CHAPTER 14

Soil warming effects on tropical forests with highly weathered soils

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Diversity of tropical ecosystems

The tropics are a region encircling the equator, delineated to the north by the Tropic of Cancer (23°26′14.0″N) and to the south by the Tropic of Capricorn (23°26′14.0″S). While we often think of the tropics as consistently warm and wet throughout the year, in reality, the tropics maintain a myriad of climates. Of the 116 Holdridge life zones (a global bioclimatic classification scheme), the tropics contain more life zones than the sum of all the planet's other geographic regions combined (Holdridge, 1967). In addition to high climatic diversity, the tropics support a wide range of parent materials, landforms, geomorphic characteristics, and soil ages, and maintain all 12 soil types of the USDA soil taxonomy system (Palm et al., 2007; Porder et al., 2007; Quesada et al., 2010; Richter and Babbar, 1991; Sanchez, 1977; Soil Survey Staff, 2006; Townsend et al., 2008). Accordingly, there is no single representative tropical ecosystem. Given the diversity of tropical biomes, this chapter will focus specifically on tropical forested ecosystems and their responses to warming because of their global importance, potential sensitivity to change, and the fact that an improved understanding of how these ecosystems may respond to warmer climate conditions is of significant importance to ecology and society. Furthermore, while generally considering all tropical forest types, emphasis in this chapter is on the humid tropics for which we have most data.

While tropical forests cover just 15% of the planet's terrestrial surface, these ecosystems house the majority of Earth's biodiversity (Pianka, 1966; Sullivan et al., 2017), account for a third of global soil carbon (C) (Jobbagy and Jackson, 2000), two-thirds of plant biomass (Pan et al., 2011), and exchange more C, water, and energy with the atmosphere than any other terrestrial ecosystem (Beer et al., 2010; Foley et al., 2003; Myers et al., 2000; Townsend et al., 2011). In the coming decades, Earth System Models consistently project that the tropics will experience increased temperature variability along with unprecedented warming and extreme temperature events (Diffenbaugh and Scherer, 2011; Mora et al., 2013; Vogel et al., 2017). In particular, models suggest that temperature variability during the season with maximum *insolation* will increase by approximately 10%–15% per degree of global warming and that 70% of the seasons in the tropics will be hotter than the hottest seasons of the late 20th century (Bathiany et al., 2018; Diffenbaugh and Scherer, 2011). Considering the massive amounts of C cycled between tropical forests and the atmosphere, determining how these systems respond to changes like warming is critical for considering and forecasting future biogeochemical

cycling and climate at the global scale (Cavaleri et al., 2015; Wood and Silver, 2012; Wright et al., 2009). Here we will explore how key aboveground and belowground components of tropical forested ecosystems may respond to a warming climate within the larger context of global change.

Tropical versus higher latitude responses to a warming world

Community and evolutionary ecologists shave long debated the role of temperature in determining the diversity, structure, function, and dynamics of terrestrial biomes (e.g., MacArthur, 1965; Pianka, 1966; Zak et al., 2003). Yet our overall understanding of thermal controls on tropical biota has lagged behind that of higher latitude ecosystems (Wood et al., 2012). This may be due, at least in part, to the fact that many tropical forests are already consistently warm and because projected increases in temperature are less severe in these regions relative to other latitudes; thus warming effects were expected to be less severe for equatorial regions (Clark et al., 2003, Anderson, 2011, Diffenbaugh and Scherer, 2011). However, emerging data suggest tropical species and their physiological responses might be more sensitive to warming temperature than previously assumed (Doughty and Goulden, 2008; Schwendenmann and Veldkamp, 2006; Townsend et al., 1992), possibly more sensitive than their higher latitude counterparts (Mau et al., 2018; Wright et al., 2009).

Tropical forests are hotter than the average annual conditions found across higher latitude ecosystems with >80% of tropical forests experiencing mean annual temperatures (MAT) >20°C (Wood and Silver, 2012). Furthermore, tropical ecosystems typically experience greater diurnal variation in air temperature than that of longer term, seasonal temperature variation. For instance, air temperature can vary as much as 6–13°C within a day, while mean monthly temperature varies just 2–4°C throughout the year in many tropical forests (Vandecar et al., 2009; Wood et al., 2016). As a whole, the seasonality of temperatures that define MAT across regional or global gradients is complex. For example, maximum daily temperatures observed in certain months of many temperate regions may not differ substantially from, and may even exceed, those in tropical regions. As such, careful consideration of temperature variation (e.g., warmer cool periods vs warmer hot periods) and the scale of temperature analysis is critical to accurately assessing warming effects on ecosystems. For this reason, other metrics, such as *growing season length* or frequency of temperatures that exceed mean daily maximum

temperature, can be valuable for understanding larger scale temperature variation and the conditions under which organisms are grown (Baldocchi et al., 2001).

According to kinetic theory, we expect reaction rates will follow predictable patterns, with rates increasing exponentially with temperature up to a physiological maximum, beyond which rates are limited by a variety of processes (e.g., *Michaelis-Menten kinetics*; Davidson et al., 2006). Furthermore, reactions vary in the *activation energy* they require, and increased temperature can activate processes in unforeseen ways. This is particularly important when considering the effects of warmer daily temperatures on the diversity of C compounds in tropical soils, a high proportion of which require larger amounts of energy to decompose (*Arrhenius kinetics* or the *carbon quality-temperature hypothesis*; Davidson and Janssens, 2006). Thus, by alleviating temperature limitation to chemical reactions, warming should increase decomposition of C that was previously unreactive. Where increased decomposition rates (i.e., C loss) are not matched by increased productivity (i.e., C inputs), a site would undergo a decrease in the storage of C in soils, resulting in net increases in the amounts of C released to the atmosphere (Crowther et al., 2016, 2018; van Gestel et al., 2018). However, where warming manifests as an increase in maximum temperatures, the potential for biological reactions to surpass high temperature thresholds also increases.

Most biological processes are a complex aggregate of secondary reactions, each of which have their own temperature sensitivities. Thus while increased temperature raises the risk of enzyme denaturation or other physical damage from high temperatures, a net decline in the rate of biological processes may be due to the depletion of available or readily decomposable *substrate* (Fissore et al., 2013), or some other rate-limiting step (e.g., regeneration of enzymes). Furthermore, because rates of biological processes in tropical forests are already consistently high when water is in sufficient supply (e.g., Parton et al., 2007; Raich and Schlesinger, 1992), rate-limiting factors, like substrate limitation, may occur much sooner in tropical ecosystems relative to their higher latitude counterparts.

When considering temperature effects on biota, time is a critical factor. Tropical biota have existed for millennia under consistently warm temperatures and as such may have evolved adaptive measures for withstanding increases in temperature. For example, a recent study of microbial temperature sensitivity found that the proportion of microbial taxa that increased their relative abundance in response to warming was significantly greater

in sites with higher MAT (Oliverio et al., 2017), suggesting a high capacity of lowland tropical species to withstand, and perhaps even thrive, under warmer conditions. However, the traits that make an organism more successful at higher temperatures are likely to come at some metabolic cost (Bradford et al., 2008; Oliverio et al., 2017). For example, if enzyme rigidity is increased to reduce susceptibility to denaturation at higher temperatures (i.e., increase temperature *optima* for biological processes), this increased rigidity can also reduce the number of binding sites on the enzyme, thereby reducing the amount of C that can be processed (Bradford et al., 2008, 2010). Thus, while increased enzyme rigidity is likely beneficial to an organism growing under higher temperatures, the trade-offs associated with this enzyme adjustment mean the organism could be outcompeted by organisms with less rigid enzymes when exposed to lower temperatures and thus they would not be able to process C as quickly (Bradford et al., 2008). However, there is emerging research that suggests that enzyme inactivation may increase with increasing temperatures, with an overall reduction in catalytic power, which could explain the observed return of soil respiration rates to control values within a few years of warming in higher latitude warming experiments (Alvarez et al., 2018). Clearly, greater understanding of the capacity of organisms to *adapt* and/or *acclimate* to warmer temperatures over the longer term is central to predicting the consequences of warming temperatures for ecosystem C balance.

While tropical organisms are likely to have existing adaptations to sustained warmer temperatures and to lower annual variation in daily temperatures compared to temperate organisms, if temperatures increase beyond historical conditions, we might expect a disproportionately large effect on tropical organisms relative to their higher latitude counterparts that are adapted to larger temperature variation across days, seasons, and years. Tropical organisms may already exist closer to maximum thermal tolerances than higher latitude species (Berry and Bjorkman, 1980; Doughty and Goulden, 2008; Huey et al., 2009; Laurance et al., 2011; Lyons and Willig, 1997; Mau et al., 2018; Payne and Smith, 2017; Stevens, 1989). Animals and plants clearly have the ability to *adapt* and/or *acclimate* to the temperatures they encounter in their environment, but perhaps do not adapt well outside of that range (e.g., temperature gradients across mountain passes present greater barriers to movement for organisms of tropical lowlands than to those of higher latitudes; *mountain passes hypothesis*; Janzen, 1967). Thus the temperature variation typical of an area has an adaptive influence on the range of temperatures physiologically tolerated by the organisms that live there.

And so tropical biota, which have evolved under very narrow temperature ranges, are likely to be "thermal specialists" when compared with higher latitude ecosystems, with many tropical organisms showing high tolerance for warmer temperatures but a low capacity to adjust to substantial deviation from historic conditions. Temperature increases in the tropics are projected to occur at a relatively rapid rate when compared with historical conditions. Predicted temperature increases are also expected to shift tropical organisms beyond what has been previously experienced (Bathiany et al., 2018; Diffenbaugh and Scherer, 2011). Accordingly, we might expect tropical organisms to have low capacity to *adapt* and/or *acclimate* to the rate and magnitude of temperature increases predicted with current and future climate change (Colwell et al., 2008; Laurance et al., 2011).

In addition to affecting the geographic range and adaptability of organisms to change, temperature is also thought to play a role in maintaining the high species diversity found in the tropics. If species with narrower thermal tolerances have equal dispersal abilities as those with broad thermal tolerances, a greater proportion of the thermal specialists are consistently placed outside of their preferred habitat relative to generalists. As such, a larger number of "accidentals" (i.e., species that are more poorly suited for the habitat) occur in systems with low temperature variation, and the constant input of these accidentals artificially inflates species numbers and inhibits competitive exclusion. As a result, geographic ranges become smaller and diversity increases as one moves toward the equator (*Rapoport's rule*; Stevens, 1989). Organisms that have been found to follow Rapoport's rule with latitude and elevation are wide ranging (e.g., Fleishman et al., 1998; Lear et al., 2017; Sanders, 2002; Stevens, 1992; Tedersoo et al., 2014). There are, however, exceptions to this rule (e.g., Bhattarai and Vetaas, 2006; Roy et al., 1994), and many alternative hypotheses for the high diversity found in the tropics continue to be debated (e.g., high primary productivity, competition, predation, evolutionary time; *sensu* Gaston et al., 1998; Rohde, 1996; Schemske and Mittelbach, 2017).

Methods of measuring changing temperature effects in the tropics

To date, research on terrestrial ecosystem responses to increased temperature has focused predominantly on regions outside of the tropics. Large-scale, decade-long manipulative experiments in nontropical ecosystems have revealed responses to experimentally warmed plants and soils (e.g., Melillo

et al., 2017; Panetta et al., 2018), providing powerful information for Earth-climate model representations of global biogeochemical cycles (Beer et al., 2010; Piao et al., 2013). In tropical forests, large-scale experiments have been implemented to investigate how nutrients (Tanner et al., 2016; Wright et al., 2018), litterfall (Sayer et al., 2011; Wood et al., 2009), and rainfall (Cleveland et al., 2010; Davidson et al., 2008; Meir et al., 2015; Sotta et al., 2007; Wood and Silver, 2012) regulate ecosystem processes, but—until very recently—there have been no large-scale in situ warming experiments in this biome (Cavaleri et al., 2015; Kimball et al., 2018). Thus our understanding of how tropical forests respond to warming is currently based on a range of indirect or small-scale approaches: the study of plant and soil responses to interannual and seasonal temperature variation (Clark and Clark, 2011); the use of gradients in MAT with elevation (Malhi et al., 2010), incubating soil in the laboratory or transplanting soil across natural temperature gradients (Fissore et al., 2013; Holland et al., 1995); and incubating plants and soil in mesocosms and growth chambers (see Fig. 1A–F; Cheesman and Winter, 2013; Liu et al., 2017; Slot and Winter, 2017a). These approaches, described below, provide valuable insight into tropical forest plant and soil temperature responses, but findings from these studies would benefit greatly from empirical support from sustained field-warming experiments that consistently push systems into the novel realm of predicted future temperatures. Indeed, the absence of tropical ecosystems in recent syntheses of field-warming experiments (Carey et al., 2016; Crowther et al., 2016) severely limits our ability to test model predictions at a global scale (Cavaleri et al., 2015).

Responses of tropical forests to variations in temperature have been evaluated in long-term studies of forest plots spanning 10 years or more (e.g., Fig. 1A; Clark and Clark, 2011; Feeley et al., 2007) and in studies of soil and atmospheric gas exchange responses to seasonal and interannual climate variation (Anderegg et al., 2015; Liu et al., 2017; Schwendenmann and Veldkamp, 2006). Long-term studies of forest plots in Costa Rica have shown that recent increases in mean annual minimum temperatures are tightly correlated with increases in tree mortality and reduced net primary productivity (NPP) (Clark et al., 2010, 2013), while warming over recent decades shows strong relationships with changes in tropical tree community ranges along elevation gradients in Costa Rica and Perú (Duque et al., 2015; Feeley et al., 2013). Studies of responses to seasonal climate variability and extreme events have revealed temperature responses of tropical forest respiration. For example, a high seasonal temperature sensitivity of soil
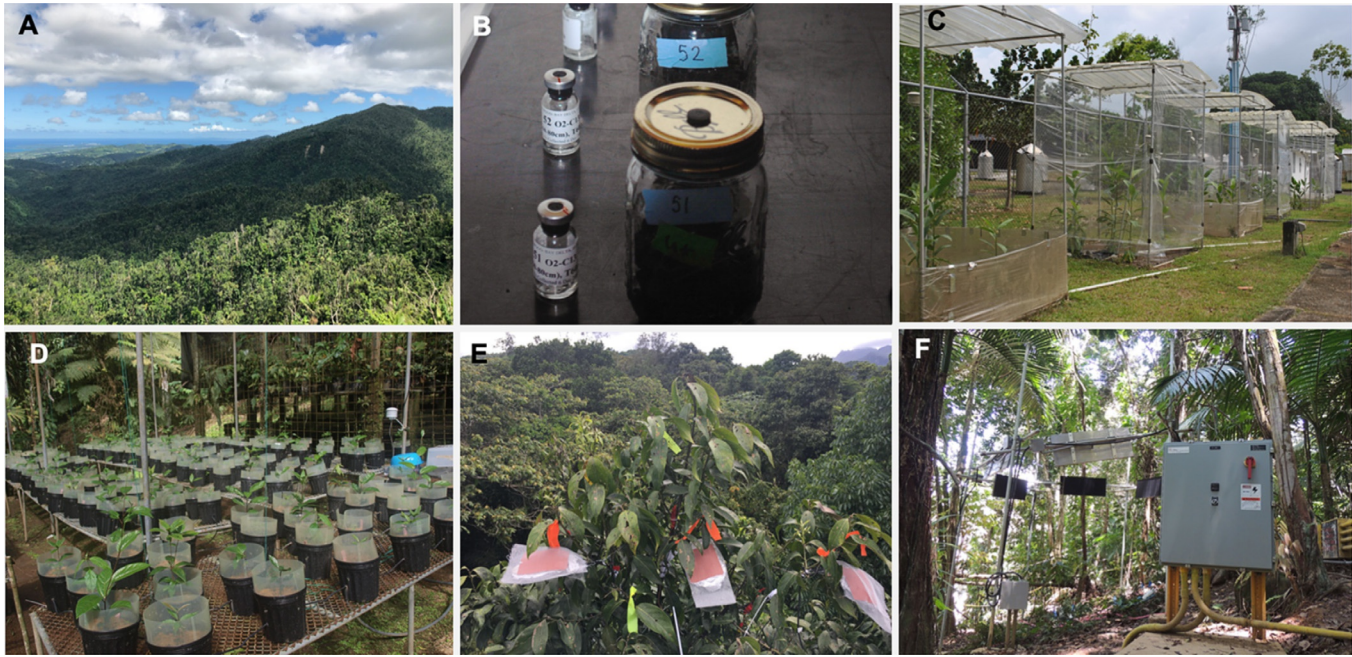
Fig. 1 Photographs of common methods used to study warming in tropical forested ecosystems. (A) Long-term monitoring and the use of natural gradients, such as the Luquillo Long-Term Ecological Research Program and the elevation gradient in the Luquillo Experimental Forest in Puerto Rico, United States. (B) Soil incubation experiment evaluating heterotrophic responses to controlled experimental conditions. (C) Growth chamber experiment in Gamboa, Panama. (D) Pot warming experiment in Las Cruces, Costa Rica. (E) Individual leaf warming experiment in the Luquillo Experimental Forest, Puerto Rico, United States. (F) Tropical Responses to Altered Climate Experiment (TRACE), a field warming experiment using infrared heaters in the Luquillo Experimental Forest, Puerto Rico, United States. Photographs (A), (B), and (F) by Tana E. Wood; (C) by Martijn Slot; (D) by Shafkat Kahn; and (E) by Kelsey Carter.

respiration was shown in lowland forest in Costa Rica (Schwendenmann and Veldkamp, 2006). Studies of atmospheric C dynamics have shown that interannual variation in the terrestrial C sink was most strongly related to nighttime temperatures, and probably associated with respiratory losses from tropical regions (Anderegg et al., 2015); and that warming (but possibly also drying) during the 2015–16 El Niño may have caused large respiratory C losses from tropical regions (Liu et al., 2017). The value of such long-term research is that we capture a wide range of natural variability, including more extreme events, which enables us to assess trends that may not be observable over the short term (Clark and Clark, 2011; Melillo et al., 2017). However, the temperatures predicted for lowland tropical systems in the future are typically warmer than the warm end of natural gradients. In addition, it is challenging to disentangle the multiple potential controls over responses across multiple gradients (e.g., factors other than temperature vary with elevation). While manipulations also have their challenges, complementary field-warming studies should greatly advance our understanding as they can provide mechanistic explanations for these observations to evaluate temperature regimes that currently do not exist (Cavaleri et al., 2015).

Elevation gradient studies are proven to be powerful tools for evaluating how long-term temperature differences affect ecosystem properties (Figs. 1A and 2; Sundqvist et al., 2013), such as ecosystem C storage (Selmants et al., 2014), C storage in coarse woody debris (Iwashita et al., 2013), plant productivity, litter decomposition, belowground C flux (Giardina et al., 2014), microbial community composition (Geml et al., 2017; Wagai et al., 2011), as well as plant community composition and processes (Girardin et al., 2014; Rapp et al., 2012). An important feature of elevation-based temperature studies is that each location along the elevational temperature gradient has been exposed to a warmer temperature than higher elevation sites for very long periods of time, and thus current observations integrate centuries to millennia of biotic adjustments. However, an important consideration when interpreting findings from elevation gradients is that other ecosystem properties including rainfall, geology, and vegetation can also vary with elevation/temperature (Körner, 2007), complicating or even confounding observed MAT patterns. Disentangling the effects of multiple covarying factors can limit inferences about any single factor, highlighting the value of constrained MAT gradients (Giardina et al., 2014). For example, the use of a highly constrained (i.e., consistent geology, vegetation, soil moisture, and disturbance history) elevation gradient in tropical forest in Hawai'i,
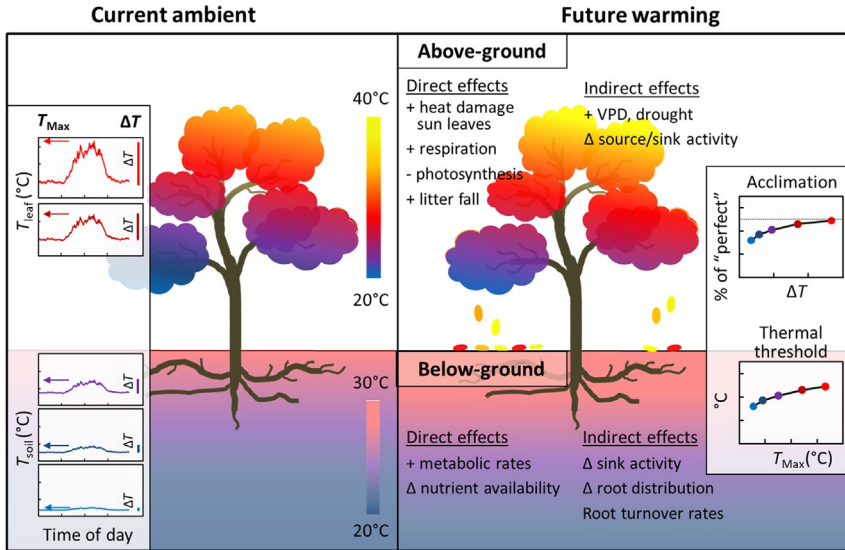
Fig. 2 Illustration of how the temperature of tropical vegetation can vary depending on where plants are assessed (i.e., forest stratum-dependent warming), as well as the direct and indirect effects of warming. Insets on the left-hand side of the figure illustrate current patterns in diurnal organ temperature ranges, highlighting the maximum amplitude (ΔT) and maximum temperature (T_{Max}). Insets on the right-hand side of the figure show how ΔT and T_{Max} may affect the acclimation potential and thermal thresholds under future warming conditions, respectively. The + signs indicate an increase in the direct or indirect effects and the Δ sign indicates a change that is expected, however, the direction of the change will depend upon other factors.

enabled scientists to demonstrate a long–term steady state in soil organic matter (SOM) turnover where warmer sites exhibited higher soil respiration rates (i.e., C loss) that were both driven and balanced by higher total belowground (root and mycorrhizal derived C) and aboveground (litter) C inputs, rather than by accelerated turnover resulting in a net loss of mineral associated organic matter (Giardina et al., 2014). While these approaches are especially valuable for investigating effects of warming on tropical montane ecosystems, this methodology is limited in its ability to evaluate responses of forests at the warm end of the temperature spectrum because projected climate regimes do not currently exist for these ecosystems (Cavaleri et al., 2015; Wood et al., 2012; Wright et al., 2009), or perhaps any ecosystem today (Williams and Jackson, 2007). Furthermore, new temperature regimes are likely to appear much more quickly than the evolutionary timescales that shaped these communities.

Laboratory incubation experiments (Holland et al., 1995) and organic matter transplant experiments across elevation gradients (Nottingham et al., 2015b; Zimmermann et al., 2009) have been used creatively to explore short-term responses (5 years or less) of soil processes to temperature (Fig. 1B). Incubation experiments have been used to evaluate respiratory and growth adaptation of the microbial community (Karhu et al., 2014), the temperature sensitivity of different soil C pools (Cusack et al., 2010), and warming-related changes in microbial community composition (Oliverio et al., 2017). Transplant experiments have been used to evaluate temperature responses of both respiration and decomposition (Zimmermann et al., 2010) to evaluate the potential for positive soil–climate feedbacks under future warming (Davidson and Janssens, 2006). Transplant experiments have also been used to evaluate the C quality-temperature prediction of kinetic theory (Craine et al. 2010) by comparing the temperature sensitivity of decomposition of different organic matter pools, such as SOM (Zimmermann et al., 2009), leaf litter (Salinas et al., 2011), and wood (Meier et al., 2010). Transplant experiments across elevation gradients have similarly been used to investigate adaptive responses among soil microbial communities. For example, soil translocation across an elevation gradient in montane forest in Costa Rica provided 10 months of +4°C warming, which resulted in increased soil enzyme activities and fungal richness under warmed conditions (Looby and Treseder, 2018). Soil translocation across an elevation gradient in Perú provided a 15°C temperature manipulation over a 5-year period, which shifted the relative abundance of microbial communities (Nottingham et al., Unpublished data) in a manner consistent with thermophilic responses shown across global ecosystems (Oliverio et al., 2017). While these experiments provide invaluable insight into mechanistic controls of temperature on soil processes, they are not without experimental artifacts. For example, soil removal can break up soil aggregates and increase exposure of soils to air, the role of roots and other plant–soil feedbacks that are known to affect soil and microbial processes are not considered, and soil incubations are often necessarily short term in nature (Reed et al., 2012). In summary, laboratory incubation and organic matter transplant studies provide valuable insight into short-term warming (5 years or less) on the tropical C cycle and biotic communities, but provide limited information on medium-term (e.g., decadal) responses of biotic communities, such as plants and associated changes in aboveground C inputs to soil.

Tropical plant responses to warming have been investigated through the study of natural temperature gradients and responses to climatic variation (Clark, 2004; Clark et al., 2010, 2013; Doughty and Goulden, 2008), growth chamber experiments with seedlings or small trees (Fig. 1C and D;

Cheesman and Winter, 2013; Slot and Winter, 2016, 2017a), and leaf and branch-scale temperature manipulation experiments in tree canopies (Fig. 1E; Doughty, 2011; Slot et al., 2014a). This research has focused on the capacity of plants to acclimate to warming, a process that can include physiological, morphological, or biochemical adjustments that occur within the lifetime of individuals. Plant growth chamber experiments offer great control over environmental conditions, reasonable replication, and are generally appropriate to address mechanistic questions about temperature effects on seedling growth and physiology. For example, Cheesman and Winter (2013) used a growth chamber study to show that nighttime warming stimulated growth in seedlings of two early-successional tropical tree species, Slot and Winter (2017a) demonstrated photosynthetic acclimation to growth temperatures, and Scafaro et al. (2017) showed that thermal acclimation of photosynthesis in temperate and tropical species was underpinned by changes in leaf Rubisco content. It is unlikely, however, that quantitative results obtained on potted seedlings grown in growth chambers translate to mature forest trees (e.g., Slot et al., 2016). More realistic (but less controlled) scenarios can be simulated in field-warming experiments in the form of seedling mesocosms grown directly in the soil using passively or actively warmed chambers (e.g., Slot and Winter, 2018), or in the form of targeted leaf or branch warming in the tree canopy (Cavaleri et al., 2015; Doughty, 2011; Slot et al., 2014a). Medhurst et al. (2006) described sophisticated whole-tree chambers that have been used to manipulate aboveground CO_2 and temperature conditions in boreal (northern Sweden) and subtropical (southeastern Australia) conditions, but to date, these chambers have not been implemented in the tropics. Given the importance of big trees for forest C storage and dynamics (Lutz et al., 2018), studying the temperature response of canopy branches and leaves is particularly relevant. Ideally the whole plant would experience experimental conditions to avoid the treatment causing imbalances, for example in *source-sink relations*, which in turn would affect plant growth response. Furthermore, for this volume we found no tropical examination of warming effects on plant reproductive efforts for the tropics (see Chapter 3). Biosphere 2 in Arizona, and the Eden Project in Cornwell both contain pockets of tropical forest vegetation (Prance, 2002; Van Haren et al., 2005). Despite the artificial conditions of these tropical "forests" in temperate climates, the whole-plant warming capabilities of the set up may offer valuable insights if applied to investigate temperature responses in tropical forest.

In summary, all approaches to warming have benefits and drawbacks, and the suite of warming options are best used in combination. Warming approaches have revealed both strong temperature responses of C cyling in the short term (days to weeks) and a steady state or adaptation of C cycling to temperature differences in the very long term (centuries to millenia). Incubation experiments reveal high temperature sensitivity of soil C decomposition (e.g., Holland et al. 1995) and adaptation or acclimation responses of soil microbial communities and plants (Bradford et al., 2010; Cheesman and Winter, 2013), while elevation gradient studies reveal a long-term look at C dynamics for plant and soil processes (e.g., Giardina et al., 2014). However, without field-warming experiments in tropical forested ecosystems, these studies are limited in their ability to address how results align with whole ecosystem responses to the rapid and novel warming predicted over periods of years to decades. This is true not only for tropical forested ecosystems, but even in better studied higher latitudes given constraints on whole forest warming (Cavaleri et al., 2015). Recent methodological advances enabling warming of the tropical forest understory (Fig. 1F; Kimball et al., 2018) and soil profiles (Hanson et al., 2011; Kimball et al., 2018) provide valuable tools to address this knowledge gap, particularly when combined with modeling experiments that enable integration of responses across a wide range of temporal and spatial scales (Cavaleri et al., 2015; Luo et al., 2011; Norby and Luo, 2004).

Tropical soil responses to warming

Soils contain the largest stock of detrital C in the terrestrial biosphere, exceeding by a factor of three the C contained in the atmosphere (Jobbagy and Jackson, 2000). Despite suggestions of slow turnover of soil C (e.g., mean residence time for SOC ≈ 100s of years), even relatively small proportional increases in the decomposition of this enormous C pool could transform soils from a net sink of atmospheric CO_2 to a net source if losses are not balanced by additional inputs from aboveground vegetation (Cox et al., 2000; Holland et al., 2000). Terrestrial biogeochemical models predict that where moisture is available, C decomposition rates in mineral soils increase exponentially with temperature (*kinetic theory*; Bradford et al., 2008; Conant et al., 2008; Davidson and Janssens, 2006; Schimel et al., 1994). At the same time, nutrient cycling is expected to change in response to changes in climate (e.g., Yuan et al., 2017), which could affect the fate of soil C (e.g., Cleveland and Townsend, 2006) and constrain aboveground

productivity (e.g., Elser et al., 2007). Accordingly, understanding the temperature response of soil C processes, including soil C formation and decomposition, as well as nutrient cycling, will be important for determining whether tropical forests are sources or sinks of atmospheric CO_2 in a warmer world.

Warming can exert long-term (millennial) influences on soils, resulting in distinct *physicochemical* characteristics. For example, warm climate soils often contain clay minerals that are structurally simpler and have lower charge densities and cation exchange capacities than cool climate soils (e.g., kaolinite or iron and aluminum oxides vs smectites or vermiculite; Birkeland, 1984). Similarly, pedologically older, more crystalline subsurface soils may be less effective at protecting C from decomposition than young, less crystalline subsurface soils (Torn et al., 1997). Conversely, temperature may negatively influence soil C quality (Amelung et al., 1998, 1999; Dalias et al., 2001), such that soil C is more stable in warm than cool climates (Fissore et al. 2008, 2009). However, in the near future (decades to centuries), warming can be expected to exert only very small influences on the physical properties of soil or on clay mineralogy. As such, this section focuses on soil processes that are likely to respond to temperature on shorter timescales. We will first discuss temperature effects on soil organic carbon (SOC) and nutrient cycling, followed by a review of temperature effects on microbial communities. We will end this section by exploring the potential for integrative effects of temperature on plant-soil feedbacks.

Soil organic carbon

Because tropical forests and grasslands store substantial amounts of soil C, by some estimates more than 40% of Earth's soil C (Jobbagy and Jackson, 2000), the lack of detailed information for tropical SOC responses represents a critical source of uncertainty in forecasting the future C balance of the terrestrial biosphere (Bradford et al., 2016). Classic expectations suggest a strong sensitivity of mineral soil C to temperature, but recent work has yielded conflicting findings—that longer term responses of soil C decomposition to warming may differ substantially from the well-studied short-term response (Conant et al., 2011), including that of tropical soils (Bird et al., 1996; Giardina et al., 2014; Trumbore et al., 1996). Reconciling these contrasting findings is critical to accurately modeling climate change effects on C storage in tropical ecosystems (Bradford et al., 2016). However, widely varying methods for examining soil C decomposition and a poor

understanding of the factors that control soil C decomposition, and especially formation rates, constrain confidence in model predictions (Bailey et al., 2018; Coleman et al., 2004). Taken together, tropical forest studies demonstrate high vulnerability of SOM stocks to short-term warming (Salinas et al., 2011; Zimmermann et al., 2009) but reveal longer term temperature acclimation responses in organic matter dynamics (Bird et al., 1996; Giardina et al., 2014; Nottingham et al., 2016b). Long-running in situ manipulative warming experiments, especially where whole ecosystems can be heated, would provide critical insights into whether acclimation of SOM dynamics will occur as climate warming increases temperatures across the tropics.

Although the temperature sensitivity of various C pools has rarely been quantified in tropical forests, despite being generally a large fraction of terrestrial totals (Jobbagy and Jackson, 2000; Pan et al., 2011), their exposure to high MATs is assumed to result in smaller turnover responses (i.e., lower sensitivity) to warming compared with responses documented in high-latitude warming experiments (Romero-Olivares et al., 2017; Wilson et al., 2016). This temperature sensitivity prediction is based on *thermodynamics* and the *kinetic theory* of chemical reactions, whereby the sensitivity of respiration rates to a given temperature increase ("Q_{10} value," where $Q_{10} = 2$ describes a doubling of reaction rates with a 10-degree temperature increase in the Celsius or Kelvin scales) is greater for colder temperatures (Davidson and Janssens, 2006). Although many soil-warming experiments support this prediction, there are several reasons why the long-term effects of warming in tropical forest soils could be significant. First, C turnover time in soils and vegetation of low-latitude ecosystems is substantially faster than that of higher latitude ecosystems (mean of 15 vs 255 years, respectively; Carvalhais et al., 2014), such that even small changes in rate could result in substantial increases in the magnitude of C cycled. Furthermore, the higher biodiversity and abundance of plant-microbial associations in tropical forests (LaManna et al., 2017) may result in large variations in the warming effects among species, with associated community composition changes. Because species can vary in the organic C of their soil footprints (e.g., Reed et al., 2008), changes to community composition could alter C dynamics in unpredictable ways.

While much work needs to be accomplished in the tropics to secure an understanding of tropical SOC response to warming temperatures, the evidence we do have provides insight into potential responses. For example, a range of soil incubation experiments show that microbial respiration of SOC

increases exponentially with temperature up to a maximum, and that warming will likely initially enhance decomposition rates and microbial CO_2 release from tropical soils (Cusack et al., 2010; Holland et al., 2000). But, changes to microbial biomass would also affect the overall exchange between soil microbes and the atmosphere, and some studies suggest significant declines in soil microbial biomass with warming, which could reduce SOC decomposition and ultimately slow the loss of SOC from these systems (e.g., Frey et al., 2008; Joergensen et al., 1990). Furthermore, warming-stimulated increases in soil CO_2 emissions may also be constrained if warming results in significant soil drying, in which case responses would be dependent on interactions between temperature and soil moisture (Machmuller et al., 2018; Wood et al., 2013). The extent to which soil CO_2 emissions increase under warming will also depend on changes in substrate supply (e.g., plant production), which has a strong influence on the temperature sensitivity of decomposition (Fissore et al., 2013), soil CO_2 efflux (Giardina et al., 2014), and soil microbial community composition (Nemergut et al., 2010). Longer term shifts in substrate supply and communities could also constrain warming-induced increases in SOM decomposition, with initial increases driven by warming disappearing as time passes (e.g., Bradford, 2013). Thus the effects of increasing temperature on community structure, biomass, and activity of microorganisms, along with effects on moisture and substrate supply, will interact to determine the overall changes to tropical forest C cycling, and will have effects that vary over temporal scales.

Comparing soils across a latitudinal gradient, Bird et al. (1996) used ^{14}C methods to interpret elevated ^{13}C:^{12}C ratios in high-latitude soils compared with tropical and temperate soils. They hypothesized that higher ^{13}C:^{12}C ratios in high-latitude soils represented: (1) temperature effects on photosynthesis; (2) isotopic discrimination relating to vegetation type; or (3) slower incorporation rates of ^{13}C-depleted CO_2 into soil. To test this third hypothesis, Bird et al. (1996) used bomb ^{14}C dating to estimate C residence time in the 63–500-μm fraction of soils with depths of 0–2 cm, which they determined to contain the most labile C in soil. The ^{14}C-based residence time in soil did not differ between temperate and tropical forest soils (<5 years for both). However, Trumbore et al. (1996) also used radiocarbon analyses of recent and archived soil samples to examine the residence time of C fractions in soil from temperate and tropical sites. In contrast to Bird et al. (1996), they found a strong exponential relationship between turnover time of labile soil C and MAT. One explanation for the discrepancy may be

that Trumbore et al. (1996) compared sites where disturbance generally increased with MAT, whereas Bird et al. (1996) compared only undisturbed forests. In line with results from Bird et al. (1996) and Trumbore et al. (1996) for acid-insoluble SOC, Giardina et al. (2014) found that ^{14}C-based estimates of SOC turnover did not vary with MAT for any SOC fraction or depth. They did find that mineralogy exerted a strong influence over turnover time, confirming previous findings of the important role played by mineralogy in SOC turnover (Torn et al., 1997).

The longer term response of decomposition and microbial respiration rates to warming are dependent on "adaptive" changes in microbial communities and function, often summarized by changes in *microbial growth efficiency*. Microbial growth efficiency is broadly defined as the proportion of C from the environment that is used for growth relative to respiration. Over a period of years to decades, warming can increase microbial growth efficiency, as found in a temperate forest soil warmed by 5°C for 18–26 years (Frey et al., 2013; Melillo et al., 2017). Temperature adaptation of microbial metabolism is also suggested by studies of the thermal optima for bacterial growth in higher latitude ecosystems, which tracked MAT across a latitudinal gradient (Rinnan et al., 2009) and shifted in response to artificial warming in the laboratory (Bárcenas-Moreno et al., 2009; Birgander et al., 2013) and in the field (Rousk et al., 2012). These adaptive changes in microbial growth efficiency or in the thermal optima for growth, can be explained by temperature adaptive changes in microbial community composition and enzyme function (Allison, 2014; Wieder et al., 2013), which, together, attenuate the total C loss that might otherwise be predicted with warming.

In tropical forests, largely due to a lack of experimentation, evidence for near-term temperature adaptation of soil microbial C cycling remains scarce, although elevation gradient studies provide examples of long-term adaptation. For example, temperature has been found to affect soil microbial community composition (Geml et al., 2014; Nottingham et al., 2016a; Wagai et al., 2011), enzyme function (Nottingham et al., 2016b), and microbial substrate use (Whitaker et al., 2014) across a range of elevation gradient studies in tropical forests, which together can partly explain observations of SOC equilibrium for a constrained elevation gradient in Hawai'i (Giardina et al., 2014). Shifts in microbial community composition in the latter study were smaller than in multiforest studies (Selmants et al., 2016), which may explain the equilibration of SOC across the elevation and temperature gradient. While relatively scarce, short-term data do provide important insight into microbial controls over tropical SOC in a warmer world. In a short-term (90-day) incubation study

of microbial respiration temperature adaptation in global soils, the three tropical forest soils included in the study did not respond in a manner consistent with "adaptation" (Karhu et al., 2014). In this same study, respiratory adaptation was related to nutrient stoichiometry, suggesting a role for substrate availability in modulating selection pressure and temperature adaptation. In tropical forest soils this may be manifested by P constraints to metabolism of labile C inputs or nitrogen (N) to stable SOM (Cleveland and Townsend, 2006; Nottingham et al., 2015b); where the availability of these nutrients differ widely among soil types (Quesada et al., 2010) and among montane and lowland soils (Nottingham et al., 2015a). The role for adaptive responses in microbial communities and function in constraining long-term C loss under warming in the tropics will depend on whether these adaptive responses can keep pace with the rate of warming during this century and beyond.

Most studies focus primarily on surface soils (e.g., depths of 0–10 cm), regardless of ecosystem. However, tropical soils can be many meters deep, and may store as much, or more, soil C between depths of 20–100 cm as in the top 20 cm (Jobbagy and Jackson, 2000). Thus the response of these deeper soils to warming could have significant consequences for predicting the effects of warming on ecosystem C balance in response to a warming climate. In general, the soil depth profile contains a strong gradient in resource availability, microbial diversity (Stone et al., 2014), and climatic conditions (Schwendenmann and Veldkamp, 2006) with more variability at the surface in terms of microclimate, the types and concentrations of C substrate (e.g., root exudates, litter from roots and leaves, and microbial by-products), and soil biota (e.g., a relatively high proportion of fungi and soil animals at the surface) which allow for more microbial niches and possibly greater metabolic diversity and efficiency (Fierer et al., 2003; Torn et al., 1997). But below the dominant rooting zone (~20 cm), the soil environment changes considerably. The climate is more stable with low variation in moisture and temperature, the pools of C and nutrients converge in composition (Coleman et al., 2004; Fierer et al., 2009), and the concentrations of C and nutrients, as well as microbial biomass, decline exponentially (Stone et al., 2014). The expectation is therefore that processes such as SOC stabilization and destabilization are likely primarily controlled by biotic factors, such as plant litter inputs and microbial metabolism in surface soils, and that these biotic controls are less influential with depth due to reduced C inputs and more sparse microbial density (Torn et al., 1997). If true, this would allow for factors such as mineral composition and reactive mineral surfaces to dominate biogeochemical cycling at depth.

Given that the simpler, more decomposable C tends to be concentrated in the surface soils with a larger proportion of harder to decompose C molecules in deeper soils, warming could result in a proportionally larger rate of C loss from the deeper soils via respiration, particularly from the more complex C pools, by pushing these compounds closer to the required activation energy (i.e., *carbon-quality-temperature hypothesis*). However, emerging research from higher latitude field-warming experiments suggests that, while warming does increase CO_2 production along the entire soil profile, the C respired is primarily from the decomposition of surface-derived, modern photosynthate that is only decades old, and not the old, deep C (Hicks Pries et al., 2017; Wilson et al., 2016). Thus research that investigates temperature responses of the whole soil profile is needed to fully assess the vulnerability of soil C to increased loss under warmed conditions.

Nutrient cycling

Nutrient cycling appears to be strongly affected by warming temperatures, at least for higher latitude soils (Rustad et al., 2001), and these effects are influenced by soil and ecosystem type, as well as by the mechanism through which warming occurred (Yuan et al., 2017). In a recent synthesis of artificial warming studies in temperate and boreal regions, Bai et al. (2013) reported large increases in N process rates with warming. In a tropical mesocosm study, Liu et al. (2017) reported that a few degrees of warming strongly increased both N mineralization rates and the amount of available phosphorus (P) that could be extracted from soils. Across the MAT gradient studied by Giardina et al. (2014) and Pierre et al. (2017) found that soil nitrate availability increased strongly with rising MAT, and the increase was correlated with an increase in ammonia oxidizer activity. Importantly, there is precious little known about how warming alters elements other than N and P, with no information on how warming affects their cycling in the tropics. This is particularly relevant given that trace elements such as molybdenum (Mo) may at least colimit rates of biological N_2 fixation in tropical forest ecosystems (Barron et al., 2008; Reed et al., 2013; Wurzburger et al., 2012) and that elements such as potassium (K) may be important to multiple aspects of function in some tropical forests (Kaspari et al., 2007; Kaspari and Powers, 2016; Wright et al., 2011, 2018).

Overall, data suggest that warming has significant potential to affect the cycling of N and P, which, in turn, could have strong indirect effects on ecosystem C process rates and storage. For example, a controlled soil

incubation experiment evaluating interacting effects of long-term N fertilization and increased temperature in two tropical forest soils found that the sensitivity of more slowly decomposing C pools to temperature increased with N fertilization (Cusack et al., 2010). In addition, soil P concentrations, as well as foliar P per unit area, were key explanatory factors for models of area-based V_{cmax} and $\mathcal{J}_{max}$ of photosynthesis in Andean and Amazonian moist tropical forest species (Bahar et al., 2016), highlighting how nutrients can create feedbacks to C cycling. Indeed, nutrient availability plays an important role in all terrestrial ecosystems (e.g., Elser et al. 2007), but has been suggested to potentially represent a larger control in tropical ecosystems where soil moisture and temperature are more favorable to biotic activity (Townsend et al., 2011). An improved understanding of the effects of temperature on nutrient cycles, and, in turn, the effects of temperature-induced changes to nutrient cycling on tropical forest C processes (i.e., plant growth and soil respiration), would represent an important advance in our capacity to forecast future tropical forest function and feedbacks to climate.

Microbial community

Across biomes, tropical forests contain the highest biomass of soil microorganisms of any terrestrial ecosystem type ($2–2.5\,PgC\,ha^{-1}$), a nontrivial amount relative even to the high aboveground biomass found in tropical forests ($140–197\,PgC\,ha^{-1}$) (Sullivan et al., 2017). This large microbial biomass exerts a major influence over ecosystem functioning by regulating biogeochemical cycles (Bouskill et al., 2016; Cleveland and Townsend, 2006; Pett-Ridge et al., 2013; Reed et al., 2007) and affecting plant production through plant-microbial associations (Fierer, 2017). An improved understanding of the effects of warming on the composition, structure, and activity of tropical soil microorganisms is therefore critical to understanding how warming-induced changes to microbial communities create feedbacks to biogeochemical cycles, plant-microbial symbioses, and the host of plant-microbe interactions that help determine plant community composition, structure, and function. Indeed, such shifts in enzymatic function and microbial community composition with temperature have been suggested to underpin long-term adaptive microbial growth responses under climate warming (Bradford, 2013). However, attaining an understanding of the relationship between temperature and tropical forest soil communities for such a diverse and dynamic range of tropical ecosystems has proven challenging.

Soil incubation experiments have found, when there was a sufficient supply of C, that microbial respiration can occur at temperatures at least as high as 55°C (Holland et al., 1995, 2000), and that when substrate is controlled, tropical forest microbial communities have higher thermal optima than their cooler climate counterparts (Balser and Wixon, 2009; however, see Liu et al., 2018). These results lead to important questions about microbial community composition under warmed conditions, including the role of thermophiles. A more recent study of the temperature response of microbial taxa across global ecosystems found that the proportion of microbial taxa that increased their relative abundance in response to warming (to 28°C) was higher for systems with higher MAT (Oliverio et al., 2017). This finding suggests that lowland tropical species have a high capacity to withstand, and perhaps even thrive under, small temperature increases. The results also supports the hypothesis that warm tropical environments contain a greater proportion of thermophiles (e.g., Balser and Wixon, 2009). Of course, soils exposed to such incubation have variations other than MAT and typically include just the top 5 or 10 cm of soil. These artifacts constrain our ability to know what factors drive observed responses (e.g., is it microbe physiology, community composition, or soil resource availability?) and do not address the consequences of warming for very deep soils that are common to lowland tropical forests and that contain large amounts of total C (see "Soil organic carbon" section above).

Temperature effects on C allocation below ground, soil moisture regimes, and soil nutrient cycling could also indirectly affect soil microbial community composition, and thus function. For example, elevated temperatures could affect plant photosynthesis (Mau et al., 2018; Slot and Winter, 2017a; Wood et al., 2012) and the quantity and quality of C allocated below ground (Giardina et al., 2014). Such changes to C inputs could significantly affect the soil microbial community; as demonstrated for a temperature gradient in Perú where microbial community composition was the main determinant of the rate at which different C substrates were metabolized and respired (Whitaker et al., 2014). Incubation studies show that labile C inputs can rapidly alter microbial community composition in tropical forest soils and that these shifts in community cooccur with large soil respiration losses (Cleveland et al., 2007). A field litter manipulation experiment at the same forests site where incubation soils were collected supported the idea that changes to plant inputs of C greatly affect tropical forest soil microbial community composition (Nemergut et al., 2010) and the fate of SOC (Leff et al., 2012). In this way, temperature effects on C cycling could alter

microbial communities and thus enact further changes to the tropical forest C cycle. Interactions between the direct and indirect effects of temperature on microbial communities will be complicated but important to decipher.

As discussed above, warming could also affect the cycling and availability of nutrients, such as N and P, and changes to these nutrients could in turn affect tropical soil microbial function (Cleveland and Townsend, 2006; Cusack et al., 2010; Nottingham et al., 2015a; Reed et al., 2011; Wood and Silver, 2012). For example, data from tropical forests suggest that changes to nutrient availability (via fertilization) greatly affect leaf litter and soil N_2 fixation via changes to the free-living N_2 fixer community composition and abundance (e.g., Reed et al., 2010). Thus warming-induced changes in nutrient cycling could have significant effects on how new inputs of N enter these systems. We know microbes are engines that help drive function in tropical forests and that the composition of microbial communities determines their function and response to change (e.g., Balser and Wixon, 2009; Bouskill et al., 2013); nevertheless, our lack of mechanistic understanding regarding the ways warming will affect soil microbial communities remains a critical unknown.

Plant-soil feedbacks

Increased temperature could indirectly affect tropical forest ecosystem dynamics via effects on plant and soil interactions (Wood et al., 2012), whereby plants change soil properties, which, in turn, influence plant performance, or vice versa. These "plant-soil feedbacks" can arise through interactions within a single plant species (direct or conspecific plant-soil feedback) or among species (indirect or heterospecific plant-soil feedback). The mechanisms by which they occur are wide ranging, including the biotic and abiotic effects of roots and leaf litter on soil chemistry and the soil microbiome, especially pathogenic or mutualistic plant symbionts (Van der Putten et al., 2013).

In tropical forests, *conspecific negative density dependence* has long been hypothesized to promote diversity (Connell, 1978; Janzen, 1970) and a number of recent studies (e.g., LaManna et al., 2017; Miao et al., 2018; Zhu et al., 2018) suggest that negative plant-soil feedbacks, the negative effect of soil microbial community on the growth or survivorship of plant species, is the key driver behind this effect. Indeed, in a recent global-scale analysis, tropical forest plant diversity appears to be more strongly promoted, at least in part, by conspecific negative density-dependent feedbacks between plants and their natural enemies than temperate forest species

(LaManna et al., 2017), with a portion of this feedback likely to be driven by microbial interactions. For example, seed–infecting fungi reduce seed viability (Sarmiento et al., 2017)—the strength of this effect varies with distance from conspecific fungal host individuals. Furthermore, at the seed stage, the soil–borne fungal community seems to be strongly influenced by the species identity of seeds, suggesting that pathogenic fungal species exhibit specificity in host species seeds (Sarmiento et al., 2017). The presence of microbial feedbacks on plant function, especially for rare species (LaManna et al., 2017), may explain broader relationships between the structure of tropical forest plant and microbial communities (Barberán et al., 2015). With projected increases in temperature, expected rise in activity and abundance of soil pathogenic fungi (Bragazza et al., 2013), coupled with potential decreases in activity of mycorrhizal fungi (Mohan et al., 2014), may alter plant–soil feedbacks (van der Putten et al., 2016), with the potential to change tropical plant community composition.

Soil fungal pathogens increase plant diversity during the seed-to-seedling transition by selectively increasing the mortality of different plant species thus affecting the relative abundance of different species (Bagchi et al., 2014). Tree seedlings grown in soil inocula from *conspecific* seedlings in a shade house, as well as near conspecifics in the forest, have reduced growth compared with seedlings grown in the soil inocula of heterospecific seedlings and near heterospecifics in the forest (Mangan et al., 2010). Indeed, the strength of negative density dependence is higher in tropical forests than in temperate forests, contributing to the high diversity of plants in tropical forests and the maintenance of populations of rare species (LaManna et al., 2017).

Emerging evidence suggests that climatic perturbations will influence plant-soil feedbacks with broad consequences for ecosystem dynamics (van der Putten et al., 2016). In tropical forests, the long-term effects of temperature on plant-soil feedbacks can be explored by examining changes in symbiotic plant and microbial associations and soil nutrients along elevation gradients. Plant production in higher elevation tropical forest is thought to be more N limited (Tanner et al., 1998), in contrast to stronger P or K limitation in lowland tropical forest (Nottingham et al., 2015a). These differences in nutrient constraints are reflected in differences in plant–microbial associations. In warmer, lowland tropics, arbuscular mycorrhizae and associated plant species are more abundant, a mycorrhizal association known to improve plant P acquisition in P-poor environments (Geml et al., 2017). In contrast, tropical montane and cloud forests are more abundant in ectomycorrhizae and ericoid mycorrhizae-associated plant species. In contrast to

tropical lowlands, ectomycorrhizae and associated plant species become more prominent with elevation and reach a peak around 2000 m, while ericoid mycorrhizae are common between 1500 and 3000 m (Geml et al., 2017). With changes of these fungal functional groups along elevation gradients, ectomycorrhizal-associated tree species (such as *Quercus* in the new world, and *Castanopsis* and *Lithocarpus* in the old world, all in the Fagaceae family) attain a high proportion of the stand biomass in mid- to high-elevation tropical forests (Culmsee et al., 2010). The dominance of these tree species at mid to high elevations in the tropics is partly due to soil N economy facilitated by their ectomycorrhizal partner (Corrales et al., 2016). Ectomycorrhizae are able to mine ammonium as well as organic N from the soil, which likely confers a competitive advantage to its symbiotic plant partner inhabiting N-limited environments, like tropical mountains (Smith and Read, 2010). Climate warming, especially soil warming, may increase available soil N and alters the C–N balance in the soil (Melillo et al., 2011; see "Nutrient cycling" section). Consequently, with climate change, compositional changes in mid- to high-elevation tropical forests may be mediated by responses of root fungal associates and resulting competitive advantages to the symbiotic partner plant species (Mohan et al., 2014).

Evidence from extratropical regions suggest that plant-soil feedbacks will be affected by changes in precipitation, drought, temperature, and other climatic variables (van der Putten et al., 2016). Mycorrhizal colonization and abundance also change with increased temperatures, although the direction of these changes depends on the context (Mohan et al., 2014). Artificial soil warming of subtropical soils in a replicated mesocosm experiment showed that warming resulted in increases in P availability, extractable nitrate and fine-root N content, as well as soil CO_2 efflux (soil respiration), suggesting that warming in tropical soils can lead to elevated processes that point to plant-soil feedbacks (Liu et al., 2017). Despite the important role plant-soil feedbacks play in tropical forest diversity and function, a lack of studies in tropical ecosystems examining the effects of global change on plant-soil feedbacks inhibits our ability to understand and forecast how tropical forests will change because of climate change-mediated plant-soil feedbacks (Wood et al., 2012).

Warming effects on tropical vegetation

Warming can have strong direct and indirect effects on plant physiology as well as growth, reproduction, and survival (demography). Direct effects include changes in net photosynthesis, stimulation of respiration rates,

and at very high temperatures, protein denaturation and subsequent leaf or even plant death. Indirect effects include responses to increased vapor pressure deficit (VPD), associated with higher temperatures; responses to changes in nutrients available to plants; and in the long-term, shifts in community composition toward more heat and/or drought tolerant species. When specifically considering soil warming, the focus of this book, plant performance may also be affected by changes in the *source-sink relationship* within the plant. Tropical forests have been hypothesized to be sink limited (Körner, 2003, 2009), suggesting that stimulation of sink activity should increase growth. Soil warming may also stimulate plant growth by increasing nutrients available to plants through stimulation of the activity of nutrient-mineralizing soil microbes (Rustad et al., 2001). Increasing soil temperature indeed stimulates the growth of cotton *Gossypium hirsutum* (Königer and Winter, 1993) and a tropical tree species *Ochroma pyramidale* Cav. ex Lam. (Slot and Winter, unpublished data). Interestingly, the growth stimulation observed in *O. pyramidale* was similar in magnitude to the growth stimulation achieved by application of fertilizer, suggesting the important role of nutrient availability in regulating plant growth responses. Unfortunately, soil–warming experiments with tropical species are very rare (see section entitled "Methods of measuring changing temperature effects in the tropics"), and to our knowledge there are no published studies addressing plant reproductive responses to warming manipulations in the tropics (see Chapter 3). Accordingly, here we will discuss the effects of temperature in general on tropical vegetation, making use of data from experiments, elevation gradients, tree-ring analysis, and long-term monitoring.

The effects that warming has on plants depends on the timescale over which plants are evaluated. In the absence of strong temperature seasonality, it has been suggested that tropical species may not have experienced the selective pressures that would favor the evolution of the kind of plasticity required to adjust to rising temperatures (*mountain pass hypothesis*; e.g., Janzen, 1967). Consistent with this, two metaanalyses of growth experiments using pot studies with experimental temperature manipulation concluded that while warming generally stimulated woody plant growth, it had a negative effect in the tropics (Way and Oren, 2010; Lin et al., 2010). Negative effects of nighttime warming on tropical tree growth are further suggested by long-term monitoring of tree diameter growth in a lowland tropical forest in Costa Rica, and tree-ring studies from other tropical forests (Clark, 2004; Clark et al., 2010, 2013; Vlam et al., 2014). However, diurnal temperature variation experienced by tropical plants can be substantial

(see "Diversity of tropical ecosystems" section; Rey-Sánchez et al., 2016), so it is perhaps not surprising that photosynthesis and respiration of tropical species have the capacity to acclimate in response to experimental warming (Cheesman and Winter, 2013; Slot et al., 2014a; Slot and Winter, 2017a, b, 2018). Nonetheless, not all species acclimate to the same extent (Campbell et al., 2007; Cheesman and Winter, 2013; Reich et al., 2016; Slot and Kitajima, 2015), possibly in relation to the functional groups species belong to (see "Photosynthesis" section), and possibly in relation to their predominant thermal environment (Shaver et al., 2000). Tropical forest canopies experience a steep vertical temperature gradient, both in terms of maximum temperatures experienced by the organs and maximum daily temperature amplitude (Fig. 2), and this may have consequences for the tolerance of vegetation to increased temperature. Whereas upper canopy vegetation that experiences a 20°C diel temperature range is likely to be capable of adjusting to moderate warming, such plasticity might not be present in understory vegetation or roots (Fig. 2). Similarly, upper thermal thresholds—for example, the temperature at which photosystem II functionality is reduced by 50%—are moderately higher for tissues that routinely experience high temperatures (Slot et al., 2018).

We will first discuss organ-level processes of photosynthesis and respiration before scaling up and looking at demography. We will end this section with a review of the temperature effects on stand- or ecosystem-level processes by looking at NPP.

Photosynthesis

Experimental manipulations investigating short- and long-term temperature responses of tropical seedlings, saplings, and mature trees have yielded important patterns and mechanistic relationships across biome type, successional status, leaf developmental stage, and leaf functional traits. Tropical plants differ biochemically from temperate species in a number of ways. For example, a comparison of tropical and temperate Australian seedlings found optimal temperatures for photosynthesis T_{opt} to be ∼4°C greater than for temperate species; however, the temperate species maintained high photosynthetic rates over wider temperature ranges. Similarly, a comparison of T_{opt} for the photosynthesis of canopy foliage of temperate and tropical forest trees found T_{opt} of photosynthesis of tropical trees to be ∼3°C greater than that of the temperate trees; however, maximum daily leaf temperatures in the tropical forest are already exceeding T_{opt} of these trees (Mau et al.,

2018). These results suggest a more limited capacity of tropical species to acclimate to changing growth temperatures, compared with temperate species. Consistent with this, Slot and Winter (2017a) found photosynthetic temperature response curves to narrow with increasing growth temperatures, concluding that, while tropical species may be able to acclimate to some degree, total C gain is likely to decrease with continued warming. Furthermore, late-successional species appear to be more sensitive to warming than pioneers (Cheesman and Winter, 2013; Slot et al., 2016; Vårhammar et al., 2015). For example, working on seedlings in Rwanda, Vårhammar et al. (2015) found that T_{opt} values of late-successional montane species exceeded more often, and to a greater degree, values of pioneer species, suggesting that the native late-successional species were less able to acclimate to a warming climate. In contrast, in the upper canopy of two tropical forests in Panama, T_{opt} of mature trees and lianas converged on mean daytime temperature among all species, regardless of functional group (Slot and Winter, 2017b). Leaf developmental stage is another important variable with respect to photosynthetic temperature response, and evidence points to a greater acclimation potential of newly formed tropical leaves versus preexisting leaves when subjected to warming treatments (Cheesman and Winter, 2013). An emerging trend is the ability of smaller leaves, with higher transpiration rates, to better thermoregulate (Cheesman and Winter, 2013; Fauset et al., 2018; Michaletz et al., 2016; Vårhammar et al., 2015), revealing a gradient, whereby smaller leaves with higher transpiration rates are able to maintain leaf temperatures closer to ambient air temperature at the expense of greater water loss, while larger leaves with thicker boundary layers and therefore lower transpiration rates may be less efficient thermoregulators, potentially requiring greater biochemical resilience to higher temperatures.

Partitioning net photosynthesis into component processes can yield insight into the mechanistic underpinnings of both short-term photosynthetic responses to temperature and longer term acclimation potential. Net photosynthetic temperature response is determined by the component most vulnerable to increasing temperature. For example, the maximum carboxylation rate of Rubisco, the maximum rate of electron transport, stomatal conductance, daytime respiration, photorespiration, and mesophyll conductance may all have distinct temperature responses and T_{opt} values (Lin et al., 2012). Indeed, at supraoptimal temperatures, electron transport was found to be more limiting than Rubisco carboxylation in tropical seedlings (Slot and Winter, 2017a; Vårhammar et al., 2015). However, stomatal conductance (Slot and Winter, 2017b) and increased photorespiration

(Slot et al., 2016) often become limiting to net photosynthesis at considerably lower temperatures than electron transport. Despite the importance of stomatal conductance and electron transport limitation at supraoptimal temperatures, the carboxylation rate appears to be important in the long-term acclimation to warming, as illustrated by changes in Rubisco content under warmer growth temperatures (Scafaro et al., 2017). Mature tropical tree canopies are more difficult to access and manipulate than seedlings and saplings, and therefore relatively few studies have investigated the temperature response or acclimation potential of canopy foliage. The upper canopy, however, represents a disproportionate amount of total C uptake, absorbs the majority of incoming solar radiation, and is therefore of critical importance to the study of tropical forest responses to a changing climate (Doughty and Goulden, 2008). In an in situ leaf-warming experiment, Doughty (2011) found mature canopy leaves in Amazonia unable to acclimate to experimental warming, primarily as a result of irreversible damage to photochemical machinery caused by occasional very high temperatures. The high temperature threshold for the photosynthetic machinery does not significantly increase when plants are grown at elevated temperatures (Krause et al., 2013), suggesting that long-term warming may increase leaf death associated with extreme temperatures.

Autotropic respiration

In tropical forests about two-thirds of fixed CO_2 is released in autotrophic respiration (RA) (Malhi, 2011). Of this, 30% comes from the roots, ~50% from the leaves, and the remainder from stems (Malhi, 2011). Tropical species do not appear to differ significantly from temperate and boreal species in their instantaneous temperature sensitivity, with rates roughly doubling for every 10°C warming (i.e., $Q_{10} \approx 2$; e.g., Cavaleri et al., 2008; Meir and Grace, 2002; Slot et al., 2013, 2014b). The effect of temperature has rarely been determined for soil respiration in the tropics (see section entitled "Tropical soil responses to warming"; e.g., Cusack et al., 2010; Holland et al., 1995; Schwendenmann and Veldkamp, 2006), let alone specifically for root respiration (Sayer and Tanner, 2010). For example, Wei et al. (2010) compiled a global data set on forest soil respiration of 323 plots; only two tropical sites in China had estimated Q_{10} values for soil respiration, without distinction made between autotrophic and heterotrophic respiration. Benchmark-level field observations of RA are as yet lacking for tropical forests (Clark et al., 2017), which affects our ability to accurately assess

temperature responses of bulk soil respiration due to the potential for auto-trophic and heterotrophic respiration to differ in their sensitivities to temperature (Subke et al., 2006). Nonetheless, it appears that stem and root respiration also increase steeply with short-term warming (Chambers et al., 2004; Meir and Grace, 2002; Ryan et al., 1994). Leaf respiration of tropical vegetation is downregulated during acclimation to experimental warming (Cheesman and Winter, 2013; Slot et al., 2014a; Slot and Winter, 2017b, 2018), and although the degree of acclimation differs among species (e.g., Cheesman and Winter, 2013), it is not clear whether early- and late-successional species differ systematically in their acclimation capacity. Regardless of species, however, leaves that develop under warmed conditions are better acclimated than control leaves that develop under ambient conditions and then are exposed to warming (Campbell et al., 2007; Slot and Kitajima, 2015). Similar to leaves, stem surfaces also experience large diurnal temperature variations (Pau et al., 2018), but we are not aware of any studies that experimentally tested for acclimation of stem respiration in the tropics. However, analyses of stem respiration across a Peruvian elevation gradient suggests only moderate acclimation; the sensitivity of stem respiration to mean site temperature yielded a Q_{10} value of 1.6 (Robertson et al., 2010), which is marginally lower than the instantaneous temperature sensitivity (Meir and Grace, 2002; Ryan et al., 1994). Current tropical soil-warming efforts will reveal whether the roots of tropical trees also have the capacity to acclimate to warming (Kimball et al., 2018). The difference in exposure to temperature variation among the different plant organs is likely to have an effect on the temperature responses of physiological processes and on their potential to thermally acclimate (Fig. 2). If we assume that the greater the capacity to acclimate scales with the diurnal temperature amplitude, we would expect the strongest negative effect of warming in the thermally buffered understory and in the soil.

Plant demography

Plant recruitment and demographic response across climate and environmental gradients will mediate how plant species and communities will respond to climatic changes. Response to abiotic factors and stresses in early life stages act as critical filters for recruitment into plant communities (Harper, 1977). For example, in Amazonia, seedlings of 41 habitat specialist tree species, planted across three distinct forest habitats, showed varied mortality, with seedling survivorship positively correlated with the abundance of

conspecific adult trees, suggesting seedling mortality plays a major role in patterns of species distribution (Fortunel et al., 2016). Much of our under-standing of plant demographic responses to abiotic variables in lowland trop-ical forests come from studies of drought and moisture gradients for juvenile trees (e.g., see below). Research utilizing natural variability in temperature and manipulative experiments studying community-wide patterns are needed to understand how temperature variability and increase affects low-land tropical tree species composition via demographic responses.

As increased ambient temperatures will lead to rainfall variability and associated changes in moisture availability, studies on species demographic responses to drought and moisture variability give us valuable insight into the forest composition of the future (Phillips et al., 2010). Seedlings of low-land dry forest-associated species showed higher tolerance to drought than wet forest species in Panama (Engelbrecht et al., 2005). This pattern of drought tolerance among tree species was found to correlate with tree spe-cies distributions across a rainfall gradient across the Isthmus of Panama (Engelbrecht et al., 2007). At the seedling stage, wet forest species have higher growth rates than drought tolerant, dry forest species, potentially leading wet forest species to outcompete drought tolerant species in moist conditions (Gaviria et al., 2017). In later juvenile life stages when DBH reaches 1 cm or more, distributions become more similar to that of adult tree species, suggesting that in tropical forests environmental filtering continues to play a major role in seedling-to-sapling and sapling-to-adult life stage transitions (Baldeck et al., 2013).

Epiphytic species are thought to be especially vulnerable to climatic changes (Foster, 2001). Transplant studies of epiphytic orchids show reduced germination of higher elevation epiphytes in the drier, warmer con-ditions of lower elevations (Nadkarni and Solano, 2002; Rapp and Silman, 2014). In a study examining the effects of climatic variability on the demo-graphic parameters of an epiphytic orchid *Lepanthes rupestris*, seedling pro-duction was directly correlated with the number of yearly average days without rain and the average number of reproductive adults was negatively correlated with the maximum average temperature of the previous year. However, these reductions and the observed changes in fecundity did not change population growth rates (λ) during the study period (Olaya-Arenas et al., 2011). While climate change and climatic variability may generally lead to reduced population sizes of epiphytic species overall, the demo-graphic mechanisms through which changes take place will likely be species and context dependent.

Recent evidence suggests the tree species in tropical mountains are responding to climate change by changing their altitudinal distributions. Researchers link this change in altitudinal distributions with change in temperature (Feeley et al., 2011, 2013; Duque et al., 2015). However, the exact mechanism that drives changes in plant altitudinal range may depend on a variety of local abiotic factors in addition to warmer temperatures, such as moisture availability, intensity of the dry season, as well as species–specific responses to these changes (Ibanez et al., 2006, Feeley et al., 2012). Plant migrations along environmental gradients are mediated via demographic changes in the local population (Zhu et al., 2011). At the leading edge of the range, earlier life stages, such as seedlings and saplings, recruit and expand the species range. At the trailing edge of the species range, younger size classes fail to recruit, resulting in a remnant adult population without replacement (Colwell et al., 2008; Laurance et al., 2011). Censuses along a montane gradient in northwestern Costa Rica document an increase in relative abundance of lowland species when modern censuses were compared with herbarium records. This change toward a warm climate-associated community resulted from increases in mortality of species associated with higher elevations and cooler climates (Feeley et al., 2013). A study using an elevation gradient in the Peruvian Andes documented a shift in tree genera elevation ranges, and that average rate of upslope migration was $2.0 \pm 0.9\,\mathrm{my}^{-1}$ (Feeley et al., 2011). Similar migrations rates were reported for Costa Rican mountains ($1.2 \pm 0.9\,\mathrm{my}^{-1}$; Feeley et al., 2013) and the Northern Andes ($\sim 2.0\,\mathrm{my}^{-1}$; Duque et al., 2015). Despite the migration upslope, the rate of migration was not enough to stay on par with current or projected changes in temperature on the Andean slopes (Duque et al., 2015; Feeley et al., 2011). In high-elevation tropics, recruitment and establishment of juvenile trees constrain the tree line on tropical mountains. With an increase in mean temperatures, however, current tree lines on tropical mountains have remained stable as extreme frost events limit recruitment of tree seedlings beyond the tree line (Rehm and Feeley, 2015).

Net primary productivity

Tropical forests are underrepresented in climate change studies, despite accounting for 33%–35% of terrestrial productivity (Saugier et al., 2001; Bonan, 2008; Cavaleri et al., 2015). For example, a global synthesis of forest ecosystem C cycling that relied on 513 eddy-covariance and biometric studies revealed that although tropical wet forests represented 20% of the global

forest area, only 3% of the studies conducted to date were conducted in these forests (Luyssaert et al., 2007). This lack of geographic balance is disproportionately important because productivity is often several fold higher in tropical wet forests compared with temperate and certainly boreal forests (Saugier et al., 2001), while C storage in tropical forests exceeds all other forest types combined (Bonan, 2008). As a result, climate controls on tropical forest productivity are poorly constrained (Girardin et al., 2010; Litton and Giardina, 2008; Robertson et al., 2010; Ryan, 2010), hampering efforts to model effects of future climate change for tropical C balance (Cavaleri et al., 2015; Clark et al., 2017). We further identify a need to understand how gross primary productivity (GPP) is partitioned to NPP and RA, as this allocation question can exert an enormous influence on how much detrital C enters the soil and C balance in tropical forests. This balance is predicted to be sensitive to changes in climate (Bonan, 2008; Cox et al., 2000; Friedlingstein et al., 2006), with potentially important but poorly understood effects on atmospheric CO_2 concentrations.

There are, however, large-scale patterns that can provide insights. For example, MAT is predicted to rise by 4–7°C in the coming century (IPCC, 2014), and because GPP, as well as the component fluxes of GPP, all increase across gradients of MAT (Giardina et al., 2014; Girardin et al., 2010; Litton and Giardina, 2008; Luyssaert et al., 2007; Raich et al., 2006), it is reasonable to anticipate that GPP and component C fluxes will increase in response to local warming, assuming other limitations do not become exacerbated or disturbance regimes change. However, as mentioned above, there are several lines of evidence to suggest a negative effect of warming on tree growth in the tropics (Clark, 2004; Clark et al., 2003, 2010; Lin et al., 2010; Vlam et al., 2014; Way and Oren, 2010). Thus an explicit assessment of gross and net fluxes is needed. Furthermore, understanding why short-term responses to interannual variation in climate can have apparently contrasting effects as gradient-based MAT effects on NPP in tropical forests requires substantially more study.

Most dynamic global vegetation models do not account for thermal acclimation of photosynthesis and RA (Mercado et al., 2018). To inform such models, data are needed on the processes underlying the thermal acclimation responses of net photosynthesis of tropical trees—such as the acclimation of the maximum rate of carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}), their activation energies, their temperature optima, and the sensitivity of stomatal conductance to VPD—and of autotrophic and heterotrophic respiration. Establishing ecosystem-scale

warming manipulations in the tropics, combined with controlled laboratory and gradient studies, will greatly enhance our ability to understand and project plant ecophysiological and ecosystem C, water, and energy balance responses to continued warming.

Conclusions and future directions

While absolute degrees of warming are projected to be greater for higher latitudes, tropical organisms are typically adapted to stable climatic conditions and narrow temperature regimes, and may already exist near upper ranges of thermal tolerance (e.g., Mau et al., 2018). In fact, 70% of future tropical seasons will be hotter than any season of the late 20th century (Bathiany et al., 2018; Diffenbaugh and Scherer, 2011). While future higher latitude habitats can be populated by species currently existing in downslope sites or sites closer to the equator (Colwell et al., 2008; Huey et al., 2009; Lyons and Willig, 1997; Mohan et al., 2009), tropical locations of today do not have such a ready source of organisms preadapted to future tropical climate conditions (Williams and Jackson, 2007). Akin to high-elevation endemics facing warming-induced extinctions by "falling off the tops of mountains," lowland equatorial species already exist at the warm end of geographic thermal gradients. What will be the geographic source of taxa for future lowland tropical rainforests, as well as other equatorial ecosystems?

As underscored in a recent study addressing the role of nighttime warming for terrestrial C storage (Anderegg et al., 2015), additional tropical warming considerations include the need to assess not just the overall amount of climate change but the dynamics of temperature increases. Warmer cool seasons and nighttime hours may well have very different implications for species and ecosystems than warmer warm seasons and daytime hours. An additional benefit of longer term studies is the ability to capture extreme events, like the 2015–16 El Niño, which had global-scale C importance (Liu et al., 2017) but may have been missed in shorter term investigations.

Exacerbating efforts to understand warming effects on tropical species and ecosystems is the relative lack of climate warming experiments currently taking place in the tropics. The small number of ecosystem-scale manipulative warming experiments in the tropics bears global implications, for example in projecting effects of future warming for global soil C storage and dynamics (Carey et al., 2016; Crowther et al., 2016; Van Gestel et al., 2018). Critically, one of the first such experiments in a tropical forest

(Tropical Responses to Altered Climate Experiment (TRACE); Kimball et al., 2018) was affected by Hurricanes Irma and Maria in 2017 (Fig. 3)—highlighting the need for future research to investigate the consequences of projected increases in both the intensity and frequency of the strongest storms for tropical forested ecosystems. Given that the tropics are particularly at risk of future "nonanalog" climatic conditions (Williams and Jackson, 2007), establishing additional tropical warming manipulations as well as investigating natural climate gradients (Feeley et al., 2011, 2013; Giardina et al., 2014) remains critical.

Despite tropical soils accounting for up to 40% of terrestrial soil C (Jobbagy and Jackson, 2000; Pan et al., 2011), soil C dynamics and, specifically, turnover times for various pools of soil C have rarely been
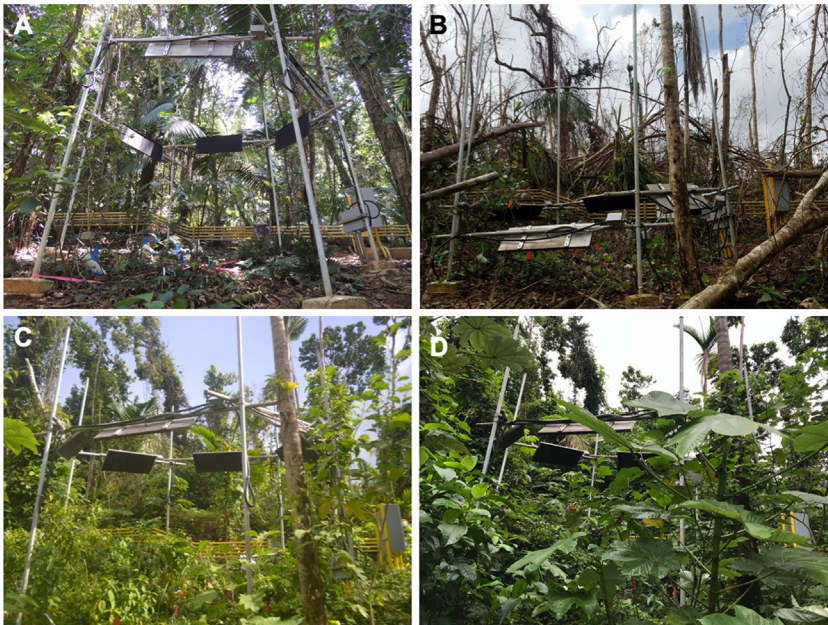
Fig. 3 A series of photographs taken of a single experimental plot in the Tropical Responses to Altered Climate Experiment (TRACE), a field warming experiment in the Luquillo Experimental Forest, Puerto Rico, United States, to demonstrate the effects of hurricane disturbance and subsequent forest recovery. (A) Photograph taken April 2015, prior to Hurricanes Irma and Maria which struck Puerto Rico in September 2017. (B) Photograph from 1 month after the hurricanes (October 2017). (C) Photograph taken 8 months after the hurricanes (June 2018). (D) Photograph approximately 1 year after the hurricanes (October 2018). Photograph (A) by Tana E. Wood; (B and C) by Aura M. Alonso-Rodríguez; and (D) by Helena Kleiner.

determined for tropical soils. Whereas soil C efflux generally increases, at least initially (months–years) with warming in higher latitude soils (Luo et al., 2001; Melillo et al., 2002, 2011, 2017; Peterjohn et al., 1994; Rustad et al., 2001), direct responses of tropical soil C to warming are less clear (Bird et al., 1996; Giardina et al., 2014; Holland et al., 2000; Townsend et al., 1997; Trumbore et al., 1996). Furthermore, while issues such as below–freezing temperatures are important for determining soil C dynamics in high-latitude ecosystems, low SOM and prevalence of highly weathered, more crystalline clay soils in tropical systems suggest an enhanced role of soil minerology for determining temperature effects on SOC including reduced soil C protection (Torn et al., 1997; see Chapter 9). On the contrary, increased temperatures may reduce soil C quality (Amelung et al., 1998, 1999; Dalias et al., 2001), resulting in enhanced soil stabilization in warmer climates (Fissore et al., 2008, 2009). However, over century timescales warming will likely have relatively small effects on soil clay minerology, compared with effects on ecosystem carbon, SOC, and nutrient biogeochemistry. Globally, warming often increases rates of decomposition and soil C efflux if adequate moisture and nutrients are available. Thus, it is important to consider the effects of warmer soils for tropical soil C balance in light of the warming effects on water, P, and in some cases N (Giardina et al., 2014; Nottingham et al., 2015b).

As well as playing a critical role for tropical soil C and nutrient dynamics, microbes play a principle role in tropical vegetation diversity and functioning. Indeed, plant-soil feedbacks mediated by soil microbes may be a causal factor explaining the high diversity of tropical vegetation (Bagchi et al., 2014; LaManna et al., 2017; Mangan et al., 2010; Sarmiento et al., 2017). Coupled with elevational gradients in N and P availabilities (Nottingham et al., 2015a), these plant-soil feedbacks may account for the shifting dominance from arbuscular mycorrhizal-associated trees in tropical lowlands to ecotymycorrhizal and ericoid mycorrhizal plants dominating at higher elevations (Culmsee et al., 2010; Geml et al., 2017; Smith and Read, 2010).

Pot studies using temperature manipulations to assess tree growth found that, unlike species from higher latitudes, tropical plants declined in biomass with nighttime warming (Way and Oren, 2010). This may be due at least in part to enhanced nighttime plant respiration, as tropical plant respiration as well as photosynthesis have been shown to be sensitive to experimental warming (Cheesman and Winter, 2013; Slot et al., 2014b; Slot and Winter, 2017a, 2018). In addition to respiration, optimal temperatures for photosynthesis T_{opt} are generally higher for tropical species than for temperate

(Mau et al., 2018), but the temperature range for adequate photosynthesis is narrower for tropical taxa (Cunningham and Read, 2002, 2003). Thus tropical vegetation may be at greater risk of negative C gain with warming (Slot and Winter, 2017a). Importantly, from a biodiversity standpoint it is worthy to note that late-successional tropical plant species have been shown to be more negatively affected by warming than early-successional pioneer species (Barberán et al., 2015; Krause et al., 2013; Slot and Winter, 2016) and thus may be at greater risk from warming.

Another important consideration for vegetation response to warming—namely, that native temperatures may affect plants responses to warming (Shaver et al., 2000)—is particularly relevant for tropical species, given that emergent trees and other vegetation growing 55 m or more above the ground cooccur with midcanopy and low-statured species in many tropical forest biomes (Janzen, 1983). Steep vertical gradients in forest temperatures mean the vertical niche a species occupies determines the degree of daily temperature fluctuations historically experienced. Whereas species inhabiting the upper canopies of tropical forests may experience diurnal temperature ranges of ~20°C, species and structures closer to and in the ground have evolved with much lower variations in temperature, and thus may be less plastic in response to, or even intolerant of, warming. But given that current maximum daily temperatures in tropical forests can already surpass photosynthetic T_{opt} (Mau et al., 2018), even these lofty taxa may exhibit C deficits as local mean temperatures continue to increase.

In summary, while tropical forests contain a vast amount of the planet's terrestrial biodiversity and 33%–35% of terrestrial productivity (Bonan, 2008; Saugier et al., 2001), and together with tropical grasslands up to 40% of Earth's soil C (Jobbagy and Jackson, 2000), our understanding of tropical forest responses to climate change is extremely poor. Current and hopefully future ecosystem-scale warming experiments in tropical locations, along with continued laboratory investigations, can reveal responses to warming over short-term timescales of up to several years, and perhaps someday, decades. These experiments provide insight into mechanisms of response. A real strength of such experiments will be coupling these findings with long-term studies of natural gradients. These elevation and other gradient investigations speak to warming effects over centuries to millennial scales and integrate across multiple, sometimes divergent, underlying processes to highlight big picture effects. Unfortunately, given the rapid pace of current and future climate change and the strong potential for future non-analog climate conditions in the tropics, laboratory and natural climate

gradient studies alone will not be sufficient for projecting changes, planning for responses, and conserving the tropical ecosystems of today or the future.

Acknowledgments

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Glossary

Acclimation Changes to an individual organism—often involving synthesis of proteins, membranes, and metabolites—that enable the organism to adjust to changes in its environment in a way that maintains performance across a range of environmental conditions.

Activation energy The energy that must be available in a system to initiate a given reaction. It is an important feature of enzymes that they can lower the activation energy of numerous metabolic reactions.

Adaptation A mutation, or genetic change, that helps an organism survive in its environment. It can take several generations for the trait to become a part of the community (i.e., natural selection). While physiological changes can be included (see acclimation above), "adaptation" generally refers to genetic changes as a result of natural selection.

Arrhenius kinetics The Arrhenius equation is a formula for the temperature dependence of chemical reaction rates.

Carbon quality–temperature hypothesis The kinetics (see above) of carbon compounds that are harder to decompose having higher temperature sensitivity than easier to decompose carbon compounds.

Conspecific A member of the same species.

Growing season length The number of days when plant growth takes place. Growing season length would be determined by factors such as temperature and moisture availability.

Insolation The amount of solar and sky radiation per unit of horizontal surface.

Michaelis–Menten kinetics An equation that relates the rate of an enzyme-catalyzed reaction to the concentrations of enzyme and substrate present.

Microbial growth efficiency The proportion of carbon from the environment that is used for growth relative to respiration.

Mountain pass hypothesis The hypothesis that temperature gradients across mountain passes present greater barriers to movement for organisms of tropical lowlands than to those of higher latitudes.

Negative density dependence When specialized natural enemies, such as insect herbivores or fungal pathogens, maintain high plant diversity by elevating the mortality of plant species that occur at high density.

Physicochemical Pertaining to both physical and chemical properties.

Rate–determining step A step significantly slower than all other steps, which thus determines the rate of the full process, as a reaction can occur only as fast as its slowest step.

Source–Sink relationship A process involved in translocation of photosynthetic products in plants from regions of supply (source) to a region of utilization or storage (sink).