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RESEARCH ARTICLE

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Experimental Soil Warming Impacts Soil Moisture and Plant
Water Stress and Thereby Ecosystem Carbon Dynamics

Key Points:

- Modeling of a soil heating experiment showed increased CO₂ emissions consistent with observations, but minimal soil carbon changes
- Accurate simulation of observed CO₂ fluxes, soil carbon, roots, and soil moisture explained heating impacts on plant water stress
- Emphasizes the need to combine observational data with modeling to understand heating effects on ecosystem carbon dynamics

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Experimental soil heating experiments have found a consistent increase in soil-surface CO₂ emissions (F_s), but inconsistent soil organic carbon (SOC) responses. Interpretation of heating effects is complicated by spatial heterogeneity and soil moisture, nitrogen availability, and microbial and plant responses. Here we applied a mechanistic ecosystem model to interpret heating impacts on a California forest subjected to 1 m deep, 4°C heating. The model accurately simulated control-plot CO₂ fluxes, SOC stocks, fine root biomass, soil moisture, and soil temperature, and the observed increases in F_s and decreases in fine root biomass. We show that a complex suite of interactions can lead to a consistent increase in F_s (~17%) over the 5-year study period, with very small changes in SOC stocks (<1%). Modeled increases in leaf water stress from soil drying reduced GPP and NPP. The resulting reduction in leaf and fine root allocation increased fine root litter inputs to the soil and reduced root exudation. Soil heating led to about a 50% larger increase in root autotrophic respiration than in heterotrophic respiration, with the heating effect on both these fluxes decreasing over the simulation period. Increased heterotrophic respiration led to increased soil N availability and plant N uptake. These heating responses are mechanistically linked, of magnitudes that can affect ecosystem dynamics, and long-term observations of them are rarely made. Therefore, we conclude that a coupled observational and mechanistic modeling framework is needed to interpret manipulation experiments, and to improve projections of climate change impacts on terrestrial ecosystem carbon dynamics.

Plain Language Summary We used observations and a mechanistic ecosystem model, *ecosys*, to study how experimental soil warming affects the carbon cycle in a Californian forest. Soil warming is an important response to climate change and can strongly affect ecosystems carbon storage. The model reasonably captured observed surface CO₂ fluxes and vertically resolved soil moisture, temperature, carbon stocks, and fine root biomass. The model also accurately captured the effects of the imposed 4°C soil heating on surface CO₂ fluxes and decreases in fine root biomass. Soil heating dried the soil, particularly near the soil surface, leading to modeled plant water stress and reduced photosynthesis and above- and belowground plant growth. This study demonstrates how difficult it is to get a full picture of how warming affects forests from experiments alone—they do not cover sufficiently large areas, last long enough, or capture all the important details about plant and soil interactions. Our modeling work demonstrates the need for more detailed measurements and better models to understand and predict how climate change might alter belowground biogeochemical and plant processes, the carbon cycle, and ecosystem carbon storage.

1. Introduction

Ecosystem soil carbon stocks are large and potentially dynamic under climate warming (Luo et al., 2020). However, current global-scale assessments of changes in these carbon pools are very uncertain, with estimates from the recent Intergovernmental Panel on Climate Change (IPCC) model intercomparison (CMIP6) varying widely in magnitude between Earth System Models (ESMs) (Varney et al., 2022). Similar discrepancies exist in site-to regional-scale terrestrial carbon cycle models (De Kauwe et al., 2017; Schaefer et al., 2012). While there are many possible explanations for these differences, ecosystem or soil temperature manipulation experiments could help identify dominant controls on carbon cycle responses to warming and necessary improvements for the next generation of land models.

Experimental soil heating can directly affect heterotrophic (R_H) and belowground autotrophic respiration (R_A), and thereby soil organic carbon (SOC) content and surface CO₂ emissions (F_s). These heating effects depend on ecosystem properties and manipulation duration (Yang et al., 2023). There have been dozens of soil heating

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experiments spanning a range of ecosystems, and several meta-analyses of their results have been performed. One consistent result from these analyses is an increase in F_s with heating. For example, Yan et al. (2022) performed an analysis with 48 heating manipulations in global grasslands and inferred an average 9.5% increase in F_s (mainly contributed by effects on R_A), and linked those increases to concurrent increases in Net Primary Productivity (NPP). Yang et al. (2023) synthesized observations from 187 field manipulation experiments in six ecosystem types and found that F_s increased with warming magnitude in short-term experiments, but adapted at longer time scales. Wang et al. (2014) analyzed 50 ecosystem heating experiments in 9 ecosystem types and found no detectable effect on R_A , but an average 21% increase in R_H (resulting in a 12% increase in F_s). We note that these robust inferences of a mean positive effect of heating on F_s obscure many reported complexities that may be relevant to interpretation of mechanisms and model development. Several independent forest ecosystem heating experiments have also reported increases in F_s following heating (Hicks Pries et al., 2017; Noh et al., 2016; Peplau et al., 2021; Soong et al., 2021). For example, in a 26-year heating study at Harvard Forest, Melillo et al. (2017) found that changes in substrate availability, microbial activity, carbon use efficiency, and community composition drove a complex response to soil heating that included increases in F_s . At the Blodgett Forest site we analyze below, Soong et al. (2021) reported a $30\% \pm 4\%$ increase in F_s under a 4°C heating, with large spatial heterogeneity between paired plots. Since most studies do not separately measure R_H and R_A , the extent to which plant roots affect the observed F_s response to heating remains an important uncertainty in interpreting experimental manipulations. Further, in addition to expected rapid increases in respiration, longer-term effects on root growth, mortality, and plant water and nutrient uptake may also be affected.

In contrast to what appears to be a clear positive effect of soil heating on F_s , studies have found that the sensitivity of SOC stocks to experimental heating varies widely. In grasslands, experimental heating effects on SOC stocks led to decreases (Verbrugghe et al., 2022), increases (Reich et al., 2020), or no changes (Chen et al., 2022). Interpreting experimental soil heating effects on SOC stocks is complicated by several factors: (a) spatial heterogeneity, particularly in forests with deeper root systems; (b) incomplete heating of the soil volume interacting with the plants, particularly in forests; (c) soil moisture effects (Reich et al., 2020); (d) nitrogen availability effects (Graham et al., 2014); (e) microbial and plant acclimation (Yang et al. (2023), but see Carey et al. (2016)) and rapid stress responses; and (f) the wide range of time scales and interconnectivity of processes that are sensitive to temperature. Regarding the first point, Finzi et al. (2020) studied the potential impacts of Harvard Forest spatial heterogeneity on interpretation of soil heating experiments, and concluded that SOC stock measurements were impractical as a method to infer statistically significant heating effects. If that conclusion is generalizable for forest soil heating experiments, quantification of soil heating effects on SOC stocks may only be possible through modeling analyses carefully evaluated and benchmarked against other observed responses. These complications to interpreting experimental heating effects on ecosystem carbon cycling imply the importance, either with measurements or modeling, of evaluating the coupled ecosystem process responses.

Since forest soil-heating experiments often heat only a small portion of the soil volume occupied by tree roots, it is often assumed that the dominant system response will be associated with local microbial and fine-root dynamics. A back-of-the-envelope estimate is that the three 2 m Heated plots occupy about 1% of the horizontal area of a single tree of 30 m crown diameter ($3\pi 2^2 / \pi 30^2$). However, as reviewed by Waadt et al. (2022), plants can respond systemically to stresses applied even to single leaves or root tips (termed Systemic Acquired Acclimation, SAA). Mittler et al. (2011) identified the Reactive Oxygen Species signal (ROS) wave generated in response to an abiotic stress (e.g., temperature, moisture, light) in a local group of cells, and that this wave can move long distances throughout the plant. Suzuki et al. (2013) showed that plant stress signaling involves both a rapid ROS wave moving through the entire plant and a stress-specific signal. Zandalinas et al. (2020) demonstrated that plants respond, signal, and acclimate systemically to combinations of stresses applied to separate leaves. The observational literature discussing these complex, multi-signal, and systemic responses to abiotic stresses is large and growing. Further, these interactions may affect experimental soil heating responses in ways not previously considered. For example, soil heating often leads to localized soil drying, potentially inducing a systemic plant response that may be proportionally larger than expected from the relatively small warmed and dried soil volume.

Since this wide range of possible heating effects on ecosystem carbon dynamics are so complex and difficult to simultaneously measure, mechanistic modeling benchmarked against available observations may provide valuable insights to coupled ecosystem behavior. Since the experimental manipulation affected only ~1% of the

horizontal extent of a typical tree, we use model results to explore the pathways by which laterally homogeneous belowground warming (as expected from climate warming) would affect whole-forest responses. To that end, here we use observations from a soil heating experiment at Blodgett Forest, a Californian mid-elevation forest, to first evaluate a mechanistic ecosystem model, *ecosys*, and then apply the model to explore ecosystem responses to the 1 m deep soil heating. We perform Control and Heated simulations and analyses to explore a possible set of interactions leading to an emergent soil heating impact on F_s and SOC stocks. We end by discussing modeling strategies and new observations needed to interpret experimental manipulations and improve carbon cycle projections.

2. Materials and Methods

2.1. Field Site and Observations

We use observations from a 1 m deep soil heating experiment at the University of California Blodgett Forest Research Station, California (120°39'40" W; 38°54'43" N, 1,370 m above sea level (Hicks Pries et al., 2017)). The site is located in the foothills of the central Sierra Nevada, has a Mediterranean climate with a mean annual precipitation of 1,660 mm (most as snow from November through April) and mean annual air temperature of 12.5°C. The area's mixed-conifer forest includes ponderosa pine, sugar pine, incense cedar, white fir, Douglas fir, and oak; most of the trees around our experimental manipulation plots are conifers, so we assumed plant functional traits consistent with a temperate evergreen conifer tree. The soil is of granitic origin with a well-developed O horizon and is classified as a fine-loamy, mixed, superactive, mesic Ultic Haploxeralfs in the Holland series. Measurements relevant to the current study include soil temperature and soil volumetric water content measured continuously at multiple depths in the top meter; fine root (hereafter, "root" refers to "fine root") biomass and SOC stocks measured from periodic cores (Riley et al., 2024). F_s was continuously monitored using a LI-8100 Automated CO₂ Flux System in conjunction with the LI-8150 Multiplexer (Licor, Nebraska, USA). Air from the headspace of each closed chamber (20 cm diameter), which was permanently installed 10 cm into the mineral soil across the six plots, was circulated through the multiplexer via a diaphragm pump. F_s was determined using SoilFLuxPro software, with flux values showing an R^2 fit of less than 0.9 being excluded from the analysis. We note that these measurements have not been used to evaluate heating effects in prior publications. Volumetric water content was converted to water filled pore space, WFPS, using measured soil bulk density and inferred porosity. Porosity (ϕ) was inferred using estimated bulk density (ρ_b (g cm⁻³)) and an assumed particle density of 2.66 g cm⁻³: $\phi = 1 - \rho_b/2.66$; ρ_b was estimated from measured soil mass, water content, and volume.

The soil heating method is described in detail in Hicks Pries et al. (2017). Briefly, three plot pairs, each with a 3 m diameter control and heated plot, were established in 2013 and heating began January 2014. Twenty-two 2.4 m steel pipes were installed vertically into the soil around each plot boundary, and heating cables were placed in the pipes. Two concentric rings (1 and 2 m diameter) of heater cables were installed 5 cm deep to compensate for surface heat loss to the atmosphere. In each heated plot, power was supplied to the vertical and surface heaters to maintain a 4°C temperature differential with its paired control plot.

2.2. Model Description

Ecosys is a mechanistic numerical model of ecosystem processes that affect carbon and nutrient (N, P) cycling, water and energy balances, vegetation dynamics, and soil microbial growth, activity, and competition. The model has been evaluated successfully over the past several decades in many ecosystems, including temperate forests (R. F. Grant, 2013, 2014), boreal forests (Robert F. Grant, 2004), tundra (R. F. Grant et al., 2019; Riley et al., 2021), agriculture (Woo et al., 2022; Zhou et al., 2021), wetlands (Chang et al., 2020; R. F. Grant et al., 2015), and others. Regional simulations (Mekonnen et al., 2019) up to continental scale (Mekonnen et al., 2016) have also been performed and evaluated. *Ecosys* is a valuable model to explore coupled soil-microbe-plant responses to perturbations because it mechanistically represents a wide range of relevant processes, including soil microbial dynamics, root nutrient and water exchanges with soil, plant hydraulics, photosynthesis and its dependencies on soil water and nutrient status, and soil thermal and hydraulic dynamics. We next describe how *ecosys* represents these processes; a detailed model description can be found in the Supporting Information S1 in Mekonnen et al. (2019) and the software is available at <https://doi.org/10.5281/zenodo.14257493> (Tang, 2024).

Modeled carboxylation and oxygenation rates, and therefore photosynthesis, are influenced by each plant's modeled water status and temperature. The model represents the effect of stomatal turgor, as affected by osmotic

potential, on conductance using the approach of Zur and Jones (1981). Additionally, the plant's nitrogen and phosphorus content, influenced by nutrient uptake from the soil, litterfall, and remobilization, also affect modeled photosynthesis. Soil heating can enhance photosynthesis by enhancing microbial mineralization and root nitrogen uptake. Photosynthesis is further affected by phenology, dehardening, and hardening in evergreen plants based on accumulated exposure to specific temperature ranges and changing day length. The model considers specific plant functional type traits, such as leaf characteristics, nutrient content, and root hydraulic conductivity. These traits affect how plants invest and retain carbon and nutrients in leaves, stems, and roots. Nutrient remobilization is driven by C remobilization when required maintenance respiration exceeds R_A , forcing remobilization and consequent litterfall, which increases carbon-to-nitrogen and carbon-to-phosphorus ratios. Leaf nutrient concentrations can decrease under nutrient limitations, impacting carboxylation rates and electron transport. Evergreen trees, characterized by higher axial xylem resistance, have slower water uptake rates and, under water limited conditions, higher stomatal water stress and reduced carbon fixation and growth. These plant traits result in variations in phenology, irradiance, CO_2 fixation rates, and water uptake, affecting competition for resources within each canopy and rooted soil layer.

Ecosys calculates canopy, litter, and soil surface energy exchange every hour and considers the movement of water and heat in a multi-layer system involving soil, roots, and the canopy. Modeled soil heating forces greater soil vapor pressure gradients and hence evaporation, causing soil drying. A specific canopy temperature for each plant population is calculated to ensure that the canopy's energy balance is consistent with modeled net radiation, latent heat flux, sensible heat flux, and changes in heat storage. This calculation is influenced by the modeled aerodynamic and canopy stomatal resistances. Canopy stomatal resistance is determined from modeled leaf resistance, which depends on the temporally variable CO_2 concentrations inside and outside the leaf, light, temperature, atmospheric CO_2 levels, and the estimated canopy turgor potential. That potential is derived from canopy water potential and osmotic water potential during the convergence calculation for transpiration and water uptake, and is used to estimate leaf water stress. The model considers both root and mycorrhizal water uptake, which are calculated based on the difference between canopy water potential and soil water potential across a series of resistances in the soil-root system. Both canopy conductance and temperature drive the calculations for canopy transpiration.

The model represents fully coupled transformations of soil carbon, nitrogen, and phosphorus through microbially driven processes. Eleven soil microbial functional groups are represented, each of which are represented in several substrate-microbe complexes. Decomposition rates of organic matter substrates are determined by interactions of active biomass within microbial populations, substrate concentrations, soil temperature, soil water potential, soil oxygen content, and microbial nitrogen and phosphorus content. These modeled decomposition rates affect net nutrient mineralization, which in turn affects the overall mineral nutrient content of the soil and plant nutrient acquisition.

The model has internal timesteps that differ between classes of processes. In the simulations used here, the baseline time step is 1 hr, which includes calculations for plant and soil biogeochemistry. Soil moisture and soil temperature are solved with time steps of 2 min.

2.3. Model Simulations

We performed a baseline simulation at the Blodgett Forest site from 1980 through 2013, and then, initializing from that simulation, two simulations from 2014 through 2018 to mimic the experimental protocol: Control and soil Heated. Soil properties (i.e., texture, bulk density; Table S1 in Supporting Information S1, and initial SOC stocks), were taken from site observations. Climate forcing (i.e., air temperature, precipitation, humidity, solar radiation, wind speed) were extracted for the site gridcell from the North American Regional Reanalysis (NARR) product (<https://psl.noaa.gov/data/gridded/data.narr.html>), and bias corrected based on weather station observations from the Blodgett Forest Research Station (Supporting Information S1). The transient atmospheric CO_2 concentration from Mauna Loa was also used to force the model (<https://gml.noaa.gov/ccgg/trends/data.html>). The model was spun up from 1980 to the beginning of the warming experiment (2014) repeating these 10 years of bias-corrected forcing. The Heated scenario was performed by ingesting into *ecosys* the hourly Control simulation's vertically resolved soil temperatures and adding energy to each control volume to raise the soil temperature by 4°C to 1 m depth, mimicking a dynamic heating control system (Figure S1 in Supporting Information S1). No parameter tuning against observations was performed for the simulations.

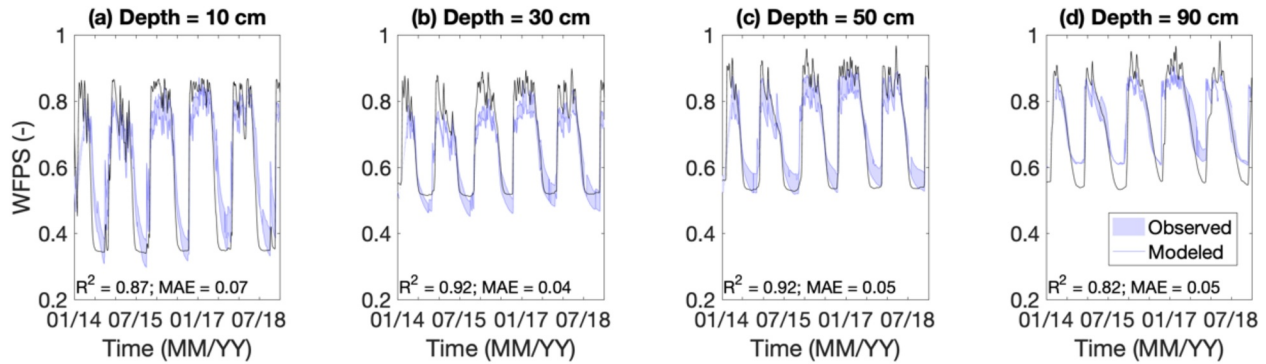


Figure 1. Modeled and observed Control plot water-filled pore space (WFPS) at soil depths of (a) 10 cm; (b) 30 cm; (c) 50 cm; and (d) 90 cm. Shading around the Observed values are for the range across the three Control plots at each time point. Modeled and observed values are smoothed with a 10-day filter for ease of visualization.

3. Results and Discussion

3.1. Model Evaluation Against Control Plot Observations

We first compared model simulation results against measured Control soil moisture, soil temperature, SOC stocks, root biomass, and soil-surface CO₂ fluxes to the atmosphere (F_s). The modeled and observed soil moisture (as water filled pore space, WFPS) were broadly consistent (Figure 1), with modest overprediction in winter between 0 and 30 cm depth and modest underprediction in summer at 90 cm depth. Modeled and observed soil temperatures are very consistent throughout the soil profile (Figure 2). The modeled heating propagated below 90 cm, reaching a mean warming of $\sim 2.5^\circ\text{C}$ at 3 m depth. Unfortunately, we do not have temperature measurements at these depths to confirm these results. However, since SOC concentrations decrease significantly

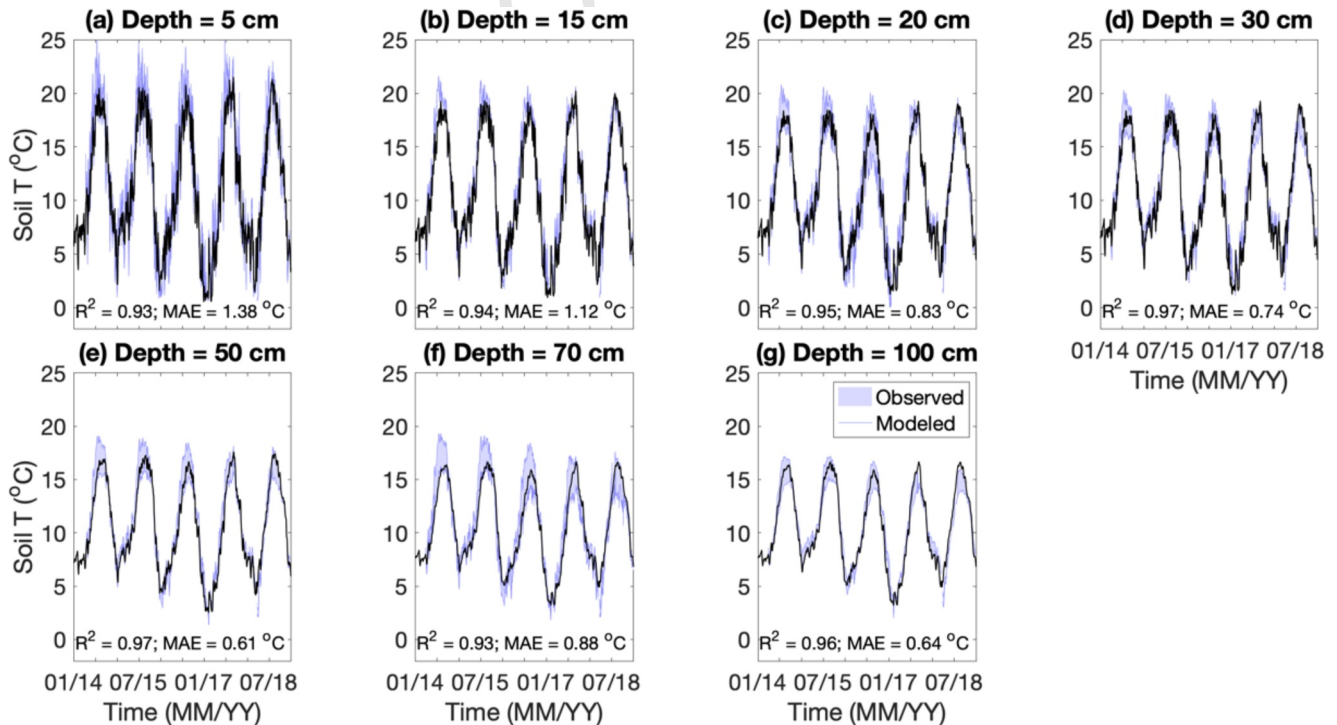


Figure 2. Modeled and observed Control plot soil temperature at depths of (a) 5 cm; (b) 15 cm; (c) 20 cm; (d) 30 cm; (e) 50 cm; (f) 70 cm; and (g) 100 cm. Shading around the Observed values are for the range across the three Control plots at each time point.

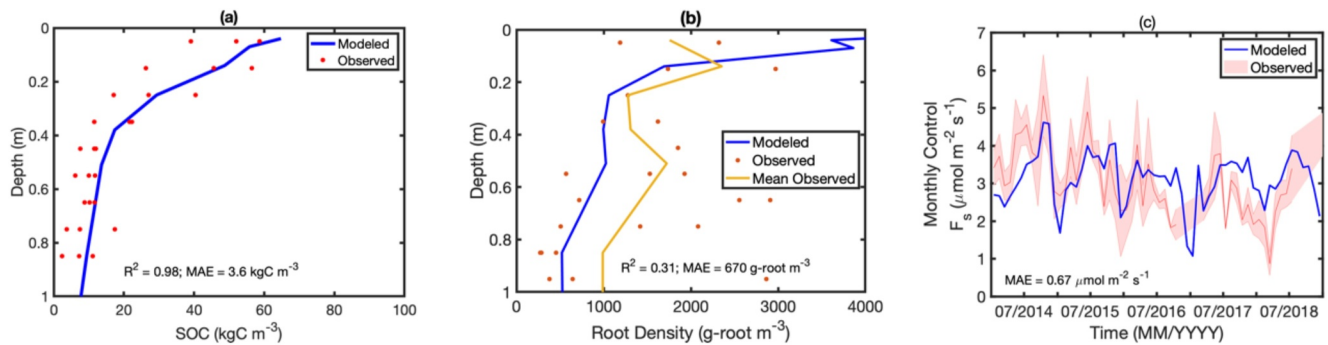


Figure 3. Modeled and observed Control-plot (a) SOC stocks ($R^2 = 0.96$, $MAE = 3.6 \text{ kgC m}^{-3}$), (b) root density ($R^2 = 0.96$, $MAE = 3.6 \text{ kgC m}^{-3}$), and (c) F_s ($MAE = 0.67 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$). The model accurately captured these three C cycle variables.

with depth at our site and the microbial activity that drives CO_2 emissions is primarily concentrated in the upper soil layers, warming below 1 m depth is unlikely to have a meaningful effect on surface CO_2 emissions.

In addition to soil moisture and temperature, we evaluated the model against observed Control-plot vertically resolved SOC stocks (Figure 3a), and found very good agreement. The model values for vertically resolved root density fell within the wide range of observed values (albeit toward the lower end of the observations) across the three Control plots (Figure 3b). The large range of observed root density values indicates relatively large spatial heterogeneity, and are consistent with the large heterogeneity in observed F_s across the three Control and three Heated plots. Simulated F_s is generally consistent with the range of observed values (Figure 3c).

3.2. Soil Heating Effects

The model successfully heated the soil by 4°C relative to Control with the dynamic heat-input approach described in Methods (Figure S1 in Supporting Information S1). Although the modeled heating was applied horizontally homogeneously and not over the relatively smaller experimentally manipulated soil horizontal extent ($\sim 1\%$, as estimated above), model simulations matched many of the observed heating effects. At Blodgett Forest, the Mediterranean climate results in soils that are relatively wet in winter and very dry in summer. Compared to observed Control plots, observed Heated plots had the largest decrease in mean WFPS at 10 cm. There were small mean decreases at 50 and 90 cm and a very small mean increase at 30 cm, but the heterogeneity at these three deeper depths was large and practically indistinguishable from no change (Figure S2 in Supporting Information S1). In the model, the vertically uniform heating resulted in decreased summer soil matric potential ($\Delta\psi_{\text{soil}}$) (up to -4 MPa) in the top few cm of soil as the system equilibrated with the atmosphere when vertical water redistribution was suppressed (Figures 4a and 4b). Below this surface layer, $\Delta\psi_{\text{soil}}$ decreases ($\sim -0.5 \text{ MPa}$) during summer were modeled down to about 1 m depth (Figure 4c), with much smaller differences below 1 m depth.

Since we do not have measurements in the top few cm of soil, it is not possible to evaluate the modeled decreased $\Delta\psi_{\text{soil}}$ predicted there. Observed versus modeled differences in the heating effects on soil moisture may be related to differences between the experimental manipulation of a relatively small portion of the soil volume compared to the simulation, and the model's coupled interactions between tree water demand and soil moisture, discussed below.

Since *ecosys* explicitly represents the coupled soil and plant hydrological system, the simulated heating effect on ψ_{soil} propagated into the plant, where it affected leaf water potential, osmotic potential, and thereby stomatal turgor pressure and conductance. The simulated heating effect (defined as the difference between Heated and Control normalized by Control, multiplied by 100%) on stomatal conductance via water stress (Zur & Jones, 1981) ranged from a few percent in the wetter winter months to between 15% and 60% from April to October, coinciding with the seasonal cycle in gross primary productivity (GPP; Figure 5). The low baseline stomatal conductance during the dry summer allows for smaller relative reductions caused by heating.

Plant water stress in the Heated simulation caused a cascading series of impacts to the plant and soil carbon cycles. Reduced stomatal conductance reduced modeled GPP and net primary productivity (NPP; Figure 6a) by ~ 260 and

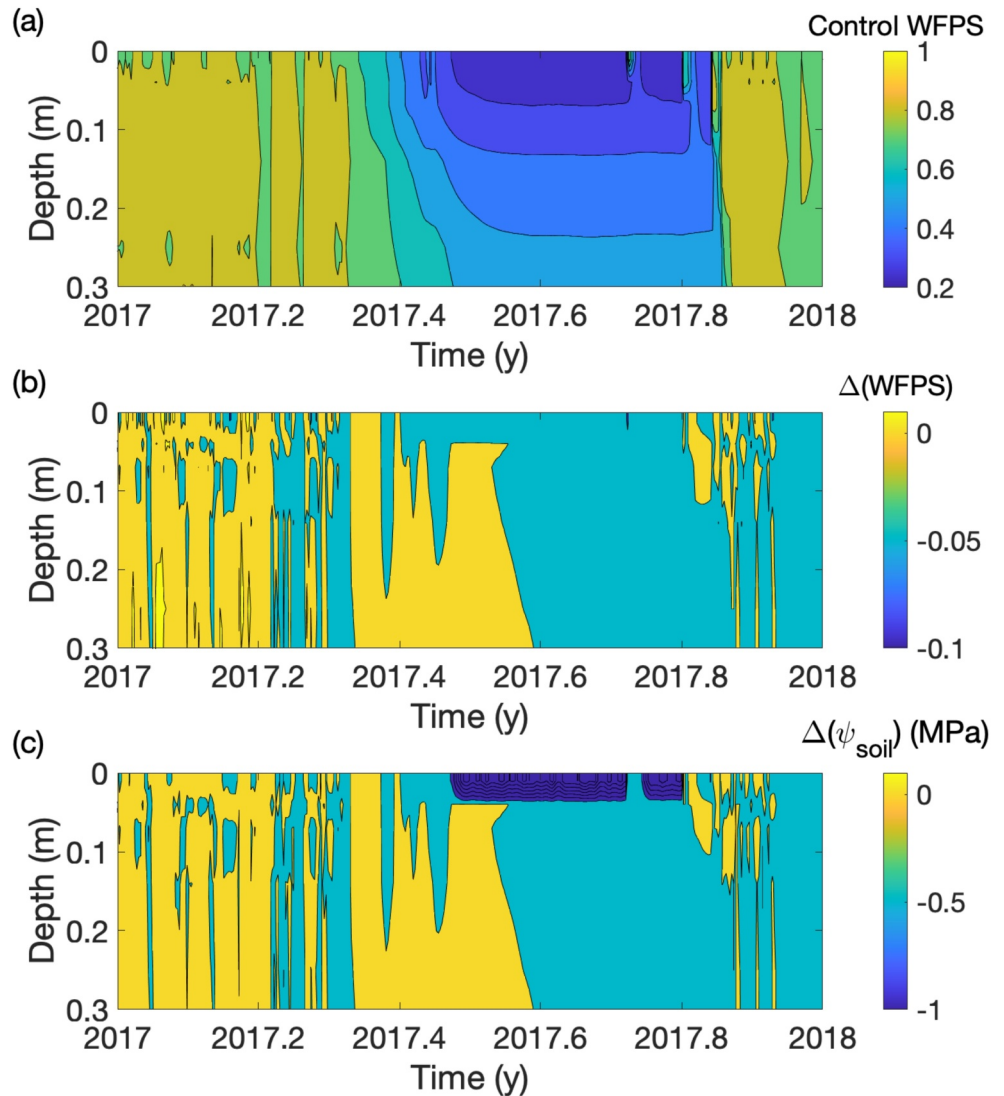


Figure 4. Modeled (a) Control WFPS; (b) differences (Heated—Control) in WFPS; and (c) differences in soil matric potential; in (b, c), negative values indicate drier soil. Between June and August, the modeled Heated soils are much drier in the top 4 cm of soil, and moderately drier (~ -0.5 MPa) to about 1 m depth. Results are shown for 2017, but all years had similar patterns. The saturated blue values in the top few cm in (c) indicate modeled $\Delta\psi_{\text{soil}}$ values approaching -4 MPa, as the system comes into equilibrium with the atmosphere when water redistribution from lower soil layers is suppressed.

$\sim 490 \text{ gC m}^{-2}$, respectively, over the 5 years. The resulting reduced plant non-structural carbon availability reduced allocation to leaves and fine roots (Figure 6b), resulting in $\sim 230 \text{ gC m}^{-2}$ reduction in fine roots by the end of the simulation period. Increased litter fall (which increased even though NPP decreased), particularly in the first 2 years, added $\sim 240 \text{ gC m}^{-2}$ to the soil (Figure 6c). Soil heating increases root maintenance versus autotrophic respiration, thereby decreasing growth, increasing senescence and non-structural C remobilization to meet the C deficit, and eventually reducing maintenance respiration to be in balance with the new autotrophic respiration. Reduced fine root biomass and belowground carbon allocation reduced root exudation by a total over the simulation period of $\sim 280 \text{ gC m}^{-2}$ (Figure 6d). Heating increased R_H by $\sim 120 \text{ gC m}^{-2} \text{ y}^{-1}$ ($\sim 18\%$) in the first year, but this increase subsided to $\sim 40 \text{ gC m}^{-2} \text{ y}^{-1}$ ($\sim 5\%$) by the end of the simulation period, resulting in a total increase of $\sim 370 \text{ gC m}^{-2}$ over the 5 years (Figure 6e). Heating increased R_A by $\sim 170 \text{ gC m}^{-2} \text{ y}^{-1}$ in the first year, subsiding to $\sim 90 \text{ gC m}^{-2} \text{ y}^{-1}$ by the end of the simulation period, resulting in a total increase of $\sim 560 \text{ gC m}^{-2}$ (Figure 6f), or about 50% more than the increase in R_H . Increased R_H led to increased mineral N availability and

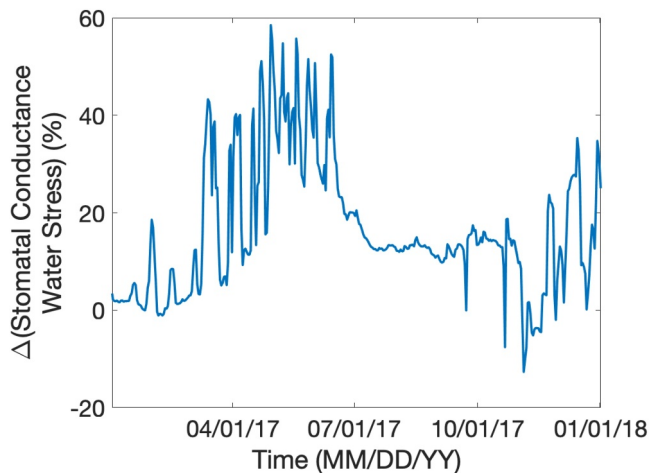


Figure 5. Percent difference in modeled Heated and Control daily maximum stomatal conductance turgor pressure stress, resulting from the relatively drier soils shown in Figure 4. For visualization, only 2017 is shown since other years during the simulation period had similar patterns.

estimates of R_A soil temperature sensitivity may result from interactions with the other known controls on plant respiration, including soil moisture (Liu et al., 2009), nutrient availability (Olsson et al., 2005), and carbon availability (Högberg et al., 2008). Our prediction that the relative increases in both R_A and R_H decreased over the warming treatment period are similar to studies that have attributed these patterns to microbial acclimation (Bradford et al., 2019). However, in our case, we attribute these decreases to reduced fine root biomass and exudation driven from the enhanced soil drying caused by the warming. However, *ecosys* does not represent some potentially relevant processes, for example, acclimation to soil moisture stress, community assembly within functional groups, or evolutionary adaptation. We therefore conclude that further model development is required to fully address the roles of these various processes on ecosystem respiration responses to warming and on assessments of microbial acclimation.

The modeled decrease in fine root biomass C of 20% with heating is consistent with that observed for root biomass (24%) and root inputs to soil at the Blodgett site (Ofiti et al., 2021). This modeled fine root biomass decrease gave rise to the decrease in root exudation. However, as discussed in Ofiti et al. (2021), previous shallow soil heating studies have reported observed root biomass to increase, decrease, or have no change, possibly because of the extent to which water limitations at each site were affected by the imposed heating. Modeled increases in litterfall are also consistent with observations at the Harvard Forest warming experiment, which reported a 9.6% increase in aboveground litterfall over the 22-year experiment (Li et al., 2018).

The modeled monthly heating effect (HE) on F_s is broadly consistent with the observationally inferred HE averaged across the 3 paired plots, although the observations are much more temporally variable (Figure 7a). Using the observed mean Heated and Control values, the observed F_s HE over the 5-year study period is 16% [−1, 30]% (the range is calculated with the minimum and maximum daily values each month), essentially equivalent to the model prediction (17%). Over the study period, the model has a small negative F_s HE trend of $-0.25\% \text{ month}^{-1}$ ($-2.9\% \text{ y}^{-1}$) while the observed HE trend is indistinguishable from 0 at $p < 0.01$. For this comparison, we reiterate the difference between the experimental manipulation, which heated only a small fraction ($\sim 1\%$) of the tree's soil volume, and the simulation, which heated the entire soil volume and therefore may have more strongly affected the plant's water demand. It is also uncertain whether stressors (i.e., soil water deficit) in the field affecting a portion of the plant's root system may have a larger than expected systemic effect on plant processes, as discussed in the Introduction. The modeled monthly R_A HE ranges from $\sim 10\%$ to over 100%, while the monthly R_H HE is more stable and varies between $\sim 0\%$ and 40% (Figure 7b). Modeled annual R_A HE decreased from about 35% to 20% and annual R_H HE decreased from about 17% to 5% over the study period, with most of those decreases occurring in the first 3 years. Since R_H is primarily driven by litterfall, this R_H HE decrease over time is consistent with the cumulative HE on litterfall, which was dominated by the first 2 years of the simulation (Figure 6c).

thereby increased plant N uptake (Figure 6g), although that additional plant N resource did not offset the water stress impacts on GPP and NPP. Note that these cumulative changes in carbon stocks and fluxes are given in the lower right-hand corner of each subplot in Figure 6, and a schematic of these interactions are provided in Figure S4 of Supporting Information S1. Our result that heating-induced soil drying affected plant water stress and thereby photosynthesis is consistent with findings from the B4WarmED full-ecosystem (i.e., plants + soil) warming experiment (Reich et al., 2018; Stefanski et al., 2023).

Our prediction that R_A and R_H increased during heating is consistent with most observational studies (Baath & Wallander, 2003; Irvine et al., 2005; Melillo et al., 2017; Rustad & Fernandez, 1998). For example, Schindlbacher et al. (2009) combined soil heating and trenching experiments in an Austrian Alps mature forest and concluded that 35%–40% and 60%–65% of increases in annual surface CO_2 emissions from heating were due to R_A and R_H , respectively. Boone et al. (1998) found, in a mixed temperate forest, that R_A was more temperature-sensitive than R_H , as did Epron et al. (2001) in a beech forest. In contrast, a meta-analysis of 50 ecosystem heating experiments (Wang et al., 2014) found that a 2°C soil heating effect on R_A was not detectable during the first few years of the manipulation. These disparate

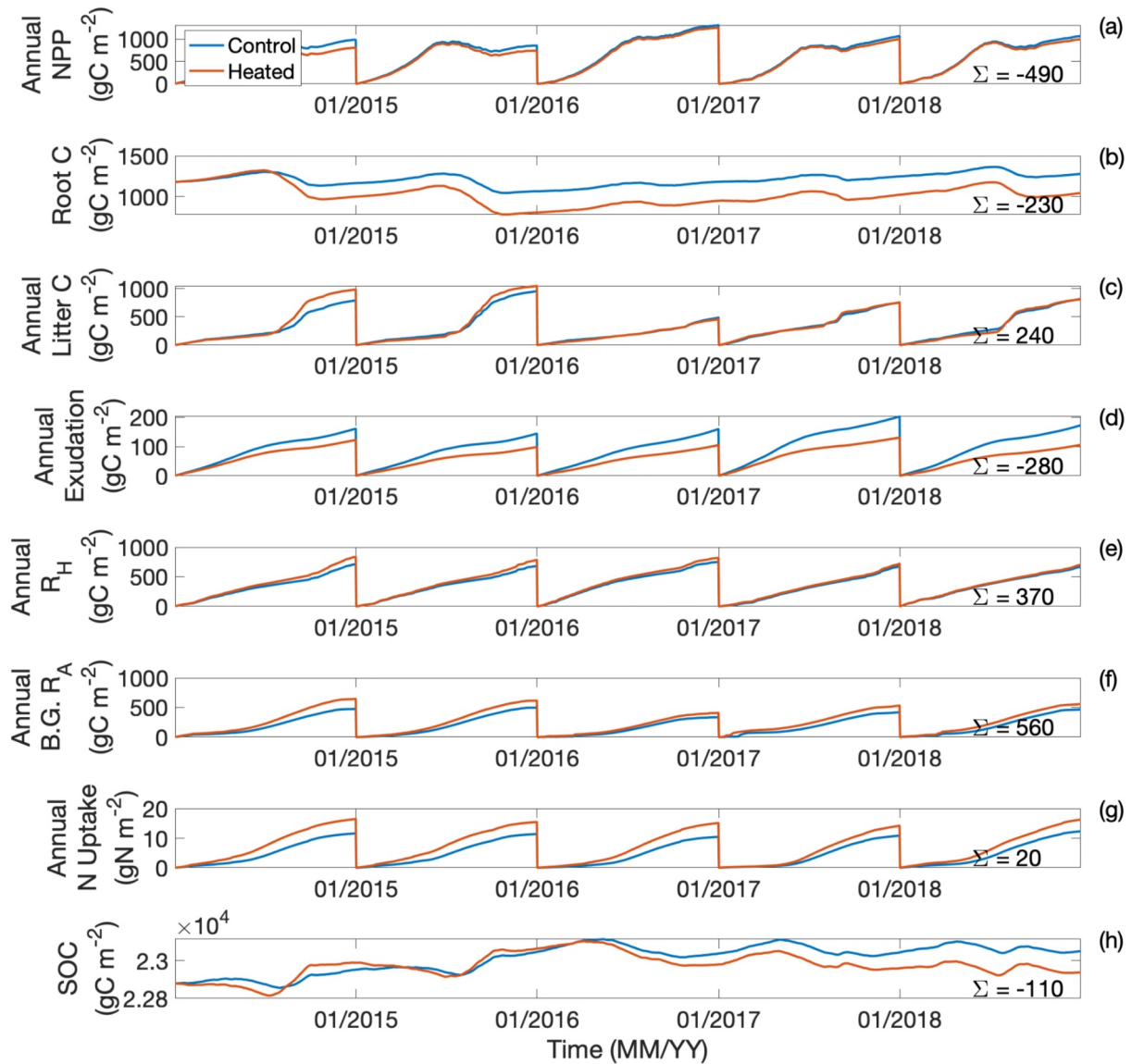


Figure 6. Heated–Control (H–C) differences over the simulation period. Modeled soil heating led to (a) reduced NPP, (b) reduced root C, (c) increased litter C inputs in the first 2 years of heating, (d) reduced root exudation, (e) increased R_H , (f) increased R_A , (g) increased plant N uptake, and (h) slightly reduced SOC. The values on the lower right hand corner of each subplot indicate the cumulative H–C differences over the simulation period in the same units as on its y-axis. “Annual” on individual y-axes labels implies cumulative flux over each year.

Finally, heating reduced modeled SOC stocks by $\sim 110 \text{ gC m}^{-2}$, which is less than 1% of the initial stock (Figure 6h) and $\sim 10\%$ of the cumulative change in modeled net ecosystem carbon exchange (NEE). Since the model maintains ecosystem carbon balance, this SOC reduction is consistent with the combination of all the heating effects on carbon cycling discussed above (e.g., reduced GPP and NPP from water stress, reduced allocation to roots, increased R_A and R_H).

Several forest experiments that heated only the soil have reported larger observed SOC losses than we modeled here, although over different periods, including previous analyses at the Blodgett site (Soong et al., 2021). For example, Tian et al. (2023) warmed the shallow (10–25 cm) soils in 6 paired plots in a 130 year old mountain forest in Austria. They found an 11% decrease in SOC content in these surface soils after 12–15 years of 4°C heating. Peplau et al. (2021) studied a naturally occurring geothermal gradient with long-term differences in soil temperature across their 4 plots. Using 4 cores from each plot, they found that topsoil and subsoil (20–80 cm)

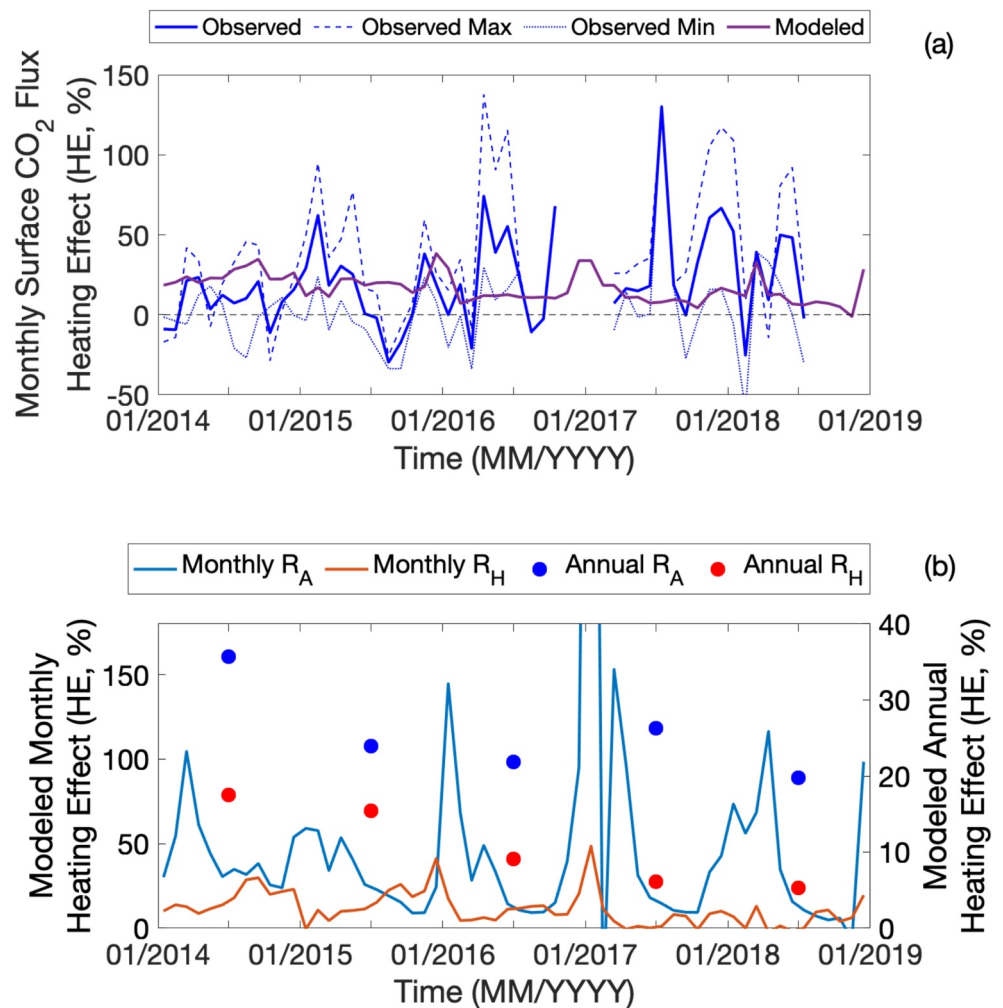


Figure 7. (a) Modeled and observed monthly soil surface CO₂ flux (F_s) Heating Effect, HE. Observed monthly HE are calculated from the monthly mean Heated and Control observations, with ranges (dashed lines) defined by the mean of the maximum and minimum monthly F_s . (b) Modeled monthly (left hand y-axis) and annual (right hand y-axis) R_A and R_H HE. Control observations were unavailable between November 2016 and February 2017, so no observed HE is shown during that period. The very large modeled monthly R_A HE in January 2017 (720%; not shown) occurred because of very low Control R_A values.

responded similarly to heating, with a total SOC loss of $3.3\%^\circ\text{C}^{-1}$ across their observed heating gradient (or 13.2% for a 4°C heating over more than 100 years). At the Blodgett site, assuming equal initial conditions in 2014, Soong et al. (2021) used 3 soil cores in each of 3 heated and 3 control plots after 4.5 years of heating to infer an SOC loss of 33% between 20 and 90 cm depth. However, that loss was associated with a very large loss in one of the 3 paired plots, while the other 2 pairs gained a moderate amount of SOC (Figure S3 in Supporting Information S1), highlighting the large spatial heterogeneity at our site, and the complexity of interpreting a relatively sparse set of SOC measurements.

Spatial heterogeneity is one of the main limitations to interpreting manipulative experiments (and most field sampling). Quantifying the effect of heating on SOC stocks can be especially difficult given practical limitations in the amount of sampling and the typically small signal relative to background variation. For example, for the Harvard Forest heating experiment, Finzi et al. (2020) estimated that it would take 103 samples to detect the changes in organic horizon SOC stocks inferred from changes in F_s at $p < 0.05$ (Melillo et al., 2017). They concluded that observed changes in surface CO₂ fluxes were “the only means of estimating soil C loss in the absence of terminating the experiment and extracting several hundred soil cores to increase statistical power.” We

found that CO₂ surface fluxes alone, however, are not a direct indication of net soil C losses, for several reasons. In the absence of a manipulation such as root-exclusion cores, surface CO₂ fluxes result from both R_H and R_A , which have different impacts on SOC stocks. We found that the modeled heating response was larger for R_A than R_H , and those responses changed over time. Further, heating-induced increases in R_H may result in more N mineralization, which can affect (a) root allocation and mycorrhizal fungi growth, and thereby R_A and (b) plant N uptake, possibly resulting in more plant C inputs to soil, and larger R_H without SOC loss. Observations in most heating experiments are not able to resolve all of these factors and interactions. Thus, the recommendation by Finzi et al. (2020) to use measured CO₂ surface fluxes alone to estimate net SOC stock changes may be insufficient.

One approach to address how spatial heterogeneity affects soil heating effects could be to make sufficient Control observations off-plot to quantify state variables, for example, SOC stocks, root and plant biomass, soil moisture and nitrogen content heterogeneity, and leaf water status and stress (the latter if the system is known to have strong water limitation, as at our Blodgett Forest site). Then a model ensemble approach could be used to evaluate whether the observed heterogeneity in those state variables can be reasonably predicted. Such an ensemble could allow for variations in soil, microbial, and plant properties, and perhaps topographical features (e.g., slope (Mekonnen et al., 2021)) to drive variations in soil moisture. Other features could be included if they were hypothesized to be important at a particular site (e.g., undergrowth vegetation (Hanson & Walker, 2019)). If the observed and modeled distributions of the chosen state variables were consistent, then one could consider the model ensemble to be a reasonable representation of the site heterogeneity and proceed to model the heating effect heterogeneity. The proposed model ensembles could also be used to establish hypotheses regarding, for example, how soil moisture and nitrogen availability affect C cycle responses to heating. These hypotheses could then be used to motivate new observations. Model ensembles could also be used to inform which observations would provide the best constraints on model structures and parameters.

Evaluating the roles of rapid (e.g., ROS wave signaling) and slower (e.g., plant or microbial acclimation, assembly, or adaptation) responses (Carey et al., 2016; Yang et al., 2023) on the C cycle will require new observations, as described in those papers. These stress signals and system responses are also related to how one should evaluate the effects of soil heating volume on ecosystem responses. Plant responses to heating were observed in our plots (e.g., reduction in root biomass) and other responses were likely (e.g., increased plant N uptake), but we have no measurements to evaluate whether the effects are systemic or localized, or how their magnitude is related to the relatively small soil volume that was warmed.

The wide range of time scales involved in ecosystem C cycle responses to heating also complicates interpretation of experimental manipulation. Modeling of a permafrost ecosystem Bouskill et al. (2020) and at the Harvard Forest warming experiment (Grant, 2014) demonstrated that directly projecting soil heating results into the future can lead to large errors because of the wide range of interacting processes expected under a longer-term climate warming. A model considering only SOC, microbes, and constant belowground NPP inputs would always result in a net loss of SOC from heating, while a model including plant interactions is likely to show very different results. Similarly, a field experiment in which only soil is warmed, such as Blodgett Forest, may result in a measured loss of soil C but does not include the plant-soil-nitrogen interactions that could compensate for such losses. In summary, this paper has shown that credible carbon cycle projections constrained by experimental manipulations will require a model that represents how the plant and soil coupled system responds to expected changes in climate forcing.

4. Conclusions

In this study we applied a mechanistic ecosystem model to interpret carbon cycle observations from a soil heating experiment in a California forest ecosystem. The model reasonably captured observed control-plot surface CO₂ fluxes and vertically resolved soil moisture, temperature, carbon stocks, and root biomass. Simulations of the imposed 4°C soil heating accurately represented the observed increases in surface CO₂ fluxes across the 5-year observational record and observed decreases in root biomass. The imposed heating decreased soil moisture content primarily near the surface in both observations and simulations. We used the model to explore coupled system responses, which were not observed by the experiment. In the simulations, the decreased soil water potential due to heating led to increased leaf water stress and decreased stomatal conductance, with cascading impacts on carbon cycle components. In particular, reductions in GPP and NPP propagated to decreased fine root

biomass and decreased root exudation. The modeled heating increased soil respiration, with a greater impact on autotrophic than heterotrophic respiration. The heating also led to higher nitrogen availability and plant uptake. Accounting for all these interactions, we found that the overall heating effect on soil organic carbon (SOC) stocks was a small reduction (<1%).

Given that most soil warming experiments have difficulty directly evaluating coupled tree and soil responses since the manipulations cover too small an area, run for too short a time, have limited observations of plant and soil processes, and cannot account for spatial heterogeneity, simulations of the coupled responses to soil heating are a necessary component of improving understanding of climate change-mediated changes in belowground biogeochemistry. Our results highlight the importance of coupled ecosystem processes to perturbations, the need for more robust measurements to quantify those processes and interconnections, and the need for robust model representations to explain observed soil heating responses and make C cycle projections.

Data Availability Statement

The observations used in this work are archived on ESS-DIVE (<https://ess-dive.lbl.gov/>; Riley et al. (2024)). The *ecosys* model and information for compiling and running it are available at <https://github.com/jinyun1tang/ECOSYS> and Zenodo at <https://doi.org/10.5281/zenodo.14257493> (Tang, 2024).

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