is relatively faster at (adapted to) native temperature ranges. The relationship is also supported for microbial respiration, which followed a similar pattern in soils collected across global temperature gradients (Li et al., 2021). Given the breadth of empirical support for this relationship (Bååth, 2018), it can be used to predict how warming will affect the intrinsic sensitivity of growth and respiration. Here, we used a T_{min} versus MAT relationship derived from the instantaneous response of microbial growth for tropical forest soils from an elevation gradient in the Peruvian Andes, where MAT varies by 20°C (Nottingham, Bååth, et al., 2019; Figure 3a, see black line; see Supporting Information for equations and on how to derive Q_{10} from T_{min}), to predict soil C emission increase for lowland tropical forests. Following this relationship, in the lowland tropics where MAT is 26°C, the intrinsic temperature sensitivity of microbial activity increases with 4°C warming according to $Q_{10\ (26\text{–}30°C)} = 2$. Importantly, each of the underlying mechanisms—enzyme kinetics and microbial growth sensitivity—predict that the intrinsic temperature sensitivity of heterotrophic respiration should be lower in the tropics with high MAT compared to higher latitudes (i.e. Q_{10} increases for lower MAT; see curve (1) in Figure 3b). However, whether these patterns have large consequences for the future temperature sensitivity of soil C mineralisation under climate warming and field conditions in tropical forests is not directly addressed in short-term incubation studies.

3.2 | Field experiments: In situ warming and translocation

The response of tropical soil C to longer term warming has great uncertainty and will depend on how the response is further modified by adaptive changes in the microbial community, soil physico-chemical properties and the community composition and productivity of plants. The prediction that the impact of warming on soil C in the tropics will be lower than that of soils from higher latitudes is based not only on kinetic theory (Davidson & Janssens, 2006), but also on the generalisation that strongly weathered tropical soils have relatively lower C concentration compared to soils from higher latitudes (Jackson et al., 2017; i.e. not accounting for the large tropical soil C stores found at depth, nor accounting for high C turnover rates; Sanchez & Logan, 1992; Trumbore et al., 1995). Until recently, there were no warming experiments in tropical forests to test these predictions in the field, (Cavaleri et al., 2015), but a few are now in operation. Two experiments focus heating on the soil profile: in lowland tropical forest in Panama on strongly weathered Inceptisols, the SWELTR experiment (Soil Warming Experiment in Lowland TRopical forest) uses below-ground resistance cables to heat the full

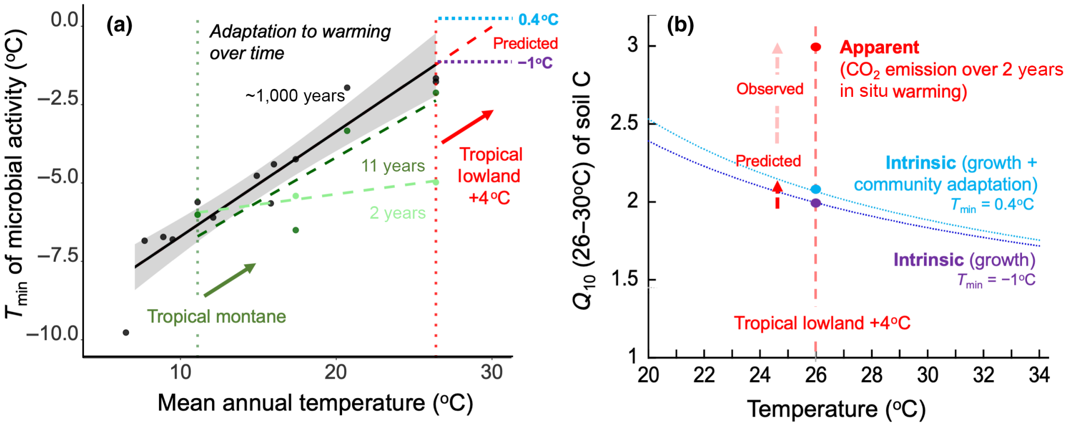


FIGURE 3 Adaptation of microbial community activity to warming in tropical montane to lowland forest soils (a), and the predicted and observed response of lowland tropical forest CO_2 emission to 4°C warming (b). Panel (a) shows the relationship between MAT and the temperature adaptation of microbial community activity (based on the T_{min} of bacterial growth) over three different time-scales (2, 11 and ~1,000 years). The long-term adaptation (~1,000 years; see black line) is based on the intrinsic temperature response of bacterial growth across a 20°C MAT gradient along an elevation transect in tropical forest in Peru; fungal community growth (data not shown here) follows a similar pattern (Nottingham, Bååth, et al., 2019). Based on these data, warming by 2°C was predicted to increase microbial activity by 28% for the cooler montane sites but by 15% for the warmer lowland sites (Nottingham, Bååth, et al., 2019). Adaptation of montane tropical forest activity to 2 and 11 years of warming (by 6 to 15°C) was determined following translocation of soil to lower elevations (see dashed dark green and light green lines). On average, 77% of growth adaptation to temperature change occurred after 2 years and was complete after 11 years (i.e. not significantly different to the long-term controls; see black line; Nottingham et al., 2021). Extrapolation of this relationship predicts that adaptation of community growth to warming by 4°C in lowland forest soils will increase the T_{min} of bacterial growth from to −1 to +0.4°C (see 'predicted', red dashed line). (b) A microbial growth model based on results in (a) predicts that the intrinsic sensitivity of activity and soil C release follows a Q_{10} of 2, while adaptation of the microbial community will increase it following Q_{10} of 2.1. However, field measurements far exceed this expectation (see 'apparent' red point in b; Q_{10} of 3; Nottingham et al., 2020). The mechanisms behind this high apparent sensitivity are unresolved (see Figure 1)

soil profile by 4°C (Nottingham et al., 2020), an experimental design also being used to heat deep volcanic tropical soils in Hawaii (McGrath, 2019). In lowland tropical forest in Puerto Rico on clay-rich Ultisols the TRACE experiment (Tropical Responses to Altered Climate Experiment) uses infrared lamps to heat both the forest understorey and soils by 4°C (Kimball et al., 2018; Reed et al., 2020). These in situ warming experiments have also been complemented by translocation experiments across tropical mountain gradients, where soil mesocosms have undergone temperature incubations in Costa Rica (Looby & Treseder, 2018) and Peru (Nottingham, Whitaker, et al., 2019; Zimmermann et al., 2012).

Contrary to the predicted response based on the instantaneous temperature sensitivity of microbial growth (see 'Intrinsic (growth)' in Figure 3b, predicted $Q_{10\ (26\text{–}30°C)} = 2$), 2 years of soil warming in tropical forest resulted in a larger increase in the heterotrophic CO_2 efflux (Nottingham et al., 2020; see 'Apparent' in Figure 3b, observed $Q_{10\ (26\text{–}30°C)} = 3$). The increase (55%) was greater than that observed in similar experiments at higher latitudes, for example a 37% increase over 2 years of full soil profile warming for temperate forest in the United States (Hicks Pries et al., 2017). Consistent with these observations, temperature manipulation of soils by translocation across an elevation gradient in Peru found that warming resulted in increased heterotrophic respiration rates and declines in labile C after 2 years (Zimmermann et al., 2012), and substantive declines in soil C after 5 years (Nottingham, Whitaker, et al. (2019); responses that represented the combined warming of upland soils and cooling of lowland soils. Thus, at least over a duration of 2 years of tropical soil warming, concurrent evidence suggests that even for strongly weathered soils where the ambient temperature is already high (e.g. 26°C), substantial increased CO_2 emissions from soil organic matter sources can occur, mediated by the soil microbial community.

A critical question emerging from these findings is when these large CO_2 emissions will eventually decline, as the availability of easily decomposable substrate decreases. This is a common expectation based on findings from outside the tropics (Melillo et al., 2017) and has been associated with an observed decline in microbial C and C use efficiency (the proportion of C used for growth relative to other processes such as respiration; CUE; Li et al., 2019; Manzoni et al., 2012). There is, however, no evidence from tropical soil warming experiments to indicate substrate limitation of microbial metabolism, at least over a few years: under soil warming in two different lowland tropical forests, microbial biomass C remained stable (Nottingham et al., 2020) or even increased (Reed et al., 2020); and while there were no significant changes in the total elemental nutrients, there were seasonal increases in the abundance of available inorganic nutrients, especially phosphate (Reed et al., 2020).

Another critical question is whether CO_2 emissions will be affected by thermal adaptation of soil microbial communities, with potentially large effects predicted by models (Wieder et al., 2013), either through changes in physiology (including altered gene expression) or community composition, manifested by change in CUE or T_{min}. In cooler montane tropical forest in Peru, by using translocation, soil warming of 4–12°C for 5 years led to increased CUE, determined from the stoichiometry of microbial biomass and enzyme activity (Nottingham, Whitaker, et al., 2019). In another study from the same site, 2 and 11 years of warming led to, respectively, 77% and complete adaptation of community growth to the new temperature, with T_{min} increasing by 0.3°C with each 1°C warming (Nottingham et al., 2021; Figure 3a, see green dashed lines). Although several mechanisms could contribute to this thermal growth adaptation, community compositional shifts appear to be important, as observed in warmed soil from temperate zones (Donhauser et al., 2020; Rousk et al., 2012) and in two separate montane forest soil warming studies, in Peru (Nottingham, Whitaker, et al., 2019) and Costa Rica (Looby & Treseder, 2018).

Whether such changes in microbial community composition and its functioning (e.g. parameters CUE and T_{min}) occur with longer term (>2 years) warming in lowland tropical forest soils remains unclear. Based on the observed relationship between T_{min} versus temperature for soils across a tropical mountain gradient (Figure 3a), we predicted that adaptation of the soil microbial community to 4°C warming would increase the T_{min} of microbial growth and activity by 1.4°C (Figure 3a); this adaptation is expected to increase soil C emissions following a change from $Q_{10\ (26\text{–}30°C)} = 2$ to $Q_{10\ (26\text{–}30°C)} = 2.1$ (see 'Intrinsic (growth + community adaptation)' in Figure 3b; see Supporting Information for equations). However, this predicted change in intrinsic sensitivity cannot explain the observed high apparent temperature sensitivity of soil C mineralisation over 2 years of experimental warming ($Q_{10\ (26\text{–}30°C)} = 3$, Figure 3b). A research priority is to understand how changes in the microbial community, in its composition and function, might be contributing to this high sensitivity of tropical soil C mineralisation to warming.

4 | HISTORICAL EVIDENCE FOR SENSITIVITY AND STABILITY OF SOIL C TO WARMING

4.1 | Inter-annual warming events

The inter-annual variation of the atmospheric CO_2 growth rate (1 ppm CO_2 ~2.128 Pg C) reflects variation in fluxes between C pools in the atmosphere and in the land or ocean, including fossil fuel emissions. The atmospheric CO_2 record reveals a striking pattern: positive growth rate anomalies coincide with warm ENSO events, with the exception of 1- to 2-year periods following major volcanic eruptions (Figure 4). These anomalies have been explained regionally via several processes, including CO_2 outgassing from tropical oceans (Feely et al., 1999), but there is now strong evidence from atmospheric $^{13}CO_2$ records indicating that terrestrial ecosystem processes are the primary cause (Langenfelds et al., 2002). These terrestrial processes include decreased photosynthesis (Gloor et al., 2018), increased respiration from soil and vegetation and C released via fires (Wang et al., 2014). Negative precipitation anomalies and decreased photosynthesis appears to play a major role, as indicated by recent evidence of water storage changes via satellite measurements (Humphrey et al., 2021). However, further lines of evidence suggest

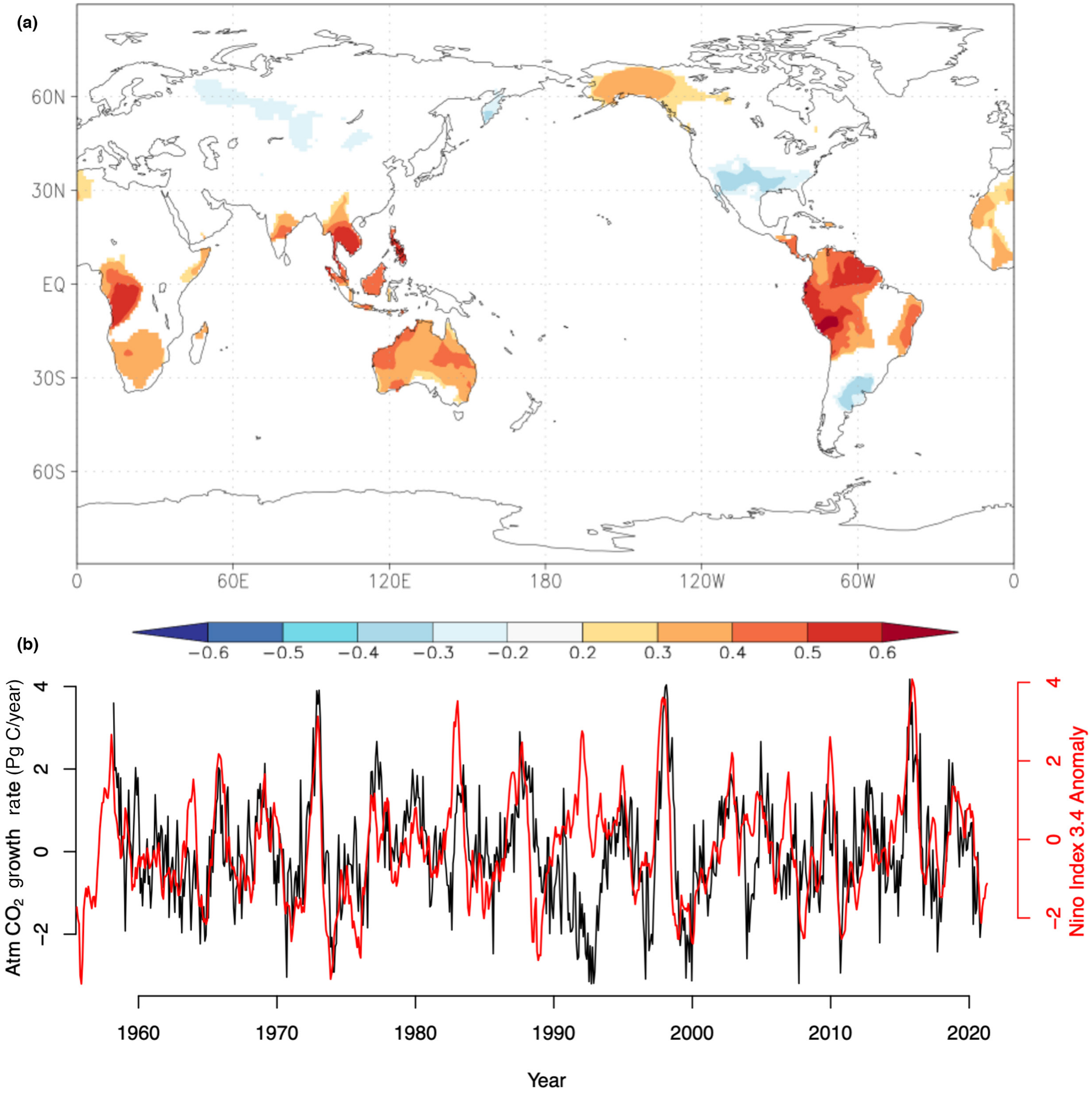


FIGURE 4 The land surface atmospheric C exchange: warm El Niño Southern Oscillation events are associated with increased inter-annual atmospheric CO_2 growth over the tropics. (a) Map of pointwise correlation coefficient of atmospheric CO_2 growth variation with land surface temperature. Temperature fields are based on observed data from meteorological stations and interpolated spatially using splines; from the Climate Research Unit East Anglia, version TS4.04. (b) The measured atmospheric CO_2 growth rate anomaly (black line) and the El Niño 3.4 index anomaly (red line; defined when the sea surface temperature anomaly between the central and eastern equatorial Pacific exceeds +0.5°C for 3-month period)

a contribution of warming and increased CO_2 emission from soils rather than decreased photosynthesis alone. For example, strong positive correlations between tropical land surface temperature anomalies and atmospheric CO_2 growth (Wang et al., 2013, 2014) and a doubling in the sensitivity of CO_2 growth with inter-annual warming over the last 50 years (Wang et al., 2014). Meanwhile, in Africa during the 2015–2016 ENSO event, remote sensing data showed a large land–atmosphere CO_2 flux (Gloor et al., 2018; Liu et al., 2017) but above-ground biomass measurements showed that forests remained a net C sink (Bennett et al., 2021). Furthermore, the release of C from warmed soils is plausible given the observation that the Eastern Amazon has been an increasingly large source of atmospheric CO_2 emissions over the last 40 years, during which time the mean annual temperature increased by 2°C (Gatti et al., 2021).

Overall, however, the contribution from soils still remains difficult to disentangle from the large interacting effects on CO_2 emission from vegetation responses, drought, deforestation and fire (Gatti et al., 2021; see below).

To explore whether a relationship between soil heterotrophic activity and temperature anomalies during ENSO cycles is plausible, and to evaluate the sensitivity of the tropical land–atmosphere CO_2 exchange to an increased temperature sensitivity of tropical soil C, we performed simulations with the CASA (Carnegie-Ames-Stanford Approach) land vegetation model. First, using the standard model formulation, we simulated land–atmosphere heterotrophic CO_2 efflux from 1981 to 2016 and considered whether there is a correlation between temperature and CO_2 growth anomalies. The standard formulation simulations suggest that heterotrophic respiration is correlated with positive flux anomalies on the order of 1 Pg C/year with 0.5°C of surface warming (averaged over all tropical lands, integrating the 1998 ENSO; Figure 5). Second, we tested the temperature sensitivity of soil C pools in the model, by defining the Q_{10} value for heterotrophic CO_2 efflux in the tropics according to the observed response to in situ warming (Nottingham et al., 2020) for pools: (1) *microbial* and *structural* C (i.e. relatively labile); and (2) *microbial*, *structural* and *slow* C (i.e. relatively stable, although we did not include the slowest pool defined as *armoured*) and with no change to precipitation anomalies or parameters relating to NPP. By increasing the sensitivity of heterotrophic respiration, from the standard CASA formulation ($Q_{10\ (26–30°C)} = 1.5$) to the experimentally defined response ($Q_{10\ (26–30°C)} = 3$), global flux anomalies during warm ENSO events increased by (1) 0.1 and (2) 0.2 Pg C/year, for the two respective C pools (e.g. integrate over 1998 ENSO event; Figure 5). The cumulative increase in C emissions from 1981 to 2016 was (1) 0.5 Pg C and (2) 7 Pg C, respectively, and was constrained by the respective C pool sizes (Figure 5). While recognising that the land CO_2 emission anomalies observed during ENSO events (Figure 4) result from combined interactions between warming, drought and fire on plants and soils, these simulations confirm that warmed soils alone can contribute significantly to CO_2 emission and soil C loss in the tropics (e.g. 0.2 to 0.4 Pg C/year per 1°C warming; Figure 5).

4.2 | Historical evidence for tropical soil C persistence

Tropical soil C exists that pre-dates historical warming events and its persistence can be partly explained by the environmental conditions under which it occurs. For example, tropical soil C can be protected by permanent anoxic conditions in water-saturated soils. Using radiocarbon dating, C held in tropical peatlands has been found to be as much as 47 kyr old (Ruwaimana et al., 2020). These C stores therefore remained intact throughout both the Holocene thermal maximum, a period of warming between 5,000 and 9,000 years B.P.

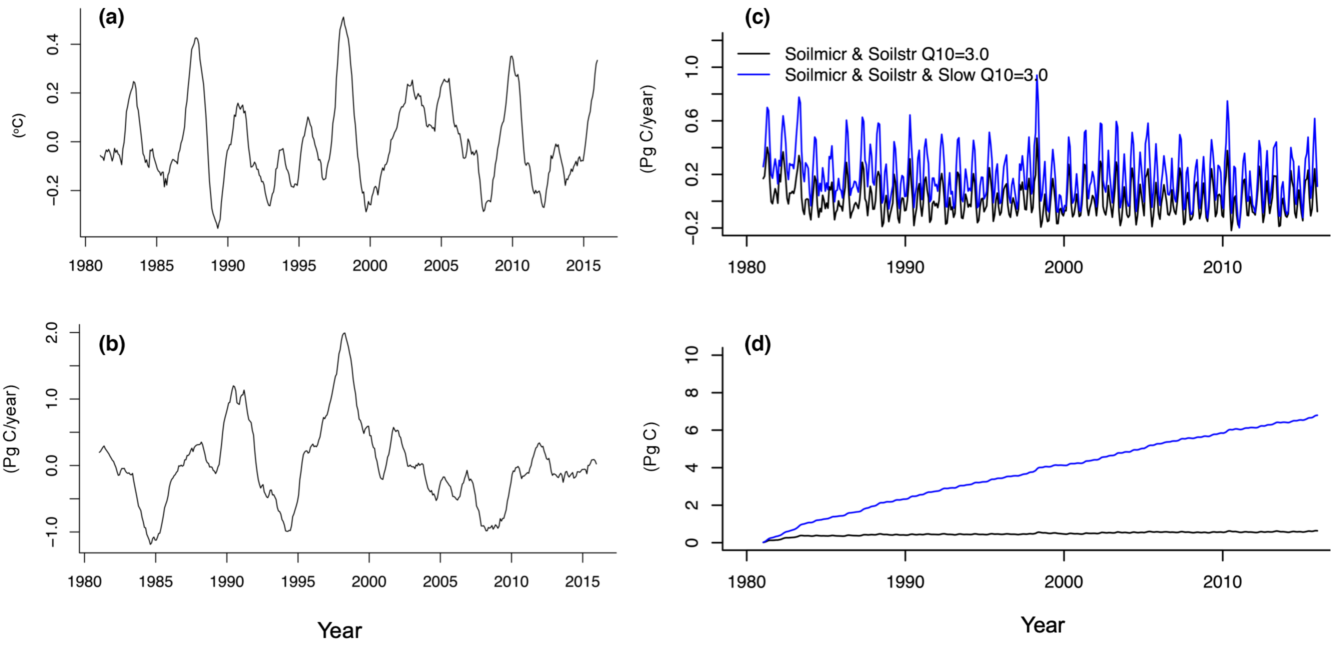


FIGURE 5 The modelled sensitivity of tropical land–atmosphere heterotrophic CO_2 exchange when accounting for the response of soil CO_2 emission to experimental warming. The model sensitivity simulations were performed using the Carnegie-Ames-Stanford Approach (CASA) land vegetation model. Panel (a) shows the tropical land (20S to 20N) temperature anomalies. Panel (b) shows the model predicted global land to atmosphere CO_2 flux anomalies for standard CASA formulation of heterotrophic respiration. Panel (c) shows the predicted global land–atmosphere heterotrophic CO_2 efflux difference where soil C pools are determined by the standard CASA formulation ($Q_{10\ (26–30°C)} = 1.5$) compared to the experimentally defined response ($Q_{10\ (26–30°C)} = 3$). Two predictions are shown, where the modified Q_{10} response applied to (1) relatively labile soil C pools (soil microbial and soil structural C pools) and (2) relatively stable soil C pools (soil microbial, soil structural and slow C pools); pools as defined by the model structure. Panel (d) shows the cumulative heterotrophic CO_2 efflux for the same model predictions over the same period. All time series are de-seasonalised and detrended

when MAT was >1°C warmer in the tropics than at present (Marcott et al., 2013), and the glacial–interglacial warming period (15 kyr BP, warming by 5–6°C, Zimov et al., 2006). The interaction of warming and drying will be critical in determining the stability of these large soil C stocks currently held under anoxic conditions.

Another example of tropical soil C persistence throughout historical warming events is provided by the presence of Amazonian dark earth (ADE) soils, locally known as 'terra preta' (Sombroek et al., 2003). These soils are Anthrosols most likely formed through centuries of human management including nutrient deposition and burning (Glaser & Birk, 2012) and are, consequently, extremely fertile and rich in organic matter. The C concentration in ADE soil is five times higher than in surrounding Oxisols, with the largest fraction occurring as aromatic compounds in particulate form, with a further large fraction stabilised on mineral surfaces of Fe and Al oxides (Glaser et al., 2000). Radiocarbon dating of charcoal in ADE soils suggests they were formed up to 7,000 years ago (Neves et al., 2004), although recent evidence suggests that cultivation and landscape modification in the Amazon began as long as 11,000 years ago (Lombardo et al., 2020). The presence of ADE soils therefore suggests millennial-scale stability of SOM to periodic warming over the Holocene (Marcott et al., 2013), and that the mechanisms for this stability occur via a combination of their aromatic structure and physical occlusion. The presence of ADE soils has wider relevance to natural tropical soils, both directly for soils modified by the influence of fire and indirectly by demonstrating how C in organo-mineral complexes can be stabilised over long time-scales.

Counter to these data suggesting long-term stability in soil C, there is also evidence for high sensitivity of tropical soil C mineralisation to historical warming, and that tropical soil C release may have contributed to the earth's past climate fluctuations. During the glacial–interglacial transition (15 kyr BP, when global temperatures increased by about 5–6°C), ice core data suggest a 100 ppm rise in atmospheric CO_2 (Zimov et al., 2006). Many hypotheses have been proposed to explain this large atmospheric CO_2 rise, including a dominant effect of changes in deep ocean circulation and oceanic outgassing (Shakun et al., 2012) and breakdown of large organic C stores held in permafrost (Zimov et al., 2006). However, new evidence from ^{14}C dating of lipid biomarkers from tropical watersheds show a twofold increase in the turnover of tropical soil organic C during this period (Hein et al., 2020), pointing towards increased mineralisation of tropical soil C that may have significantly contributed to the measured atmospheric CO_2 rise.

5 | INTERACTIONS—PLANTS AND CLIMATE

5.1 | Warming effects on plants

A major factor in governing the long-term effect of warming on tropical soil C is its effect on the balance of decomposition and plant biomass production, that reaches an approximate steady state for soil C in a stable climate (Jenny, 1941). This equilibrium has been demonstrated for one tropical forest location, across an elevation gradient in Hawaii (Giardina et al., 2014). However, whether these observations are relevant to the rapid warming predicted this century depends partly on whether (and the rate at which) plants increase in productivity, and the fate of that plant-derived C, whether stabilised or released as CO_2, following its allocation below-ground. Outside the tropics, experimental warming has induced increased plant production and below-ground C inputs for temperate (Melillo et al., 2011) and cold artic ecosystems (Sistla et al., 2013). In contrast, results for tropical trees suggest an overall decline in plant C uptake under warming, based on leaf-level responses of saplings grown in growth chambers (Slot & Winter, 2017) and branch-level manipulations in the Amazon (Doughty, 2011) and Puerto Rico (Carter et al., 2021), with further indirect evidence from the observation of a negative correlation between NPP and temperature over the two decades for tropical forest in Panama and Malaysia (Feeley et al., 2007) and the correlation between tropical land surface temperatures and atmospheric CO_2 growth rates (see above). The long-term response of NPP will also depend on the warming response of plant–microbe associations including mycorrhizal fungi and pathogens (see plant-soil feedbacks; Figure 1). For now, under warming alone, current evidence suggests tropical plants may not be able to accelerate below-ground C allocation sufficiently to offset C loss from soils (Carter et al., 2021; Doughty, 2011; Slot & Winter, 2017).

5.2 | Climate interactions

Warming alone is unlikely to be the ultimate constraint on soil C loss, rather interactions are expected of concomitant warming, drying, vegetation/land-use change, increased atmospheric CO_2, N deposition and fire (Brando et al., 2019; Lu et al., 2021). For example, increased atmospheric CO_2 may moderate the negative effect of warming on tropical forest NPP (Smith et al., 2020), although evidence from field experiments suggests that an NPP increase may not result in further soil C storage due to increased priming (Sayer et al., 2019; Terrer et al., 2021). Such interactions have likely contributed to C loss from the Amazon over the past 40 years, where warming, drought, deforestation, fires and associated feedbacks have been linked to increased CO_2 emission (Gatti et al., 2021). A broad discussion of such interactions is beyond the scope of this paper; however, because warming directly increases evaporation, we consider the interaction of warming and drying on tropical microbial C dynamics.

Drought generally reduces microbial activity and slows decomposition and CO_2 emission (Wood & Silver, 2012). However, the inverse can sometimes occur under drying and rewetting cycles. In moist tropical forest soils, moderate soil drying can increase oxygen supply, which stimulates the precipitation of ferrous to ferric iron, releases soluble P and increases C mineralisation (Hall & Silver, 2013). Further increase in C mineralisation occurs where drought is followed by rewetting, through post-drought oxidation (the 'Birch' effect; Birch, 1964) and lignin mineralisation due to abiotic Fe oxidation and an increase in reactive oxygen species (Hall et al., 2015). These changes have occurred alongside microbial community change, including an increased dominance of rare fungal groups conferring increased drought tolerance (Bouskill et al., 2016; Buscardo et al., 2021) and increased enzymatic capacity to degrade C (Bouskill et al., 2016). Together, this evidence suggests warming and drying could interact to, overall, accelerate C degradation in tropical forest soils. This interaction may also have large effects on C cycling via plant–microbe interactions. For example, a field experiment in the Brazilian Amazon tropical forest found that 14 years of drying resulted in a decline in fungal pathogens (Buscardo et al., 2021), which could explain the separate observation of reduced negative density dependency for seedlings under experimental warming (and an interaction with drying) for tropical forest in Puerto Rico (Bachelot et al., 2020).

The interaction between warming, drying and fire frequency will have clear consequences for soils that occur in tropical wetlands. Drying of peatlands can trigger high oxidative enzyme activity which, in turn, can stimulate hydrolytic enzyme activities—together accelerating the degradation of C stores (Freeman et al., 2001). For example, drying through human disturbance of peatlands has led to C losses dating from 5,000 year BP (Moore et al., 2013), while burning of tropical forest on peat soils had little effect on CO_2 exchange but almost doubled CH_4 emission (Lupascu et al., 2020). A priority for improved understanding of these interactions must be the development of factorial experiments and standard protocols to compare responses among existing long-term studies.

6 | CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

In a warming climate, the response of tropical forest soil C and microbial communities will vary across temporal and biogeographical scales, and understanding the mechanisms driving this variation remains a major research challenge. In the short term, microbial activity and the tropical soil C store appear to be highly sensitive to warming, as demonstrated in field-based experiments (Figure 3; Nottingham et al., 2020; Reed et al., 2020). Likely explanations for this short-term sensitivity include accelerated enzymatic activity, stimulated activity of thermotolerant microbial communities and the rapid degradation of particulate organic C—exacerbated by priming effects due to high plant inputs to soil and high soil C turnover rates (Figure 1). Together, these mechanisms may explain a small contribution (e.g. an additional 0.2 to 0.4 Pg C/year per 1°C warming; Figure 5) from soil C to the atmospheric CO_2 growth rate over the tropics during warm ENSO events (Jones et al., 2003; Wang et al., 2014) and during the warming observed over recent decades (Gatti et al., 2021). Consistent with these experimental observations, the historical record demonstrates the potential for a large release of tropical soil C under warming (Hein et al., 2020). However, the historical record is also suggestive of mechanisms enabling long-term stability of soil C, including physico-chemical protection, anoxic conditions and through changes in plant growth and related C inputs to soil (Figure 1). Through these mechanisms, the tropical soil C pool could be protected from microbial degradation during future warming. For example, soil C stores can be protected or even increased by conserving intact tree communities and their mycorrhizal associations and the large transfer of C below-ground they enable (Averill et al., 2014), by the conservation of anoxic conditions in peatlands (Moore et al., 2013) and by the application of C residues and their mineral stabilisation (Abramoff et al., 2021), as observed in ADE tropical soils (Glaser & Birk, 2012).

Biogeographical variation also requires attention. Tropical forests are diverse not only in their above-ground composition (ter Steege et al., 2013), but also in their geology (Figure 2; Quesada et al., 2010; Sanchez & Logan, 1992). Studies are required across the breadth of soil types found in the tropics, and including the major C stores found in subsoils, tropical wetlands and montane systems. Representing the diversity of soil communities and plant–microbe interactions remains a challenge. However, some broad generalisations are possible, based on key functional plant–microbe groups. For example, we predict large differences in the manner of plant–soil interactions and C dynamics under warming between arbuscular versus ectomycorrhizal dominated forests, where the presence of saprotrophic ectomycorrhizae may strongly influence below-ground C transfer and decomposition rates under warming.

To understand responses across temporal and biogeographical scales requires bringing together multiple lines of evidence, from long-term in situ experiments to intensive monitoring and historical observations. To better generalise across these approaches, standard protocols are needed for the monitoring of below-ground C exchange, including key parameters needed to inform microbial soil C models (Hagerty et al., 2018). Building these measurements into existing networks of intensively studied forest plot networks offers the opportunity to understand soil C change in the context of above-ground processes; and the development of these measurement networks is needed urgently because baselines are shifting rapidly (e.g. Bond-Lamberty et al., 2010, 2020). We identify key factors to provide a focus for future research in warming impacts on tropical soils across broad spatio-temporal scales: (1) the response of soil communities to unprecedented but possible future maximum temperatures, and the consequences for soil processes; (2) the formation and stability of mineral-associated C in strongly weathered tropical soils; (3) the consequences of highly coupled plant–microbe interactions for both soil C and forest function under warming; and (4) the interactions with warming, including drought, elevated CO_2, N deposition and land-use change.

The response of tropical soil microbial communities to warming will be a major determinant for the future of tropical forest ecosystems and the global atmosphere. However, we are only beginning to understand the vital role they play, enabled by rapidly growing developments in methods to characterise microbial communities and their functioning, their role in C cycling and in maintaining plant species diversity. To fully understand their response to warming, and for their accurate representation in models, requires applying methods to study systems that span temporal and spatial scales representing the biogeographical heterogeneity of tropical forest plants and soils. Together, these approaches will reveal the impacts of warming on tropical soil microbes and, in turn, the role of microbes in the maintenance and functioning of tropical forests—both as a major store of terrestrial C and as a refuge for global biodiversity.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.T.N. conceived the idea and wrote the first draft of the paper. E.G. performed the CASA model simulations. All authors contributed to the discussion and revision of the paper.

DATA AVAILABILITY STATEMENT

There are no data to archive.

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