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Tropical Forest Soils in a Warmer World

Consequences for Climate and Biodiversity

Andrew T. Nottingham

ABSTRACT. Climate warming poses detrimental but poorly understood consequences for tropical forest biodiversity and carbon storage, especially through its impact on soils. To address this uncertainty, the Soil Warming Experiment in Lowland Tropical Rainforest (SWELTR) was initiated on Barro Colorado Island in Panama; one of a few emerging experiments designed to understand the effects of a warmer climate on the tropical land-surface. In this chapter, I describe results following up to three years of experimental whole-profile soil warming, showing high sensitivity of soil organic matter degradation and an unexpectedly large release of carbon dioxide (CO_2) to the atmosphere. I consider the biogeochemical mechanisms that may be contributing to this CO_2 emission and, finally, the research priorities to understand the longer-term and wider-scale implications of warming on tropical forest soils. Better understanding of these feedbacks is vital for developing mitigation strategies to conserve the biodiversity and carbon storage of tropical forests in a warming world.

Keywords: biogeochemistry; global warming; microbial ecology; soil carbon storage; soil microbiology; soil warming; tropical forest ecology

INTRODUCTION

Over the coming century, the tropics are predicted to warm by 3–4°C (Intergovernmental Panel on Climate Change, 2021), moving significantly out of their historically stable climatic regime (Mora et al., 2013). A warming climate is of concern both for the large stores of carbon (C) found in tropical forests and for the diverse biota they harbor. Soils contain more than twice the amount of C held in vegetation and four times the amount that is held in the atmosphere—and a third of all soil C resides in the tropics (Jackson et al., 2017). Soils are also environments of high microbial biodiversity, which regulates ecosystem function and structure by influencing processes, such as decomposition, and by interacting with plants (Bardgett and van der Putten, 2014). Soil biodiversity may be of particular importance in tropical forests, where the interactions between plants and microbes have been shown to contribute to high plant biodiversity (Mangan et al., 2010; Bagchi et al., 2014). The response of tropical forest soils to warming is thus of major consequence for ecosystem C storage, our future climate and for the persistence of tropical forest biota.

School of Geography, University of Leeds, Seminary Street, Woodhouse, Leeds, UK. Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Ancón, Republic of Panama.
Correspondence: A.Nottingham@leeds.ac.uk
https://orcid.org/0000-0001-9421-8972

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UNCERTAINTY: WARMING EFFECTS ON TROPICAL FOREST SOILS

Increased temperature can stimulate the decomposition of soil organic matter representing a positive feedback on further climate change (Cox et al., 2013; Crowther et al., 2016). This effect has been described in Earth system models by a Q_{10} function (Todd-Brown et al., 2013) based on theories of chemical reaction rates (Arrhenius, 1889; Michaelis and Menten, 1913). When applied to soils, these theories commonly predict that the temperature sensitivity of reaction rates (i.e., Q_{10} value) is lower at warmer temperatures, greater for more recalcitrant (less reactive) substrates and reduced under conditions of low substrate availability (Davidson and Janssens, 2006). For tropical soils, where temperatures are already warm, soil C temperature sensitivity is therefore predicted to be relatively low when compared with observations from cooler climates (Carey et al., 2016; Crowther et al., 2016; Hicks Pries et al., 2017). However, the temperature sensitivity of soil C measured under field conditions ("apparent" Q_{10}) can depart from this theory, as warming affects the soil environment, including the soil biotic community composition, plants, and moisture (Davidson and Janssens, 2006; Nottingham et al., 2015b). Given the scarcity of information for tropical forests under field conditions, the representation of tropical forest soil C temperature sensitivity in Earth system models has lacked an empirical foundation and has limited our ability to predict the response of the land-surface to climatic change (Cavaleri et al., 2015).

Warming may further affect tropical forests and climate through changes in the community composition and diversity of both soil biota and plants. Plant species diversity peaks in the tropics (ter Steege et al., 2013). Soil bacterial and fungal diversity has also been observed to increase in warmer climates (Tedersoo et al., 2014; Zhou et al., 2016; Nottingham et al., 2018) although soil pH is often a dominant influence on bacteria irrespective of temperature (Fierer and Jackson, 2006). One explanation for a correlation between temperature and biodiversity, whether of plants or microbes, is a positive influence of temperature on evolutionary rates (e.g., energy-diversity theory; Wright, 1983). Consistent with this theory, soil microbial diversity has been observed to increase under experimental warming in cooler climates (DeAngelis et al., 2015; Zhou et al., 2020). Whether or not this pattern occurs in tropical soils, where warmer temperatures may exceed thermal limits for certain species, had until recently, remained untested. A change in the tropical forest soil microbial community and diversity under warming could have further direct implications for plant growth and survival, given evidence that tropical forest plant diversity is increased through interactions between plants and their microbial partners (e.g., conspecific negative- density dependency interactions between plants mediated by microbial pathogens) and evidence that the presence and activity of diazotrophic bacteria or mycorrhizal fungi feedback on plant productivity (Mangan et al., 2010; Bagchi et al., 2014; Sarmiento et al., 2017, Nottingham et al., 2023; Spear and Mordecai, 2024). Thus, any change in microbial species diversity and community composition may have consequences for the performance and even survival of plant species. Biodiversity change could have further consequences for the C cycle and CO_2 emissions from soil as many studies have demonstrated correlations between diversity and ecosystem processes for both plants (Tilman et al., 2012) and soil microbes (Strickland et al., 2009; Bardgett and van der Putten, 2014).

TROPICAL WARMING EXPERIMENTS

Despite the dominant influence of tropical forests on the terrestrial carbon cycle (Pan et al., 2011), we have extremely poor understanding of their response to a warming climate (Cavaleri et al., 2015). Indeed, metanalyses of global field warming experiments lack any study from the tropics (Crowther et al., 2016). Emerging field experiments, however, are now addressing this uncertainty (Wood et al., 2019; Nottingham et al., 2022a). To understand how a warming climate might affect the large stores of C and microbial biodiversity held in tropical soils, the Soil Warming Experiment in Lowland Tropical Rainforest (SWELTR) was initiated on Barro Colorado Island (BCI) in Panama (Fig. 1). The experiment uses a whole-soil profile warming design, the first of its kind to be implemented in a tropical ecosystem. The experiment consists of five paired warm and control plots across a 1-ha area of forest. Each warm plot contains a circular heating structure (resistance cables inside a stainless-steel frame) measuring 3.5 m in diameter and 1.2 m deep, which was buried to heat the soil profile to >1.5 m depth by 4°C. The experimental design follows similar experiments conducted at higher latitudes (Hicks Pries et al., 2017; Richardson et al., 2018). Further information on the experimental site and design is available in Nottingham et al. (2020).

For a tropical forest site on BCI, the SWELTR experiment is revealing how a warming climate will affect tropical forest function, biogeochemical cycling, and biota across multiple kingdoms—plants, fungi, bacteria, and the soil macrofauna. Results from SWELTR need to be understood in the context of biogeographical variation in tropical forests, where responses may differ with variation in biotic communities, geology, and climate. Further field experiments are being implemented that will provide this necessary context to understand the effects of warming across wider scales. Another belowground warming experiment, using a similar experimental design to SWELTR, is being used at a site initially cleared of vegetation in the Lyon Arboretum, Hawaii (McGrath, 2019). In contrast, the Tropical Responses to Altered Climate Experiment (TRACE) situated in a lowland tropical forest in Puerto Rico on clay-rich Ultisols, uses infrared lamps to heat both the forest understory and soils (Kimball et al., 2018). These in situ warming experiments are complemented by studies using temperature gradients on tropical mountains, where soil mesocosms have undergone temperature incubations in Costa Rica (Looby and Treseder, 2018) and Peru (Nottingham et al., 2019b; Zimmermann et al., 2012), and by laboratory

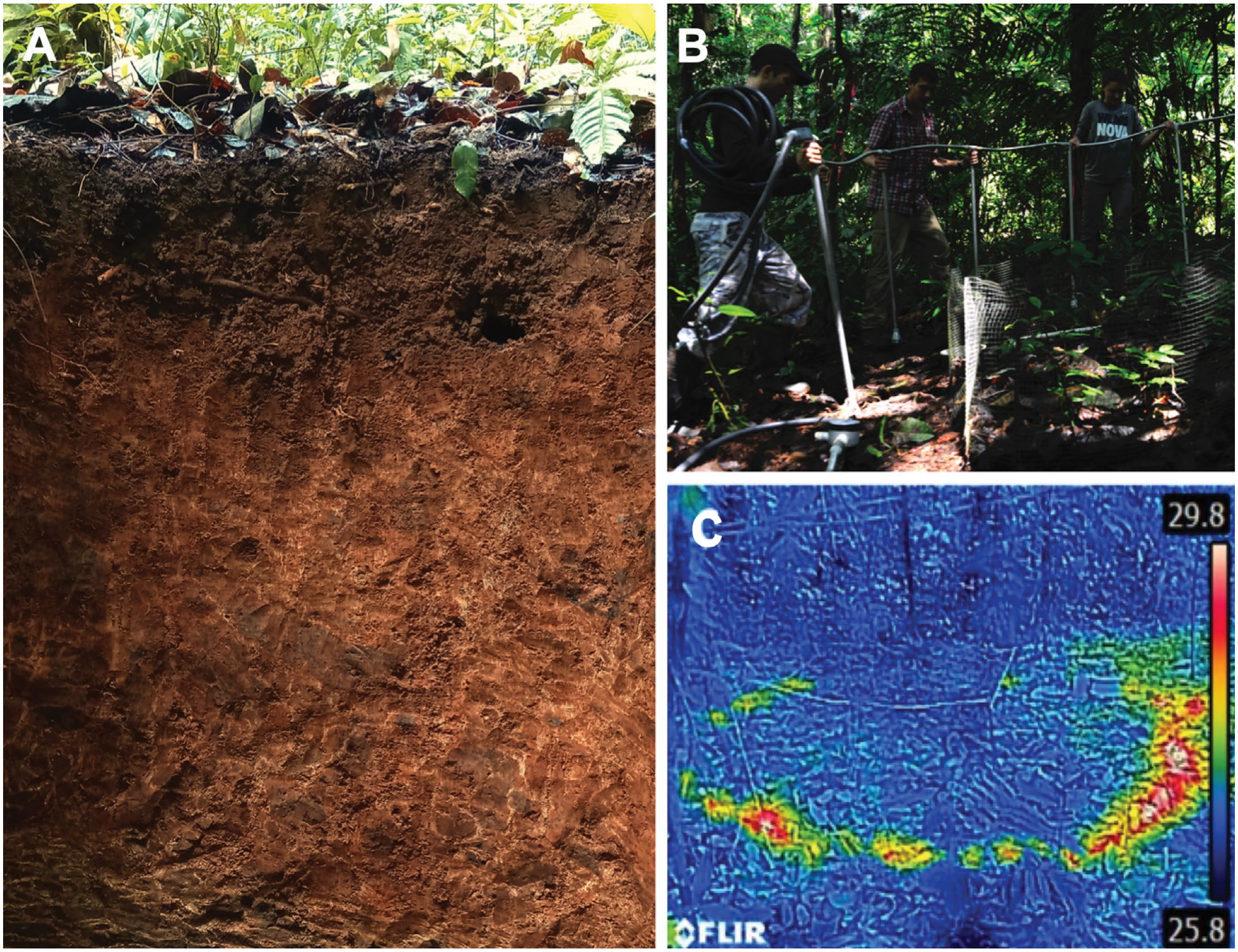

FIGURE 1. The SWELTR experiment on Barro Colorado Island, Panama (Soil Warming Experiment in Lowland Tropical Rainforest). (**A**) The tropical forest soil at the SWELTR site. The red colors originate from iron oxides, which are characteristic of the old, strongly weathered soils of the tropics. Photo © Maria Montero-Sanchez. (**B**) The installation of SWELTR heating structures, which are 1.2 m in length and buried to about 1.3 m in depth. The experiment heats >120 m^3 soil in total (5 plots × 5-m diameter × >1.3-m depth). Photo © Geetha Iyer. (**C**) A thermal image of the soil-surface temperature shortly after the warming structure was switched on; before equilibration of soil temperature across the plot area (to +4°C above ambient temperature), which occurred after a few days of heating. Photo © Jelena Bujan and Esther Velasquez.

incubation experiments (Holland et al., 2000). Although generally restricted to short-term studies, incubation experiments are useful to understand fine-scale mechanisms under controlled conditions and to allow for the broader study of a wide variety of soil types. For a wider review of these experimental approaches the reader is referred to Nottingham et al. (2022a) and Wood et al. (2019). Here, I summarize results from SWELTR on the response of tropical forest soil C and soil communities during the first three years of warming, while drawing on emerging results from companion warming experiments. Specifically, I consider the soil processes that influence the effect of warming on soil C and its emission as CO_2 (Fig. 2).

SOIL ORGANIC MATTER RESPONSE

In tropical forest on BCI, two years of soil warming by 4°C increased soil CO_2 emissions by 55% (Nottingham et al., 2020). This result, relative to a 34–37% increase observed for warmed soil in temperate forest in California using a similar full-soil-profile

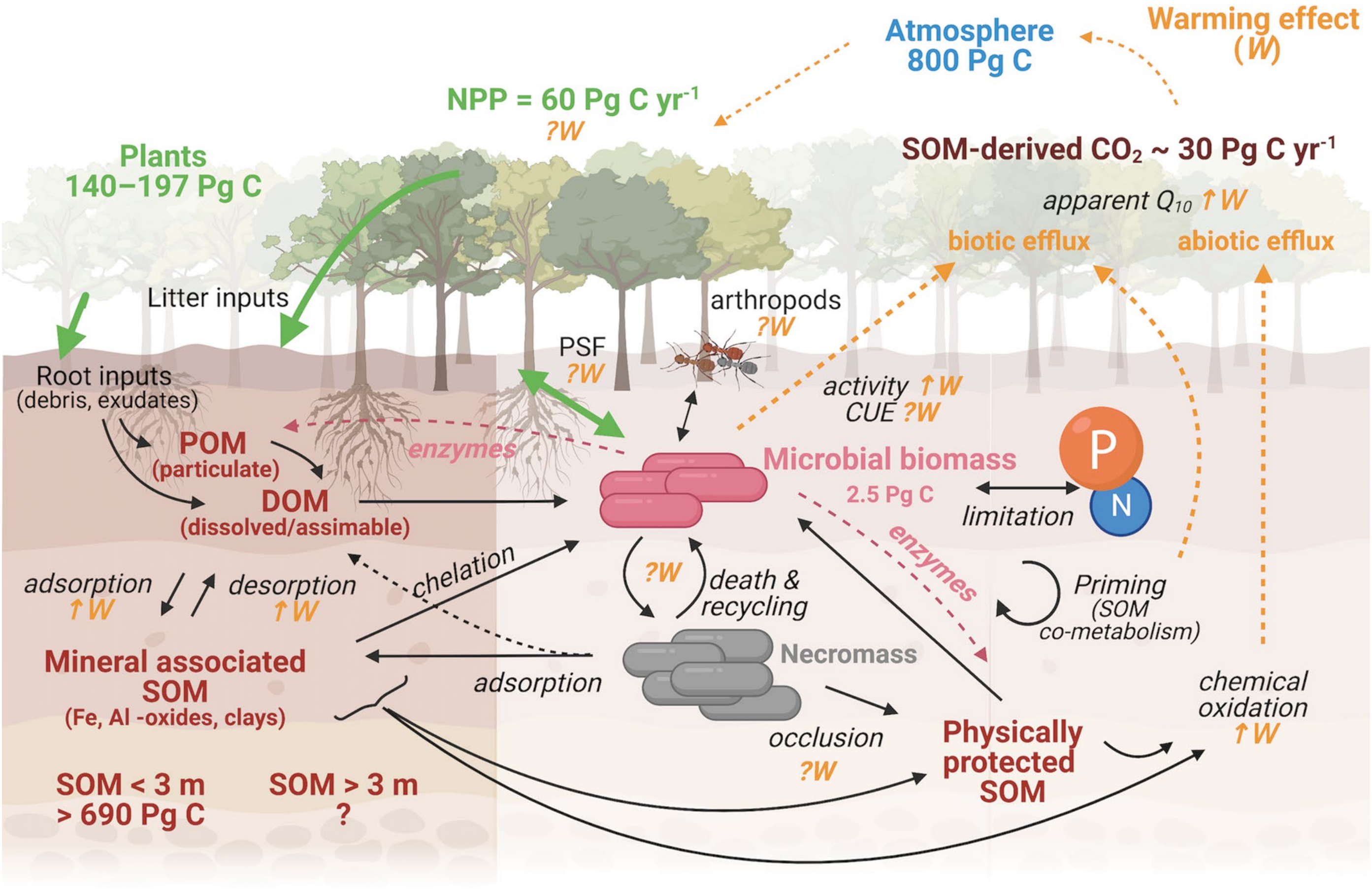

FIGURE 2. The tropical forest soil C cycle and its response to a warming climate. The temperature response of soil-derived CO_2 emission (apparent Q_{10}) is determined by the net intrinsic response of specific soil processes. Warming interactions are denoted by *W*, including the hypothesized direction of response, or a question mark where unknown. Tropical forest C pool sizes are shown for plants, net primary productivity (NPP; Pan et al., 2011), microbial biomass (Serna-Chavez et al., 2013), and soil organic matter (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 (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. 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; T, temperature. 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. Warming interactions are denoted by *W*, including the hypothesized direction of response, or a question mark where unknown. From Nottingham et al. (2022a).

heating method (Hicks Pries et al., 2017), indicates a high apparent Q_{10} of CO_2 release for tropical soils (equivalent to $Q_{10\,(26\text{-}30oC)}$ = 3.0, calculated across reference temperatures 26°C to 30°C). A physical root-partitioning method was used to quantify the source of the increased soil CO_2 emission, which showed a dominant contribution from soil-derived ("heterotrophic") rather than root-derived ("autotrophic") sources, especially during the wet season when moisture was not limiting to microbial activity (Nottingham et al., 2020). These results point toward preexisting soil C as the source of the CO_2 emission, which was confirmed by radiocarbon dating. After one year of warming, the age of soil-derived CO_2 emission was two- to threefold older in the warmed plots relative to controls (Δ^{14} C increased by 12 ‰), indicating increased microbial metabolism of older stores of C (McFarlane et al., 2023). A high sensitivity of soil CO_2 emission to warming may be representative of tropical forest soils more broadly, as another study in Puerto Rico has also reported high CO_2 emission rates from warmed forest soils (Wood et al., in review). Further study is required to examine whether these responses translate into decreased soil C storage. At least in the short-term (three years), lowland tropical forest soil CO_2 release appears to have high apparent sensitivity to warming, contrary to model predictions (Davidson and Janssens, 2006).

MICROBIAL ACTIVITY RESPONSE

What caused the high sensitivity of tropical forest soil CO_2 emission to warming, observed both on BCI and in Puerto Rico: the effect of warming on microbial activity, on biogeochemical processes and substrate supply to microbes, or on the composition of the soil biotic community (Fig. 2)? For the SWELTR site, we first explored biological mechanisms and the instantaneous temperature sensitivity of microbial growth, because microbial catabolism is the rate-limiting step for soil CO_2 emission (Hobbie and Hobbie, 2013; Bååth, 2018). Information on the instantaneous temperature sensitivity of microbial growth and respiration determined in laboratory assays of soils from the SWELTR site was used to predict the effect of warming on microbial activity (Nottingham et al., 2022a). The study found that the instantaneous temperature response of microbial activity increased CO_2 emission by 20% and therefore was insufficient to explain the 55% increase measured in situ.

Changes in substrate and nutrient availability under warming could interact with, potentially accelerating, the temperature response of microbial activity and soil C mineralization. Several studies in tropical forest soils have demonstrated phosphorus limitation to microbial C metabolism and decomposition rates (Camenzind et al., 2017), including from nearby forest in Panama (Kaspari et al., 2008; Nottingham et al., 2015a, Wright et al., 2024). For SWELTR, warming increased the availability of soil extractable PO_4 seasonally (during the early wet season; Nottingham et al., 2023), a pattern consistent with increased microbial activity and mineralization of organic phosphorus. Consistent with this, the maximum potential activity (V_{max}) for 7 out of 10 measured extracellular soil enzymes increased significantly with warming (up to 34°C), including phosphorus-degrading enzymes (Nottingham et al., 2022b). This pattern of accelerated enzyme activity at high temperatures could also result from the effect of warming on abiotic processes. For example, warming can increase the desorption of "mineral-associated" C and extracellular enzymes that form an otherwise stable pool, sorbed to the surfaces of mineral particles (Wallenstein et al., 2011; Fanin et al., 2022), and that may form a substantial pool in clay-rich tropical soils (Kirsten et al., 2021). The pattern could also result from biotic processes, where increased C release from decomposing leaf-litter can accelerate enzyme synthesis for soil organic matter mineralization ("priming"), a phenomenon observed in a nearby field experiment where leaf-litter inputs were experimentally increased (Sayer et al., 2011; Tanner et al., 2024) and in another experiment using BCI soils following the addition of ^{13}C-labeled substrates (Nottingham et al., 2012). It is therefore possible that both abiotic and biotic processes contributed to accelerated enzyme activities and, in turn, organic matter mineralization under warming.

MICROBIAL COMMUNITY CHANGE

Another mechanism by which warming can increase soil CO_2 emission is through compositional changes in the microbial community that result in increased activity and respiratory C loss (Karhu et al., 2014; Melillo et al., 2017). Such "community adaptation" to warming has been shown by models to substantially increase predicted C loss from soils (Wieder et al., 2013), although there is high uncertainty (Sulman et al., 2018) arising in part because of methodological challenges in quantifying this microbial community response (Hagerty et al., 2018). One direct method is the use of isotopic tracers to measure changes in the temperature sensitivity of bacterial and fungal growth (and the calculation of the minimum temperature for growth "T_{min}", a theoretical value representing temperature adaptation of the community (Ratkowsky et al., 1982). Using this method, studies have shown that soil bacterial and fungal communities are adapted to long-term temperature difference, with positive correlations between T_{min} and mean annual temperature observed across gradients in latitude and elevation (Rinnan et al., 2009; Nottingham et al., 2019a). The method has also shown how rapidly communities from cooler climates may adapt to warming in soils (Donhauser et al., 2020; Nottingham et al., 2021), indicating increased activity of the new community at warmer temperatures, with the potential to increase soil C mineralization.

Similar results were found following two years of warming at the SWELTR site. Warming increased the T_{min} for bacterial and fungal growth and changed the microbial community structure, with increased dominance of thermotolerant phyla (Nottingham et al., 2022b). However, soil warming on BCI also led to decreased microbial diversity, especially for bacteria (Nottingham et al, 2022b), suggesting a breakdown—at least initially (three years)—in the positive relationship between temperature and soil microbial diversity observed in cooler climates (DeAngelis et al., 2015; Zhou et al., 2020). Despite the community adaptation to warming (increase in T_{min}), microbial biomass C did not decline at BCI (Nottingham et al., 2020) nor at Puerto Rico (Reed et al., 2020). This result points to a consistency between two tropical forest sites of maintained or increased microbial biomass under short-term warming, potentially explaining sustained CO_2 emission. This contrasts with findings from warming experiments at higher latitudes where a decline in microbial biomass (because of a decline in "carbon use efficiency") was suggested to reduce soil CO_2 emission (Melillo et al., 2017). When the measured increase in T_{min} for microbial growth in warmed BCI soils was used to predict changes in respiration, however, soil CO_2 emissions were predicted to increase only marginally, from 20% to 22% (Nottingham et al., 2022b). Thus, adaptation of the microbial community, which included a reduction in diversity, can only explain a small portion of the measured increase in soil CO_2 emission under warming.

TROPHIC CASCADES

The effect of warming on soil C dynamics may be further modulated through changes in soil macrofauna and interactions across trophic levels. Soil invertebrates and their interactions with soil microbial communities play an important role in ecosystem functioning and organic matter breakdown (Folgarait, 1998; Wardle, 2006; Bardgett and van der Putten, 2014), which are often overlooked in models of soil C dynamics and its response to global change. Ant diversity and community composition were characterized for the SWELTR site following two years of soil warming. Although diversity was unaffected, warming led to a significant shift in the ant community composition with increased dominance by *Wasmannia auropuctata* (Bujan et al., 2022), a thermotolerant species associated with disturbed environments (Foucaud et al., 2013). Soil invertebrate communities were characterized in soil and litter samples collected from the SWELTR site following three years of warming. Over a full seasonal cycle, 72,000 invertebrate organisms were collected, representing more than 33 taxonomic orders. Here, declines in order-level diversity but increases in abundance were observed in both soil and litter-dwelling communities, with increased dominance by oribatid mites (Szczygieł et al., in review) known to play important roles in soil systems as decomposers and fungivores (Scheu et al., 2005). Thus, under warming, the increased abundance and activity of soil macrofauna, including important groups of decomposers, could contribute to increased soil CO_2 emission; although these effects are likely further mediated by trophic interactions and altered grazing of the soil microbial community as observed in warmed temperate forest soil (Crowther et al., 2015). In summary, findings from SWELTR show that warming affects soil communities across trophic levels (Bujan et al., 2022; Nottingham et al., 2022b, Szczygieł et al., in review), which together may be contributing to C loss from soils.

FUTURE DIRECTION

The SWELTR experiment has demonstrated high sensitivity of soil C loss to warming in tropical forest at BCI (Nottingham et al., 2020). The high CO_2 emission, which was also observed for warmed tropical forest soils in Puerto Rico (Wood et al., in review), exceeded the prediction from a microbial model calibrated with data on the temperature response of microbial activity in soils collected from the BCI field site (Nottingham et al., 2022a). Emission rates appeared to be accelerated through widespread changes in organic matter dynamics and soil biotic communities across multiple trophic levels (Bujan et al., 2022; Nottingham et al., 2022b, Szczygieł et al., in review). These results are based on the response to three years of warming, however, and it is expected that longer-term responses may differ, with further change in soil substrate availability, soil organo-mineral interactions, plant-microbial interactions, plant growth, and soil biotic communities (Melillo et al., 2017). Indeed, emerging evidence suggests species-specific differences in plant performance under warming (Slot, 2024), further supported by the response of seed germination and seedling growth in experimentally warmed forest on BCI (Diedrich et al., in review; Nottingham et al., 2023) and in Puerto Rico (Bachelot et al., 2020). The SWELTR experiment is, at present, one of only two warming experiments in tropical forests globally that, together, are providing complementary insight on the response of tropical forests to a warming climate across broad biogeographical scales. It is a key ongoing global-change experiment with wide application in empirical and modeling science; such long-term field experiments are vital to advance our understanding of how tropical forests respond to global change (Muller-Landau and Wright, 2024). Future research at SWELTR will focus on longer-term biotic and abiotic interactions between and within plants and soils, and how they may feedback on ecosystem C storage and forest function in a warmer world.

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