# Trade-off between plant and soil carbon storage under elevated CO₂

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**Abstract**

Terrestrial ecosystems remove about 30% of the carbon dioxide ($CO_2$) emitted by human activities each year[1], yet the persistence of this carbon sink depends partly on how plant biomass and soil organic carbon (SOC) stocks respond to future increases in atmospheric $CO_2$ (refs. 2,3). Although plant biomass often increases in elevated $CO_2$ ($eCO_2$) experiments[4–6], SOC has been observed to increase, remain unchanged or even decline[7]. The mechanisms that drive this variation across experiments remain poorly understood, creating uncertainty in climate projections[8,9]. Here we synthesized data from 108 $eCO_2$ experiments and found that the effect of $eCO_2$ on SOC stocks is best explained by a negative relationship with plant biomass: when plant biomass is strongly stimulated by $eCO_2$, SOC storage declines; conversely, when biomass is weakly stimulated, SOC storage increases. This trade-off appears to be related to plant nutrient acquisition, in which plants increase their biomass by mining the soil for nutrients, which decreases SOC storage. We found that, overall, SOC stocks increase with $eCO_2$ in grasslands (8±2%) but not in forests (0±2%), even though plant biomass in grasslands increase less (9±3%) than in forests (23±2%). Ecosystem models do not reproduce this trade-off, which implies that projections of SOC may need to be revised.

**Introduction**

The future of the land sink, especially of soil carbon, is particularly uncertain[9]. Soils can become either sources or sinks of carbon with rising levels of atmospheric $CO_2$, depending on the prevalence of gains via photosynthesis or losses via respiration[9,10]. This uncertainty in terrestrial ecosystem model projections reflects uncertainty in both the mechanisms and the parameter values controlling soil carbon cycling under $eCO_2$[11].

Plant growth generally increases in response to $eCO_2$[4,12], with soil nutrients identified as the dominant factor explaining variability across experiments[12–15]. The effect of $eCO_2$ on soil carbon stocks ($\beta_{soil}$) is more equivocal. Although the expectation is that soil carbon will accrue as $eCO_2$ increases plant growth[16], a few experiments show increases in $\beta_{soil}$, many show no change, and some even show losses[7]. The observed variation in $\beta_{soil}$ across experiments is puzzling, and there is large disagreement regarding the dominant mechanisms explaining this variation[7,17,18].

A positive relationship between the effects of $eCO_2$ on plant biomass and soil carbon pools is expected if increased plant production under $eCO_2$ increases carbon inputs (litter) into the soil. Indeed, a positive relationship between inputs and soil carbon storage is formalized in first order kinetics[16] and is applied in most terrestrial ecosystem models[19,20]. Because the effect of $eCO_2$ on plant aboveground biomass ($\beta_{plant}$) is strongly correlated with the effect of $eCO_2$ on litter production (Extended Data Fig. 1a, $r=0.81$) and on root production[21], a positive relationship between $\beta_{plant}$ and $\beta_{soil}$ can thus be expected based on first order kinetics. This hypothesis, however, ignores soil carbon losses associated with accelerated soil organic matter decomposition sometimes observed under $eCO_2$[7,18]. Plants acquire limiting resources from soils through carbon investment belowground in root growth, exudates, and symbiotic bacteria and fungi. Accelerated decomposition of soil organic matter fueled by plant carbon inputs can enable plant nutrient uptake (the "priming effect"[22]). The return on this belowground carbon investment is an increase in aboveground biomass production[15]. However, the priming effect can decrease soil carbon[5]. A *negative* relationship between $\beta_{plant}$ and $\beta_{soil}$ may thus emerge through the economics of plant resource acquisition.

Here, we evaluate the mechanisms of $\beta_{soil}$, including its relationship with $\beta_{plant}$, by synthesizing 268 observations of $\beta_{soil}$ from 108 $eCO_2$ experiments spanning the globe with coupled $\beta_{plant}$-$\beta_{soil}$ data (Supplementary Table 1) using meta-analysis techniques. We explore how well these mechanisms are represented in ecosystem models, and upscale the geographical distribution of $\beta_{soil}$ derived from experiments to identify regions where models might be missing important processes.

**Results**

**Predictors of SOC accrual under $eCO_2$**

Overall, $eCO_2$ increased soil carbon stocks by 4.6% across experiments (Fig. 1, 95%-CI: 1.7% to 7.5%). Given the strong variation in $\beta_{soil}$ across factors (Fig. 1), we used a random-forest approach in the context of meta-analysis (meta-forest) to quantify the importance of 19 potential predictors (Extended Data Table 1), including climate, soil, plant, and ecosystem variables and their interactions, accounting for covariation across predictors and potential nonlinearities.
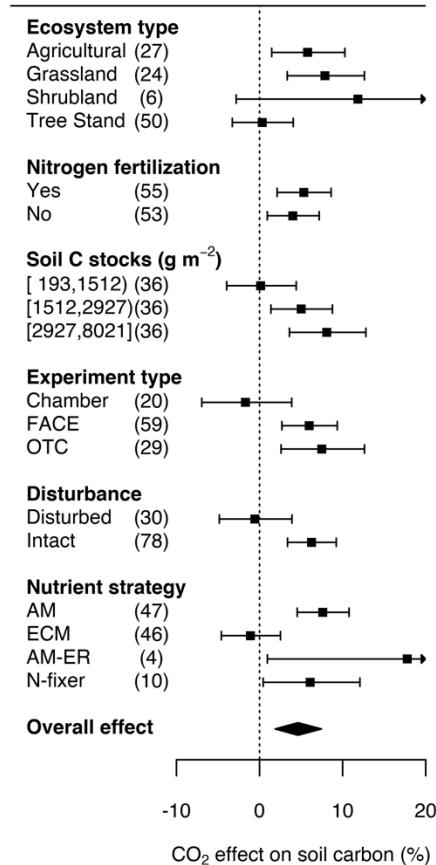
**Fig. 1. Meta-analysis of the effect of elevated $CO_2$ on soil carbon (%) across different factors.** n=108. Overall means and 95% confidence intervals are given; we interpret $CO_2$ effects when the zero line is not crossed by the confidence intervals. Arrows represent 95% confidence intervals that extend beyond the limits of the plot. Soil carbon stocks represent values in ambient $CO_2$ plots as a continuous variable, here expressed as intervals of equal sample size for illustration purposes. Values in parenthesis are sample sizes. $CO_2$ effects represent, on average, an increase in $CO_2$ from 372 ppm to 616 ppm. FACE: Free Air $CO_2$ Enrichment, OTC: Open Top Chamber, AM: arbuscular mycorrhizal, AM-ER: mix of AM and ericoid mycorrhizal, ECM: ectomycorrhizal, N-fixer: fixation of atmospheric nitrogen.

We found that $\beta_{plant}$ is the most important predictor of $\beta_{soil}$ (Extended Data Fig. 2a,b, n=108), revealing a strong coupling between $CO_2$-driven changes in plant biomass and soil carbon. In addition, $\beta_{soil}$ increased with background SOC stocks (Fig. 1), also identified as an important predictor.

Contrary to expectations from some first order models[19,20], the relationship between $\beta_{soil}$ and $\beta_{plant}$ was negative. For the subset (n=73) of field experiments with intact soils (non-potted plants and non-reconstructed soils), we found a significant interaction between $\beta_{plant}$ and nitrogen (N)-fertilization (Extended Data Fig. 2c, p<0.01). In non-fertilized experiments, the slope between $\beta_{soil}$ and $\beta_{plant}$ was significantly negative (Fig. 2a, p<0.0001, $R^2$=0.67, n=38), whereas in fertilized experiments the slope was less pronounced and nonsignificant (p=0.34, n=35) (Extended Data

Fig. 3a). In non-fertilized experiments, increases in plant biomass were associated with decreasing soil carbon stocks (Fig. 2a), consistent with the priming effect. In N-fertilized experiments, $eCO_2$ generally increased both plant biomass and soil carbon (Extended Data Fig. 3b), in line with first order kinetics.
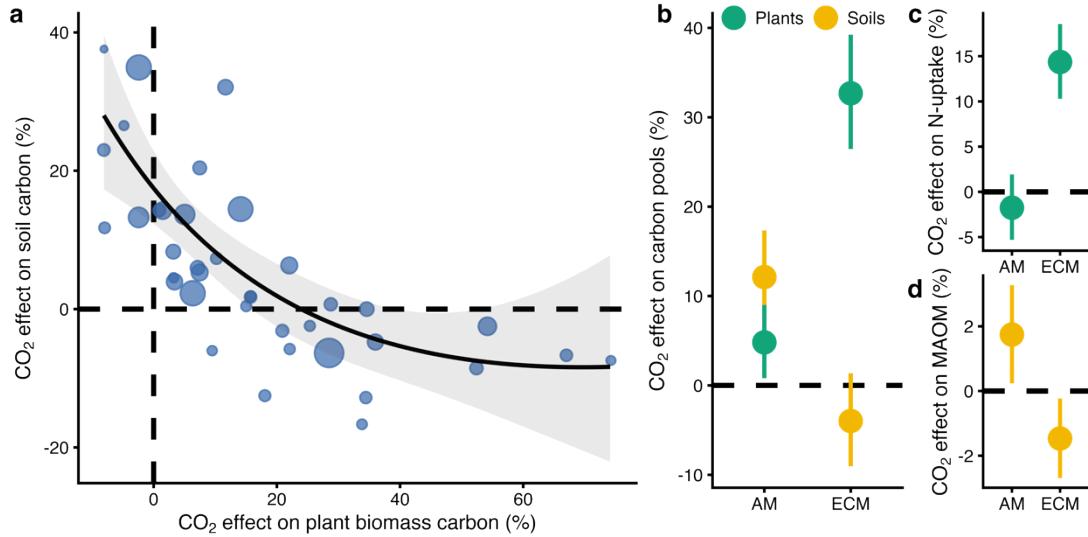


**Fig. 2. Elevated $CO_2$ experiments show an inverse relationship between the effects of elevated $CO_2$ on plant biomass and soil carbon (a).** This inverse relationship can be explained by the different efficiencies in plant nutrient uptake (c) between arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) nutrient-acquisition strategies driving opposite effects on plant biomass and soil carbon pools (b), including mineral-associated soil organic matter (MAOM) stocks (d). Regression line (a) is based on a quadratic mixed-effects meta-regression model and 95% confidence interval ($R^2$=0.67, p<0.0001, n=38). Dots in (a) represent the individual experiments in the meta-analysis, with dot sizes proportional to model weights. Dots in (b-d) represent overall effect sizes from a meta-analysis and 95% confidence intervals. Data shown here are for non-fertilized experiments (see Extended Data Fig. 3 for nutrient-fertilized experiments).

We propose a framework to explain the negative relationship between $\beta_{soil}$ and $\beta_{plant}$ based on plant nutrient acquisition strategies. Symbiotic associations between plants and arbuscular (AM) and ecto (ECM) mycorrhizal fungi mediate $\beta_{plant}$ (Extended Data Fig. 2d), resulting in much higher $\beta_{plant}$ in ECM than AM when nutrient availability is low (Fig. 2b). ECM plants efficiently increase N-uptake under $eCO_2$ (Fig. 2c, n=12), enhancing $\beta_{plant}$. However, acquiring N from soil organic matter via priming accelerates soil carbon losses[7], reducing $\beta_{soil}$ in ECM (Fig. 2b). In contrast, $eCO_2$ did not significantly affect N-uptake in AM systems (Fig. 2c, n=12). This outcome limits $\beta_{plant}$ in AM systems but stimulates $\beta_{soil}$ (Fig. 2b), likely due to increased carbon inputs through fine-root production and rhizodeposition[21,23,24] combined with decreased carbon losses[25]. The composition of the soil organic matter may mediate this effect as well; AM plants produce more easily decomposable litter[26], which enhances mineral-associated soil organic matter (MAOM) formation[27] and results in a greater fraction of soil carbon in MAOM under AM relative to ECM systems[28,29]. Indeed, $eCO_2$ increases MAOM more strongly in AM systems than in ECM systems (Fig, 2d, n=19). Because MAOM is less accessible to microbial decomposers[30], greater MAOM in AM systems could limit priming-induced losses and promote long-term soil carbon storage.

We considered three alternative mechanisms that could potentially explain this tradeoff. First, grasses allocate more carbon to roots than trees, which is associated with greater SOC stocks[31,32]. Because grassland species associate with AM fungi and the majority of tree species in the dataset associate with ECM, the observed increase in $\beta_{soil}$ in AM could be driven by ecosystem type rather than mycorrhizal type. However, we found that $eCO_2$ effects on root biomass and fine-root production were generally lower in grasses than trees, and also in AM than ECM trees (Extended Data Fig. 4). Second, in non-fertilized experiments with available data (n=16), $eCO_2$ increased litter C:N by 8%, which could reduce the decomposability of litter and the stabilization of carbon in the soil[27]. If litter quality is reduced more in ECM than AM, this could help explain why $eCO_2$ increased SOC in AM, but not in ECM. However, the effect of $eCO_2$ on litter quality was similar between mycorrhizal types (Extended Data Fig. 4). Finally, contrasting $\beta_{soil}$ in AM vs. ECM could be driven by larger background SOC in grasslands vs. forests, given that higher SOC is associated with higher $\beta_{soil}$ (Fig. 1). We found, however, that background SOC was similar between mycorrhizal types and ecosystem types (Extended Data Fig. 4). Thus, differences in root allocation, litter quality and background SOC in grasses vs. trees cannot explain the tradeoff between $\beta_{soil}$ and $\beta_{plant}$. Instead, losses in SOC associated with plant nutrient uptake (priming effect) in ECM, and gains associated with rhizodeposition in AM, are likely key. Experiments including both AM and ECM tree species should be targeted to better understand the impacts of nutrient-acquisition strategies under $eCO_2$.

**Upscaling**
To explore the potential geographical distribution of $\beta_{soil}$, we simulated a global FACE experiment (Fig. 3a). Unlike Fig. 1 where predictors are analyzed individually, our meta-forest model can upscale $\beta_{soil}$ from experiments while accounting for all important predictors simultaneously on a grid (Extended Data Figs. 5-6, 10-fold cross-validated $R^2 = 0.51$). Grasslands, croplands, and shrublands showed a stronger potential to accumulate soil carbon in response to experimental $eCO_2$ than forests (Fig. 3a,b). Soils in semi-arid herbaceous ecosystems were particularly responsive to $eCO_2$, consistent with the results from the Mojave desert FACE experiment that showed $eCO_2$-driven increases in soil carbon, but not biomass[33]. We identified large areas not currently sampled with $eCO_2$ experiments, particularly in the tropics and high latitudes (Fig. 3c,d, Extended Data Fig. 6), where new experiments would help reduce uncertainties.
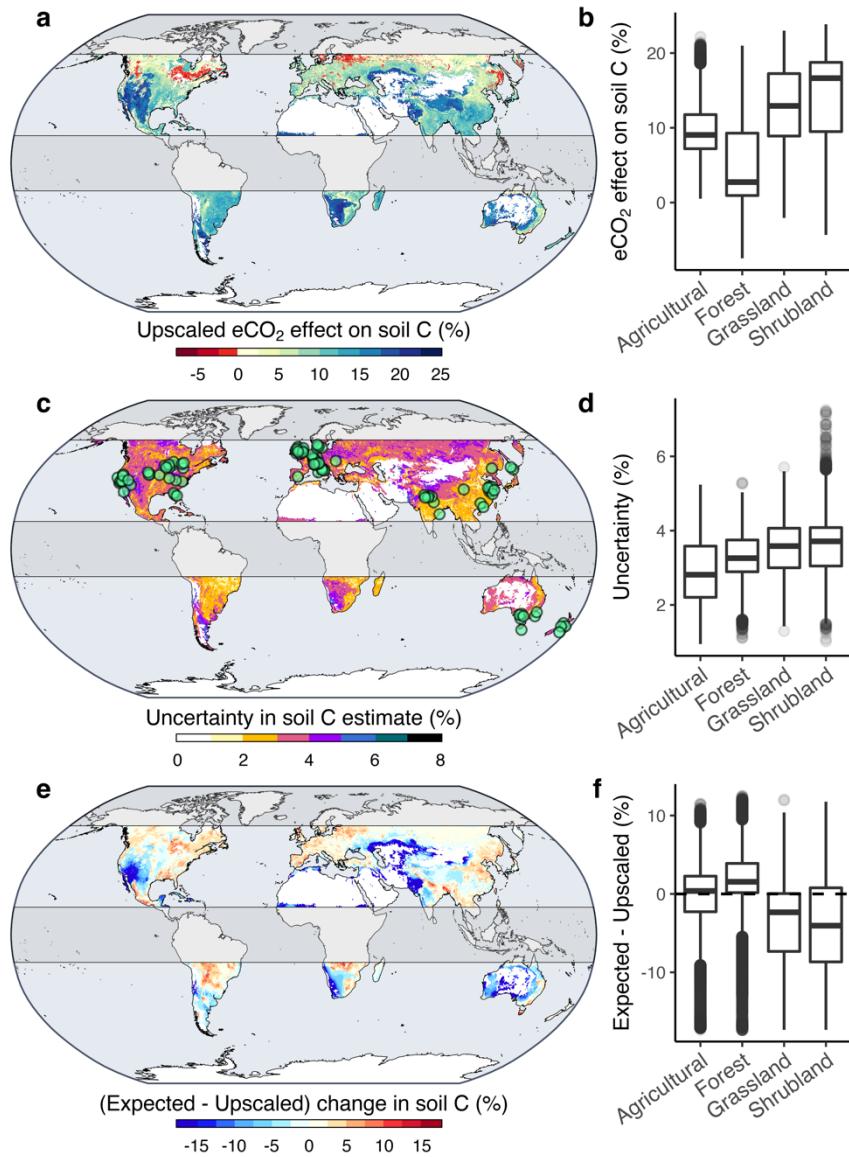
**Fig. 3. Effect of elevated CO$_2$ (~240 ppm) on soil carbon stocks upscaled from 108 CO$_2$ experiments.**
(a,b) Relative effect of elevated CO$_2$ on soil carbon upscaled based on a meta-forest approach with data from CO$_2$ experiments. (c, d) Standard error in (a). Green dots represent the location of the CO$_2$ experiments included in the analysis. (e,f) Difference between expected CO$_2$ effects on soil carbon stocks based on CMIP5 models and upscaled based on experiments (shown in a). Expected values result from the relationship between β$_{soil}$ and β$_{plant}$ coded in models. Positive values (red color) indicate an overestimation by models; negative values (blue color) indicate an underestimation by models. Shaded areas between -15 to 15 and from 60 to 90 degrees in latitude represent ecosystems not well sampled by experiments and are excluded from the analysis.

## Data-model comparisons

In addition to the negative relationship between β$_{soil}$ and β$_{plant}$, we also found a significantly negative relationship between β$_{soil}$ and the effect of eCO$_2$ on aboveground biomass *production* (Extended Data Fig. 1b, R$^2$=0.55, *p*<0.001), which is strongly correlated with litter production (Extended Data Fig. 1a, R$^2$=0.63, *r*=0.81, *p*<0.01). This result questions the positive relationship between litter inputs and soil carbon stocks encoded in most ecosystem models. Thus, we

investigated the relationship between $\beta_{soil}$ and $\beta_{plant}$ in models from three different model ensembles (description in Extended Data Table 2). First, models from the FACE model-data synthesis project (FACE-MDS)[34] mimic the experimental treatment in six $eCO_2$ experiments and allow for a direct comparison with respective observations. While observations from the six experiments included in FACE-MDS showed a *negative* relationship between $\beta_{soil}$ and $\beta_{plant}$ (Fig. 4a, blue line, $R^2=0.99$, $p<0.001$), the twelve models simulated a *positive* relationship when pooled by experiment (Fig. 4a, red line, $R^2=0.91$, $p<0.01$). The relationship across all models individually was positive as well (Extended Data Fig. 7a, dashed line, $R^2=0.37$, $p<0.0001$), and none of the individual models was able to reproduce the observations. Second, to investigate whether the same relationships emerge across the globe and in simulations where $CO_2$ increases gradually, we evaluated global century-scale relationships between $\beta_{soil}$ and $\beta_{plant}$ from the TRENDY and CMIP5 model ensembles (Fig. 4b,c). Overall, TRENDY and CMIP5 models did not simulate a negative relationship either (Fig. 4b,c). Instead, most models simulated a positive relationship and the vast majority of model simulations fell into the upper-right quadrant (Extended Data Fig. 7b,c), reflecting that inputs drive SOC accumulation in the first-order decomposition soil model structure common to the models.

In TRENDY and CMIP5 model simulations, $\beta_{soil}$ was estimated over a much longer time period than in experiments (Extended Data Table 2). Given the relatively slow turnover times of SOC pools, and the slow pace of evolutionary pressures on both plants and soil microbes, long-term effects likely differ to those found in experiments. However, first order models also simulate a positive relationship $\beta_{plant}:\beta_{soil}$ when they are forced to simulate the temporal scale of experiments (Fig. 4a), suggesting important processes are missing in models. By including explicit links between plant growth, belowground carbon allocation and SOC decomposition rates, models may more effectively reproduce the observed negative relationship between $\beta_{soil}$ and $\beta_{plant}$ and improve long-term projections.
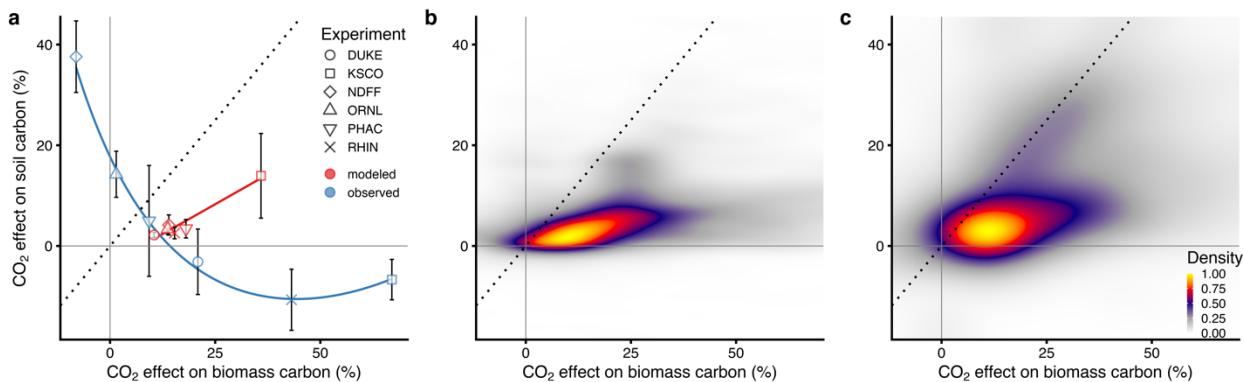


**Figure 4. Comparison of modeled and measured relationships between aboveground biomass and soil carbon responses to $CO_2$.** (a) Relationship observed (blue) and modeled (red) across 6 $eCO_2$ experiments. Model results are based on 12 models applied to the same 6 experiments with a common forcing and initialization protocol. Experiments included are Duke FACE (DUKE), Kennedy Space Center (KSCO), Nevada Desert FACE (NDFF), Oak Ridge FACE (ORNL), Prairie PHACE (PHAC), and Rhinelander (RHIN). Regression line across observations in (a) is based on a quadratic meta-regression model. Modeled simulations averaged in (a) for each experiment are from the FACE Model-Data-Synthesis project phase 2. (b,c) Global-scale relationship simulated by ecosystem models (b) from the TRENDY ensemble for the historical increase in $CO_2$ since the year 1700 and (c) from the CMIP5

ensemble for an increase in $CO_2$ from 372 ppm to 616 ppm as in $eCO_2$ experiments. Dotted lines are the 1:1 line.

To estimate the error in terrestrial ecosystem model projections of $\beta_{soil}$ caused by ignoring the tradeoff between $\beta_{soil}$ and $\beta_{plant}$, we calculated "expected"-$\beta_{soil}$ as a function of our upscaled $\beta_{plant}$ and the ratio $\beta_{soil}/\beta_{plant}$ simulated by CMIP5 models. CMIP5 models overestimated $\beta_{soil}$ for forests (Fig. 3e,f, red color). In contrast, CMIP5 models underestimated $\beta_{soil}$ in large areas dominated by grasses (Fig. 3e,f, blue color), likely because they do not account for the effects of rhizodeposition on $\beta_{soil}$[21]. Results with TRENDY models were similar (Extended Data Fig. 8).

**Discussion**
In summary, our synthesis of experiments shows that soil carbon stocks can increase by ~5% in response to a 65% step increase in $CO_2$ concentrations, with a strong coupling between $CO_2$-driven changes in plant aboveground biomass and soil carbon. However, the coupling between plant biomass and soils is an inverse relationship (Fig. 2a, Extended Data Fig. 1b), opposite to that simulated by many ecosystem models (Fig. 4). The effect of $eCO_2$ on soil carbon storage is dependent on a fine balance between changes in inputs and changes in turnover[18], where the latter is dependent on root-microbe-mineral interactions in the rhizosphere. Our results suggest that rhizosphere responses, and especially priming, explain much of the variation in $\beta_{soil}$ across experiments (Fig. 2). Most models focus on carbon inputs and underestimate rhizosphere effects[11,20,35], likely explaining the disagreement in $\beta_{soil}$ between observations and models (Figs. 3,4). We propose a framework to explain $\beta_{soil}$ based on nutrient acquisition strategies[15,36,37]. On one end of the spectrum, substantial acquisition of soil N is possible via priming[5] in ECM plants, causing a stronger plant biomass sink at the expense of soil carbon accrual. On the other end, low nutrient availability strongly constrains the plant biomass sink[38] in AM plants. However, the ecosystem-level sink is not necessarily eliminated; instead, $eCO_2$ can trigger soil carbon accrual through plant carbon-allocation belowground[21,23,24]. When plant growth is severely limited by N or other nutrients, $eCO_2$ may only cause a transient priming effect in ECM, with high soil decomposition and insufficient nutrient uptake rendering no ecosystem-level sink[39].

Our results underline the potential of grassland soils to store carbon as atmospheric $CO_2$ levels continue to rise. The results also suggest that current state of the art models may overestimate the soil carbon sequestration potential of forests in large parts of the world. Previous studies suggest that the potential of vegetation to take up $CO_2$ will slow later in this century due to nutrient constraints[12–14,38,39]. Our synthesis indicates that these nutrient constraints extend to carbon storage in ecosystems as a whole — through a partial tradeoff between increased plant growth and soil carbon storage whereby ecosystems where plant growth is more nutrient limited accumulate more carbon belowground. The apparent mismatch between observations and how most models represent the biomass-to-soil link suggests that many terrestrial ecosystem models do not adequately represent the critical processes driving soil carbon accumulation. Models are evolving to include more sophisticated representations of soil nutrient cycling, and some now include microbial activity explicitly[36,40]. This change towards coupled carbon-nutrient cycling mediated by plant-soil interactions is important for more realistically and accurately modeling the carbon cycle today and for projecting the land sink in the future.

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## Methods

**Overview.** Here, we collect data on the effects of elevated $CO_2$ on soil carbon stocks ($\beta_{soil}$) in both relative and absolute terms and synthesize them through meta-analysis. We also collect data on climatic, experimental, and vegetation characteristics that could potentially explain variability in $\beta_{soil}$ ("predictors"). In Fig. 1, we show a descriptive meta-analysis of overall $\beta_{soil}$ across different predictor factors. We next combine the strengths of meta-analysis (e.g. accounting for within-study variability, weights) with random-forest (e.g. computational efficiency, nonlinearities, interactions) – meta-forest – to quantify the relative importance of 19 predictors in explaining variation in $\beta_{soil}$ in the dataset. In Fig. 2, we describe the regression between $\beta_{soil}$ and its most important predictor ($\beta_{plant}$), and explore the possible mechanisms underlying this relationship. In Fig. 3, we apply the data-trained meta-forest model to upscale $\beta_{soil}$. Finally, we investigate whether the emerging relationship between $\beta_{soil}$ and $\beta_{plant}$ found in experiments is represented in models (Fig. 4).

**Data collection.** We have compiled the openly available Report of Mutualistic Associations, Nutrients, and Carbon under e$CO_2$ (ROMANCE) v1.0 dataset[41] with data on soil organic carbon (SOC) and plant biomass from e$CO_2$ experiments. Expanding van Groenigen et al's 2014 meta-analysis[7] of 53 experiments reporting soil organic carbon (SOC) data, we used Google Scholar to gather a total of 166 studies related to e$CO_2$ experiments, published from 1st January 2013–1st May 2019. Search terms were either "elevated $CO_2$", "increased $CO_2$" or "$CO_2$ enrichment" and either "soil carbon" or "plant biomass." To account for experiments that could have been omitted by van Groenigen et al. prior to 2013, we consulted the list of $CO_2$ experiments from INTERFACE (https://www.bio.purdue.edu/ INTERFACE/experiments.php), the Global List of FACE Experiments from the Oak Ridge National Laboratory (http://facedata.ornl.gov/global_face.html), the ClimMani database on manipulation experiments (www.climmani.org) and the database described by Dieleman et al.[42]. We recorded the structure of each e$CO_2$ experiment from the papers, taking into consideration the start date and total duration of the experiment (years), and the location of the experiment (coordinates). When the data were presented in figures, mean values and standard error were extracted using GraphClick.

For this meta-analysis, only one datum per experiment was considered to avoid pseudoreplication. The effects of e$CO_2$ on soil C pools are modulated by increases in soil C inputs from plant litter as well as feedbacks between plants and soils altering soil biogeochemical cycles that can take several years to occur. Thus, we used the most recent measurements in each experiment as the most representative data of the effect of e$CO_2$ on SOC.

For plant biomass, measurements across different time-points were combined so that only one effect size was analyzed per study. The combined effect size and variance that account for the correlation among the different time-point measurements was calculated following the method described in Borenstein et al.[43], using a conservative approach by assuming non-independency of multiple outcomes ($r = 1$) and performed using the MAd package in R[44]. We collected data on both aboveground biomass stocks and production. When aboveground biomass production data were unavailable, we collected plant data in the following order or preference: NPP, aboveground biomass increment, foliage production and yield. When biomass or soil data were not reported, studies were excluded. We also included the data on litter production reported by Song and Wan[45] to study the interactions with aboveground biomass and production data.

Soil carbon measurements in the dataset were reported at different depths, varying from 5 to 30 cm maximum depth, with an average depth of ~20 cm. When upscaling e$CO_2$ effects on

SOC through meta-forest, we included a fixed value of 0-30 cm in depth as a covariate to control for the influence of soil depth, interpolating predictions for the same soil depth of models.

SOC data reported as concentrations were transformed to stocks (g m$^{-2}$) using soil bulk density. When bulk density was not reported, we used data reported for similar experiments within the same site or assumed a bulk density of 1 g cm$^{-3}$. Assumptions are indicated in the dataset.

Studies from ROMANCE v1.0 were not included in the meta-analysis if they met any of the following exclusion criteria: i) studies with no SOC data; ii) papers with no plant biomass data; iii) studies where the duration of the eCO$_2$ experiment lasted less than 0.5 years. A total of 138 independent experiments were collected, of which, 108 were included in the final analysis based on these exclusion criteria.

**Meta-analysis.** Two types of effect size were calculated:1) the log response ratio (mean response in elevated-to-ambient CO$_2$ plots), to measure effect sizes in relative terms (%) for each experiment; and 2) the raw mean difference, to compute effect sizes in absolute terms (g m$^{-2}$). For each experiment, we collected data on SOC stocks, standard deviation and sample size under elevated and ambient (control) CO$_2$ plots. Effect sizes were calculated using the *escalc* function from the R package *metafor*[46]. We calculated overall effects in a weighted, mixed-effects model using the rma.mv function in *metafor*. The potential non-independency of studies within the same site (e.g. different species, different treatments) was accounted for by including "site" as a random effect. Effect size measurements from individual studies in the meta-analysis were weighted by the inverse of the variance[47]. 13% of studies did not report standard deviations, which were thus imputed using Rubin and Schenker's[48] resampling approach from studies with similar means. These calculations were performed using the R package *metagear*[49].

**Variable Importance and upscaling approach.** 19 potential moderators were coded (Extended Data Table 1). Including all 19 moderators in a meta-regression risks overfitting the model. Therefore, we applied the R package '*metaforest*'[50] to identify potentially relevant moderators in predicting β$_{soil}$ across the complete dataset of 108 studies. The approach is based on the machine-learning 'random forest' algorithm, which is robust to overfitting, and is integrated in a meta-analytic context by incorporating the variance and weight of each experiment as in classic meta-analysis (see above).

As an initial step, we conducted variable pre-selection by including the 19 predictors in *metaforest* with 10,000 iterations and replicated 100 times with a recursive algorithm in the *preselect* function from *metafor*[46]. Moderators that consistently displayed negative variable importance (i.e., that showed a reduction in predictive performance) were dropped using the *preselect_vars* function. Moderators that improved predictive performance were then carried forward to optimize the model. Parameters of the meta-forest model were optimized using the *train* function from the *caret* package[51], and calculated 10-fold cross validated R$^2$ with 75% of the data used as training data and 25% for validation. Unlike maximum likelihood model-selection approaches, this method can handle many potential predictors and their interactions and considers non-linear relationships. Partial dependence plots were produced which visualize the association of each moderator with the effect size, while accounting for the average effect of all other moderators.

As a sensitivity test, and to identify important interactions between predictors, we ran an alternative model-selection procedure using maximum likelihood estimation. For this purpose,

we used the rma.mv() function from the *metafor* R package[46] and the glmulti() function from the *glmulti* R package[52] to automate fitting of all possible models containing the 5 most important predictors and their interactions (level=2). Model selection was based on Akaike Information Criterion corrected for small samples (AICc), with the relative importance value for a particular predictor equal to the sum of the Akaike weights (probability that a model is the most plausible model) for the models in which the predictor appears.

Finally, the data-trained meta-forest model was applied to global gridded data of pre-selected predictors (see Extended Data Table 1 for gridded data sources) to estimate the effect of elevated $CO_2$ on SOC. The resulting global maps are geographically constrained to ecosystems best represented by experiments. We remove the estimates for latitudes comprised between -15 to 15 degrees, corresponding to tropical ecosystems not sampled by experiments (Fig. 3c, green dots), and from 60 to 90 degrees.

**Nitrogen fertilization and soil disturbance.** We used the information reported in the papers to assess whether the soils were exposed to external inputs of N fertilization ("yes") or not ("no"). Experiments were also classified as either having "disturbed" or "intact" soils as noted in the papers. If not, experiments which used pots or reconstructed soils were categorized as disturbed. We used the same approach and classification as in ref[53].

To upscale the effect of nitrogen fertilization and disturbance on $\beta_{soil}$, we reclassified the ESA CCI land cover map https://www.esa-landcover-cci.org/?q=node/164. Reclassification files are accessible online https://figshare.com/account/projects/74721/articles/11710155. For example, we classify "Cropland, rainfed"-"Herbaceous cover" (class 11) and "Cropland, irrigated or post-flooding" (class 20) as fertilized.

**Nutrient-acquisition strategy classification.** We considered the importance of the type of symbiotic association as a driver of $eCO_2$ effects on soil C. Mycorrhizal status includes AM, ECM and a mix of AM and ericoid (ER) mycorrhizal fungal associations. Here, we also considered some plant species known to associate with N-fixing microorganisms. We refer to this classification as "Symbiotic", because it includes both mycorrhizal status and N-fixation. Together, these four symbiosis types represent different mechanisms plants use to acquire nutrients[15].

We assessed the impact of the dominant symbiotic association type by classifying all studies as ECM, AM, AM-ER, and N-fixers, using the check-lists by Wang et al.[54] and Maherali et al.[55], with additional classifications derived from the literature. Species that associate with both ECM and AM (e.g. Populus spp.) were classified as ECM because these species can potentially benefit from increased N-availability due to the presence of ECM fungi[56]. Most of the N-fixers in the dataset were associated with both N-fixing symbionts as well as AM fungi, but we classified them as N-fixers because these species can potentially benefit from N acquired through N-fixation.

**MAOM data.** We retrieved data on mineral-associated organic matter (MAOM) and particulate organic matter (POM) for the subset of studies employing size or density fractionation of soil organic matter (n = 19). Because of methodological differences, POM is loosely defined as organic matter recovered in the total coarse (typically > 53μm) or light (typically < 1.6 g cm-3) soil fraction. Where MAOM was not reported, it was estimated based on mass balance by subtracting the POM fraction from total C.

**FACE Model-Data-Synthesis.** We use data from the FACE Model-Data Synthesis (FACE-MDS) Project Phase 2[34,57–61], in which 12 models were applied to 6 eCO$_2$ experiments. Each model covered the time periods representative of the FACE experiments, following a standardized protocol including meteorological forcing, CO$_2$ concentration, site history, and vegetation characteristics for each site.

Experiments included in the FACE-MDS Phase 2 were Duke FACE[62], Kennedy Space Center[63], Nevada Desert FACE[64], Oak Ridge FACE[38], Prairie PHACE[65,66] and Rhinelander[67]. Models included were CLM4.0[68], CLM4.5, DAYCENT, CABLE, JULES[69], LPJ-GUESS, OCN, TECO, ORCHIDEE[70], GDAY, ISAM, and SDGVM. See ref.[60] for an overview of model structures and processes. As in the observational data, we compared relative changes in aboveground biomass and soil carbon stocks of each experiment for eCO$_2$ relative to control treatments.

**TRENDY models** We use model outputs from the TRENDY v7 S1 simulations, where each model is driven by standardized forcings of observed increasing CO$_2$ for years 1700-2018 CE, and constant preindustrial climate and land use. We selected six models that provided outputs for aboveground vegetation carbon (taken as the sum of wood and leaf carbon), soil carbon, and NPP (CABLE-POP[71], CLM5.0[72], ISAM[73], LPJ-GUESS[74], ORCHIDEE[70], ORCHIDEE-CNP[75]). Wood carbon often includes coarse roots in models. Here, we evaluate relative changes and numbers are not sensitive to the exact definition. Description of models can be found in ref[76]. Briefly, ORCHIDEE-CNP includes an interactive N and phosphorus cycle, whereas ORCHIDEE is a C-only model. The rest have coupled C-N cycles. Relative changes were calculated based on means over ten initial years ($i$, vary depending on the model) and $j$ = 2008-2017 as $(C_j – C_i)/C_i$. To reduce effects of discrepant response timescales of soil C and biomass, we estimated the steady-state soil C storage ($C^*$) as:

$$C^* = \frac{C_j}{1 - \frac{\Delta C_j}{NPP_j}} \; ,$$

where $\Delta C_j$ is the change in soil C over the years 2008-2017. The relative change in soil C is then taken as $(C^* - C_i) / C_i$. Data shown in Fig. 4 is based on pooled data from all six models. We randomly sampled outputs from N gridcells for each model in order not to bias the visualization towards models with a large number of gridcells (i.e. higher resolution). N is chosen as the number of gridcells in the model with the coarsest resolution.

**CMIP5 Models - Expected β$_{soil}$.** We used projected SOC (Csoil) and biomass pool (Cveg) responses to rising CO$_2$ as simulated by CMIP5 models as a comparison for the upscaled values we derive from experiments. Specifically, we used data from the experiment "esmFixClim1", in which CO$_2$ is increased by 1% per year from 285 ppm. In the esmFixClim1 experiment, the increase in [CO$_2$] only affects vegetation and not the radiation code of the models, enabling a quantification of the effect of eCO$_2$ in isolation (e.g. excluding warming), and thus a close comparison with eCO$_2$ experiments. At a [CO$_2$] increasing rate of +1% year$^{-1}$, [CO$_2$] reaches 372 ppm (average concentration in ambient CO$_2$ plots in the dataset) in the 28th year and 616 ppm (average concentration in elevated CO$_2$ plots in the dataset) in the 78th year. ΔCveg and ΔCsoil were calculated as the difference between the respective carbon stocks in the 28th and the 78th year.

Though plants in both experiments and our CMIP5 dataset see a similar increase in $[CO_2]$, experiments simulate a step increase in $CO_2$ over half a decade, whereas the increase in $CO_2$ in CMIP5 models is much slower and over the course of 50 years (Extended Data Table 2). As soil organic matter turns over slowly, the resulting $\beta_{soil}$ from experiments is lower than $\Delta Csoil$ from models, and the comparison not meaningful. We thus focus on the specific relationship $\beta_{plant}:\beta_{soil}$ in experiments vs. models. Here, we calculated the spatially explicit ratio of $\Delta Cveg_{CMIP}$ to $\Delta Csoil_{CMIP}$. This was done for five Earth System Models in the CMIP5 ensemble with esmFixClim1 simulations (CanESM2; GFDL-ESM2M; HadGEM2-ES; IPSL-CM5A-LR; MPI-ESM-LR). Then, we calculate "expected" $\beta_{soil}$ from CMIP5 applying the same $\beta_{plant}$ used for experiments with the model-average $\Delta Cveg_{CMIP}$ to $\Delta Csoil_{CMIP}$ ratio:

$$expected \ (Mg \ C \ ha^{-1}) = \beta plant \times \frac{\Delta Csoil_{CMIP}}{\Delta Cveg_{CMIP}}$$

With $\beta_{plant}$ as the effect of elevated $CO_2$ on plant biomass derived from $eCO_2$ experiments. We then computed the difference between the expected (modeled) and observed (upscaled) effects of elevated $CO_2$ on $\beta_{soil}$. As both expected and upscaled $\beta_{soil}$ use the same $\beta_{plant}$, this transformation allows us to directly tackle the consequences of the different $\beta_{soil}/\beta_{plant}$ ratios between experiments and models. We acknowledge, however, that the ratio is likely to change over time, so the comparison needs to be interpreted with caution. We found, however, that first-order models also simulate a positive relationship between $\beta_{soil}$ and $\beta_{plant}$ when forced to simulate the same duration as experiments (Fig. 4a), suggesting that the sign of the $\beta_{soil}:\beta_{plant}$ relationship in CMIP5 models would not likely reverse if CMIP5 models would be forced to simulate a step increase in $CO_2$ over 5 years as in experiments.


## Code availability
The R code used in the analysis presented in this paper is available in GitHub and can be accessed at https://github.com/cesarterrer/SoilC_CO2

## Data availability
All the empirical data that support the main findings of this study have been deposited in Figshare: (https://figshare.com/account/home#/projects/74721) and GitHub (https://github.com/cesarterrer/SoilC_CO2). FACE-MDS data can be accessed at https://www.osti.gov/dataexplorer/biblio/dataset/1480327. CMIP5 data can be accessed at https://esgf-index1.ceda.ac.uk/search/cmip5-ceda/. TRENDY data can be requested at http://dgvm.ceh.ac.uk/index.html.

**Author contributions**
C.T and R.P.P. conceived the original idea. C.T. designed the paper, with R.B.J., B.A.H. and K.J.vG contributing to the development of the conceptual framework. J.R. C.T. and K.vS collected the data. C.T. ran the statistical analyses and upscaling. B.D.S ran the analysis with TRENDY models. B.N.S., C.T., and B.A.H. ran the comparison with the FACE MDS data. T.F.K, H.Z., and C.T. analyzed CMIP5 data. M.C. collected MAOM data. B.A.H. and C.T. wrote the first draft, with input from all authors. P.B.R., B.A.H., E.P., Y.C., R.D.E, R.B.J., and many others ran the experiments.

**Competing interests**
The authors declare no competing interests.

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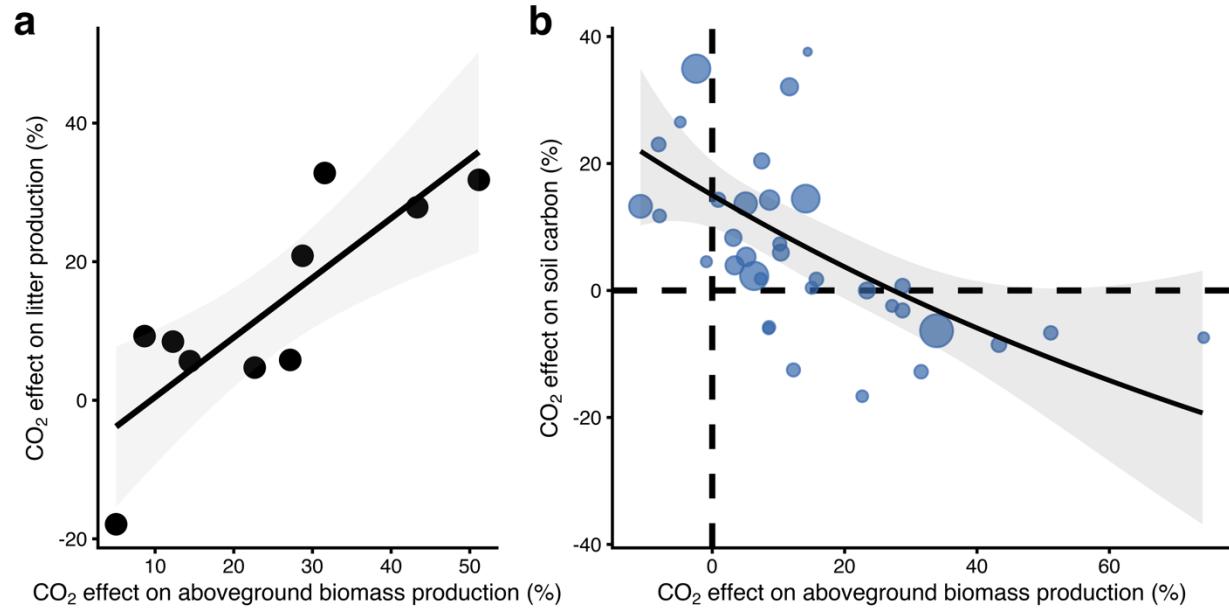
**Extended Data Figure 1 | Relationship of the effects of $eCO_2$ on aboveground biomass production with litter production (a) and soil carbon storage (b).** Results for non-fertilized field $eCO_2$ experiments (n=10, and n=35, respectively). Dots represent individual experiments, with dot size in (b) proportional to the weights in the meta-regresion.
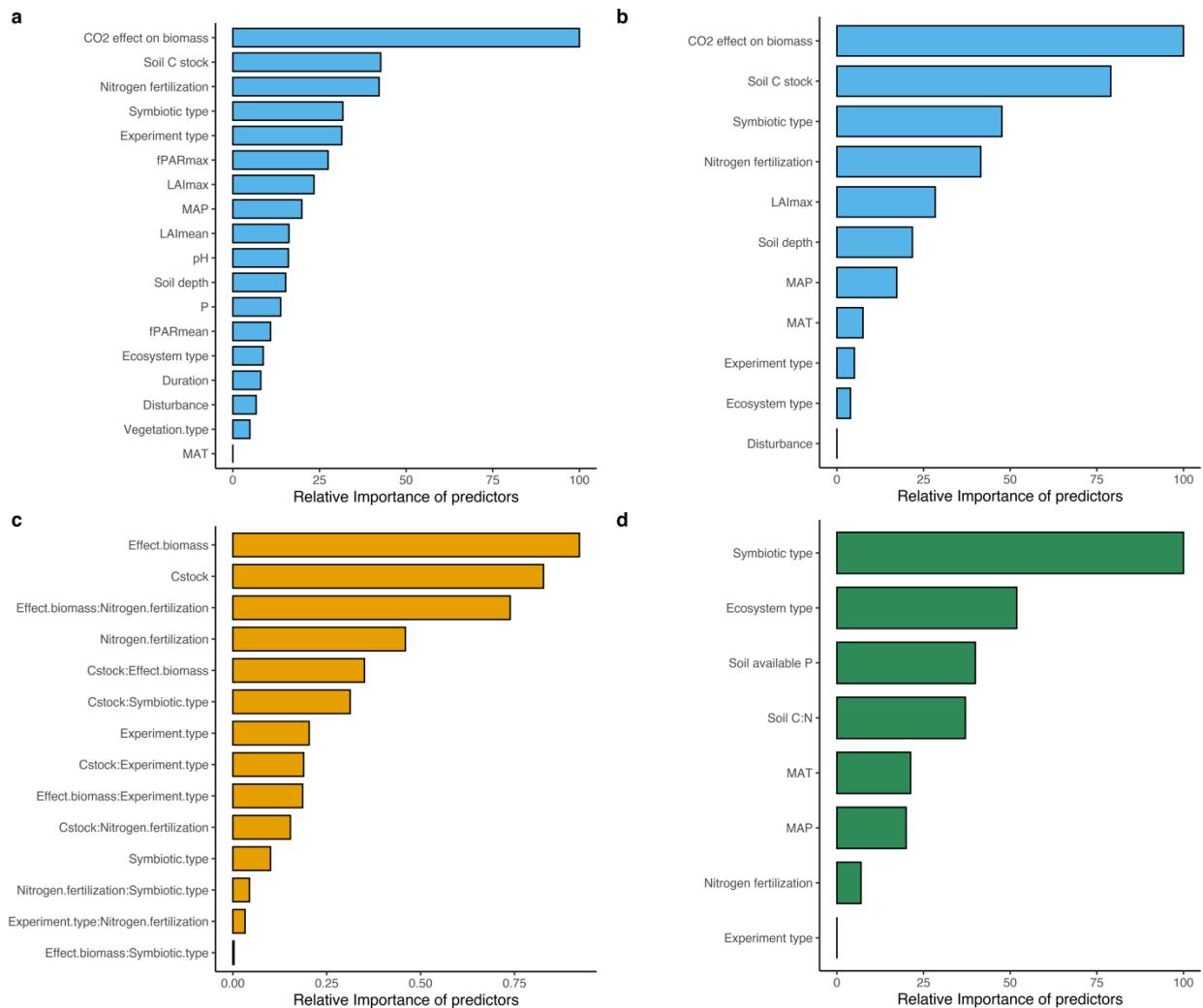
**Extended Data Figure 2 | Variable importance of 19 predictors of the effects of $CO_2$ on soil carbon and biomass stocks**. (a-b) Variable importance of the effect of $CO_2$ on soil carbon stocks in (a) relative (%) and (b) absolute terms (g m$^{-2}$) across the full dataset (n=108). (c) Variable importance of the effect of $CO_2$ on soil carbon stocks (%) across the subset of $eCO_2$ experiments in "intact" soils (n=73). (d) Variable importance of the effect of $CO_2$ on plant aboveground biomass (n=138). Variable importance in (a,b,d) is quantified based on a meta-forest model. Variable importance in (c) is quantified based on the sum of AICc weights, which allows for the quantification of the importance of interactions between predictors. As an initial step, moderators that consistently displayed negative variable importance (i.e., that showed a reduction in predictive performance) were automatically dropped.
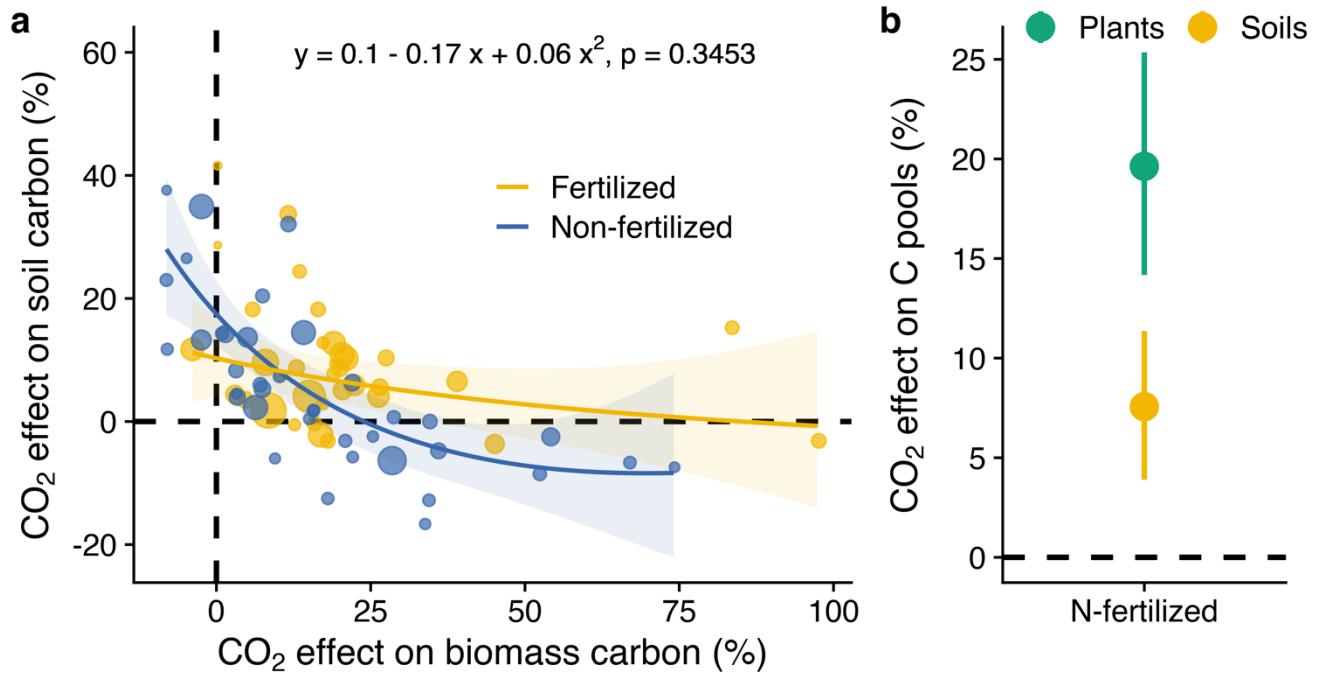
**Extended Data Figure 3 | Effects of elevated $CO_2$ on soil carbon and plant biomass in the subset of nitrogen-fertilized e$CO_2$ studies (n=35)**, expressed as a regression (a) and overall effects in meta-analysis (b). Dot sizes in (a) represent the individual studies and are drawn proportional to the weights in the model. The regression with the subset of non-fertilized studies is also shown here for comparison. Dots in (b) represent the effect sizes and 95% confidence intervals from the meta-analysis.
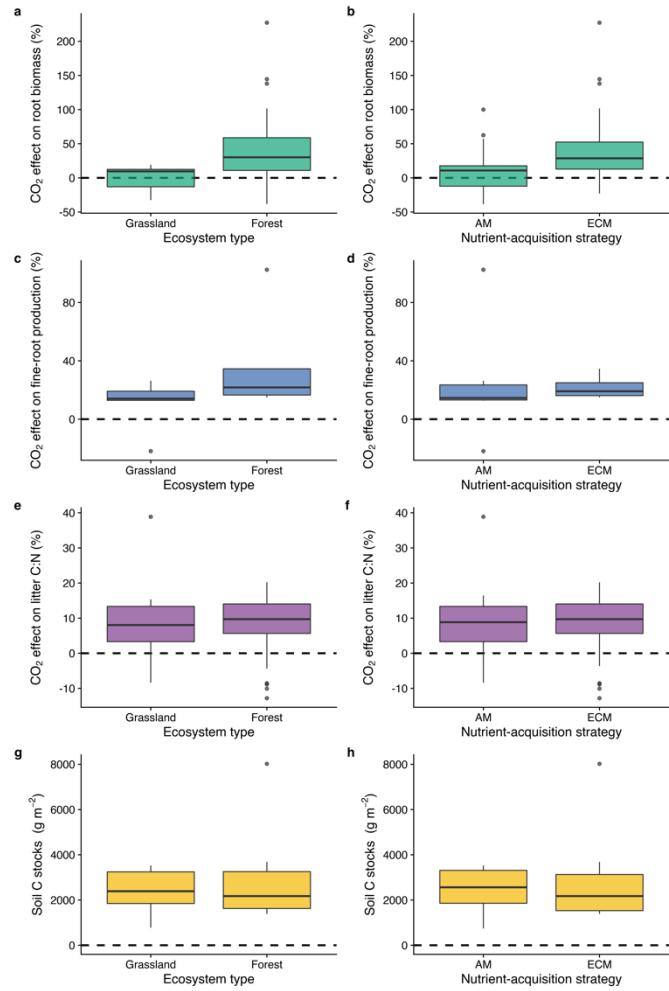
**Extended Data Figure 4 | Analysis of variables potentially explaining the observed effects of elevated CO$_2$ on soil carbon.** Effects of elevated CO$_2$ on root biomass (n=45), fine-root production (n=11), litter C:N (n=16) and background soil carbon stocks (n=38), between ecosystem types (grassland vs. forest) and nutrient-acquisition strategies (arbuscular mycorrhizae –AM– vs. ectomycorrhizae –ECM–).
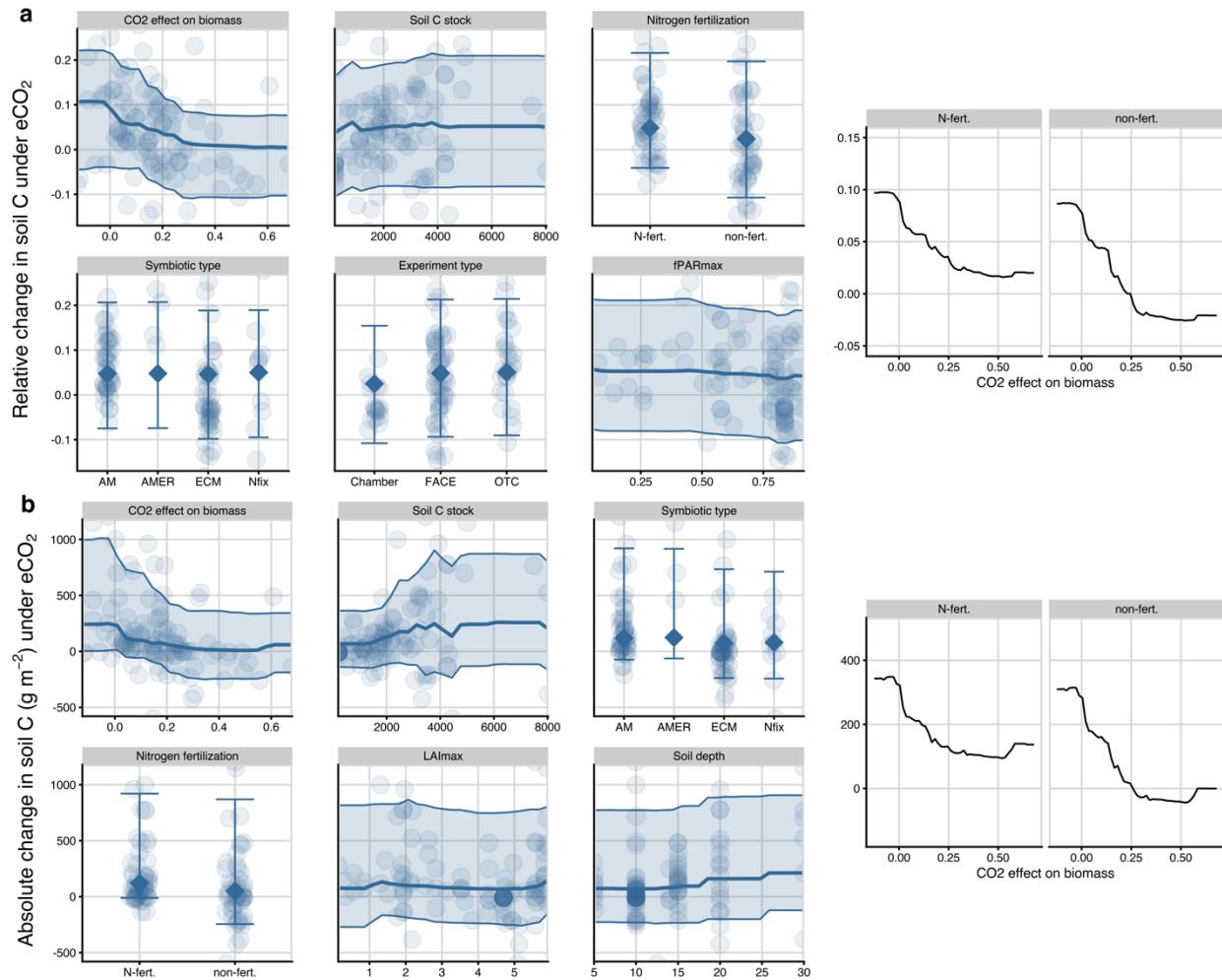
**Extended Data Figure 5 | Partial dependence plots of the six most important predictors of the effect of elevated CO₂ on soil carbon stocks across 108 experiments.** The figure shows the predicted $CO_2$ effect (yi) in relative (a) and absolute terms (b) across each predictor and the most important interaction between predictors (right panels) in a random-forest meta-analysis. Error bands represent 95% confidence intervals. Partial regression plots give a graphical depiction of the marginal effect of a variable on the response and the shape and direction of the relationship. Little variation in yi across the values of a predictor generally reflects the low predictive power of the predictor for yi. However, important predictors may show little variation in yi when involved in interactions, so the right panels show the most important interaction in the model. More details about the different predictors in Extended Data Table 1. From a total of 19 predictors, only the six most important predictors and the most important interaction are shown here.
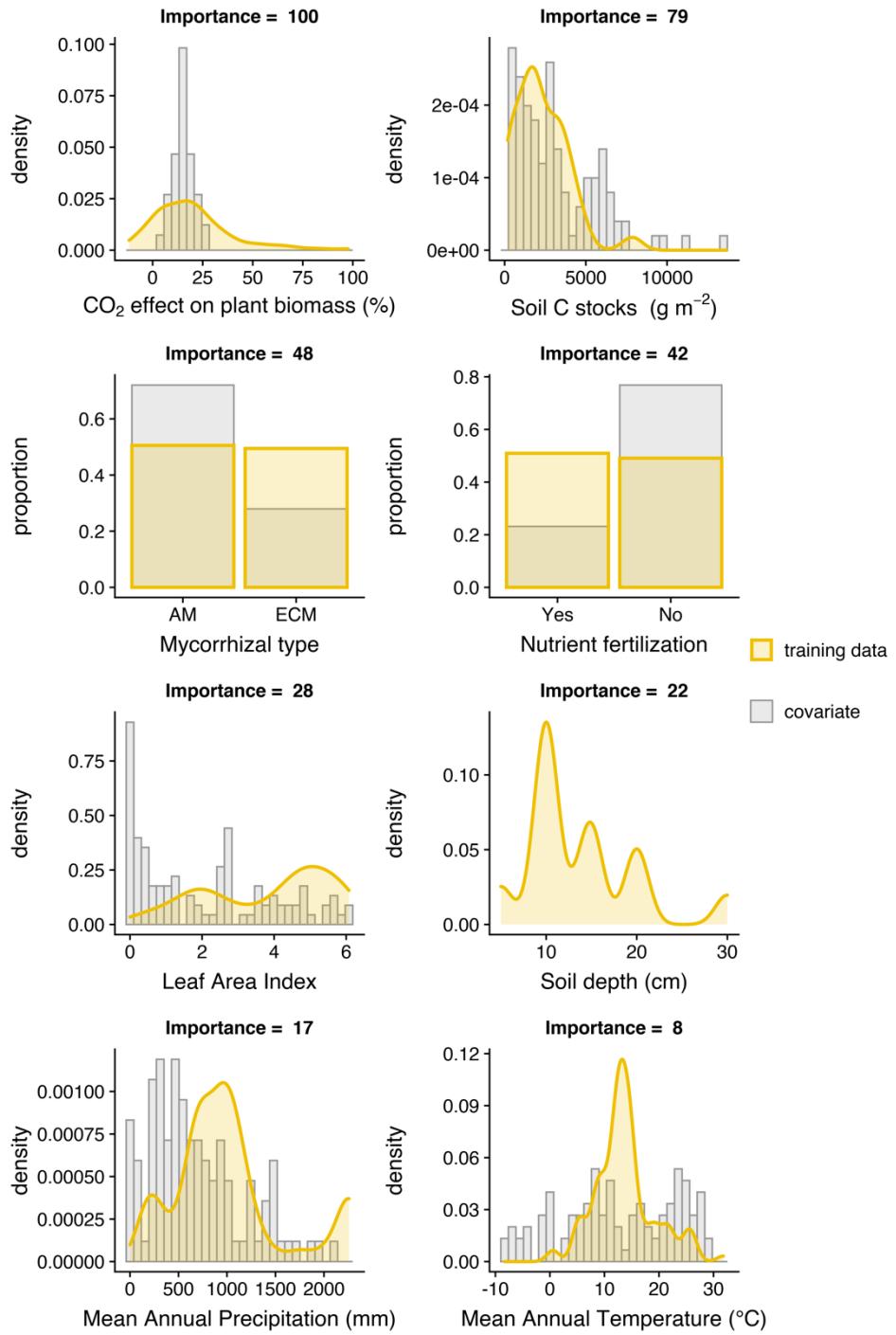
**Extended Data Figure 6 | Representativeness of the upscaling predictors of the effect of elevated $CO_2$ on soil carbon stocks.** Histograms showing the distribution of both the predictors in the training dataset of $CO_2$ experiments and the data used to upscale the global distribution of the effect. Predictions exclude regions between -15 to 15 and from 60 to 90 degrees latitude due to the lack of experiments.
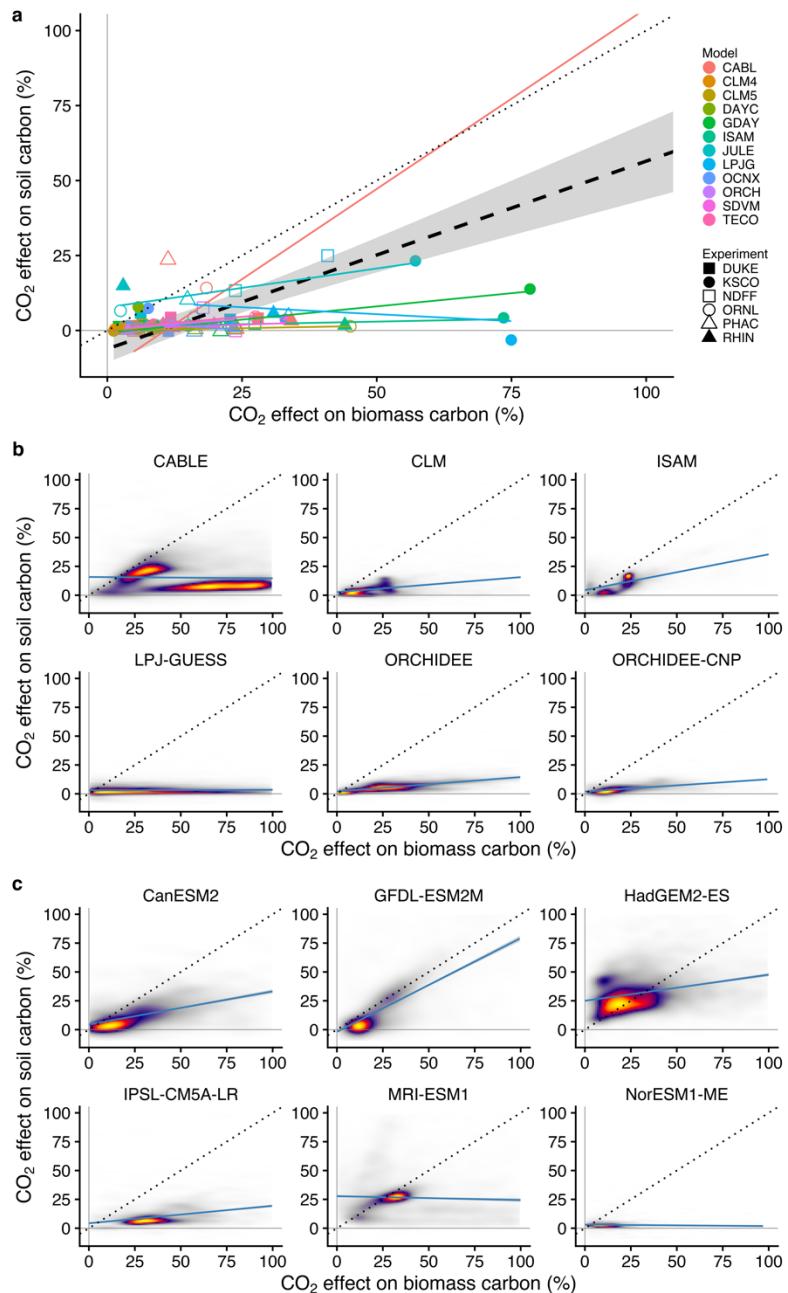
**Extended Data Figure 7 | Relationship between the effects of CO₂ on aboveground biomass and soil carbon across individual models from three model ensembles**. (a) FACE Model Data Synthesis Phase 2. Individual model results are represented by colored symbols and lines. Each symbol represents one site; lines represent model-specific linear regressions. To ease interpretation of the results and the comparison with Fig. 4 axis limits are set. Dashed line and error band represent the linear regression line and standard error across all experiment-by-model results. (b) TRENDY v7 models. (c) CMIP5 models.
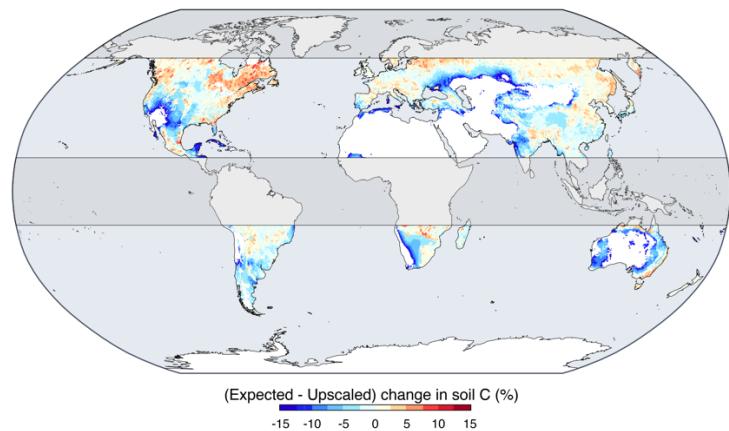
**Extended Data Figure 8 | Difference between expected CO₂ effects on soil carbon stocks based on TRENDY models and upscaled based on experiments**. Expected values result from the relationship between $\beta_{soil}$ and $\beta_{plant}$ coded in models. Positive values (red color) indicate an overestimation by models; negative values (blue color) indicate an underestimation by models.

**Extended Data Tables**
**Extended Data Table 1 | List of predictors used to examine and upscale the effects of elevated $CO_2$ on soil carbon.**

| Predictor | Source | Upscaling |
|---|---|---|
| Mean annual temperature (MAT) | reported in papers | scaled from CRU[77] |
| Mean annual precipitation (MAP) | reported in papers | scaled from CRU[77] |
| Duration of the experiment | reported in papers | non-important |
| Experiment type | reported in papers | scaled for FACE only |
| Ecosystem type | reported in papers | scaled from ESA land cover: http://maps.elie.ucl.ac.be/CCI/viewer/download.php |
| Vegetation type | reported in papers | non-important |
| Symbiotic type | reported in papers | scaled from ref[78] |
| Effect of elevated $CO_2$ on plant biomass | reported in papers | scaled from ref[12] |
| Disturbance | reported in papers | scaled from ESA land cover: http://maps.elie.ucl.ac.be/CCI/viewer/download.php |
| Nitrogen fertilization | reported in papers | scaled from ESA land cover: http://maps.elie.ucl.ac.be/CCI/viewer/download.php |
| Soil carbon stock in control plot | reported in papers | scaled from ref[79] |
| Soil depth of carbon measurements | reported in papers | scaled for 0-30 cm depth |
| Soil C:N ratio | [80] | [80] |
| Soil pH | [79] | Non-important |
| Soil available P | [81] | [81] |
| Maximum Leaf Area Index (LAImax) | 1 km year 2012 v2 land.copernicus.eu/global/products/lai | land.copernicus.eu/global/products/lai |
| Mean Leaf Area Index (LAImean) | 1 km year 2012 v2 | non-important |
| Maximum fraction of absorbed photosynthetically active radiation (fAPARmax) | 1 km year 2012 v2 land.copernicus.eu/global/products/fapar | land.copernicus.eu/global/products/fapar |
| Mean fraction of absorbed photosynthetically active radiation (fAPARmean) | 1 km year 2012 v2 | non-important |

**Extended Data Table 2 | Synthetic description of the basic characteristics of three model ensembles in terms of their treatment of CO$_2$ effects.**

| Model ensemble | Spatial extent | CO$_2$ concentration | Time CO$_2$ exposure | CO$_2$ increase |
|---|---|---|---|---|
| FACE-MDS 2 | Site-level (6 sites) | From current levels to elevated CO$_2$ ("future") | ~ 10 years | Step increase |
| TRENDY v7 S1 | Global | From preindustrial levels to current CO$_2$ ("historical") | 1700-2018 | Gradual |
| CMIP5 esmFixClim1 | Global | From current levels to elevated CO$_2$ ("future") | 50 years | Gradual |
| **Experiments** | **Site-level** | **From current levels to elevated CO$_2$ ("future")** | **~ 1-10 years** | **Step increase** |

**Supplementary Table 1 | Overview of CO$_2$ enrichment experiments included in the analysis.**

| Experiment | Type | Ecosystem | Duration | Citation |
|---|---|---|---|---|
| ArizonaFACE - wheat - high N | FACE | Agricultural | 1.5 | [82] |
| China FACE rice - high N - weakly | FACE | Agricultural | 3 | [83] |
| China FACE rice - high N - strongly | FACE | Agricultural | 3 | [83] |
| China FACE wheat - low N | FACE | Agricultural | 4 | [84] |
| China FACE wheat - high N | FACE | Agricultural | 4 | [84] |
| China OTC - low N | OTC | Tree Stand | 5 | [85,86] |
| China OTC - high N | OTC | Tree Stand | 5 | [85,86] |
| DUKE FACE | FACE | Tree Stand | 9 | [87] |
| EucFACE | FACE | Tree Stand | 4 | [39] |
| FACTS II - Aspen | FACE | Tree Stand | 11 | [88] |
| FACTS II - Aspen/Birch | FACE | Tree Stand | 11 | [88] |
| GiFACE | FACE | Grassland | 13.5 | [89] |
| Hohenheim | FACE | Agricultural | 4.5 | [90] |
| Jasper Ridge - sandstone | OTC | Grassland | 5.41 | [91] |
| Jasper Ridge - serpentine | OTC | Grassland | 3 | [91] |
| JRGCE - Control | FACE | Grassland | 14 | [92], pers.comm |
| JRGCE - N | FACE | Grassland | 14 | [92], pers.comm |
| Merritt Island | OTC | Tree Stand | 11 | [63], pers.comm |
| NewZealandFACE | FACE | Grassland | 13 | [93] |
| New Zealand Greenhouse | Chamber | Grassland | 0.75 | [94] |
| New Zealand OTC - P. radiata | OTC | Tree Stand | 6 | [95] |
| New Zealand OTC - N. fusca | OTC | Tree Stand | 6 | [95] |

| | | | | |
|---|---|---|---|---|
| ORNL FACE | FACE | Tree Stand | 11 | 96 |
| Placerville - low N | OTC | Tree Stand | 5.5 | 97 |
| Placerville - medium N | OTC | Tree Stand | 5.5 | 97 |
| Placerville - high N | OTC | Tree Stand | 5.5 | 97 |
| POPFACE - alba | FACE | Tree Stand | 2 | 98 |
| EUROFACE - alba | FACE | Tree Stand | 6 | 99 |
| POPFACE - euramericana | FACE | Tree Stand | 2 | 98 |
| POPFACE - euramericana | FACE | Tree Stand | 6 | 99 |
| POPFACE - nigra | FACE | Tree Stand | 2 | 98 |
| POPFACE - nigra | FACE | Tree Stand | 6 | 99 |
| Shortgrass Grassland | OTC | Grassland | 5 | 100 |
| SoyFACE | FACE | Agricultural | 6 | 101 |
| FACE Stillberg - larix | FACE | Tree Stand | 9 | 102,103 |
| FACE Stillberg - pinus | FACE | Tree Stand | 9 | 102,103 |
| SwissFACE- grass - low N | FACE | Grassland | 10 | 104 |
| SwissFACE- grass - high N | FACE | Grassland | 10 | 104 |
| SwissFACE- clover - low N | FACE | Grassland | 10 | 104 |
| SwissFACE- clover - high N | FACE | Grassland | 10 | 104 |
| Tallgrass Grassland | OTC | Grassland | 8 | 105 |
| UMBS - aspen | OTC | Tree Stand | 0.5 | 106 |
| WSL - loam, low N | OTC | Tree Stand | 3.75 | 107 |
| WSL - loam, high N | OTC | Tree Stand | 3.75 | 107 |
| WSL - sand, low N | OTC | Tree Stand | 3.75 | 107 |
| WSL - sand, high N | OTC | Tree Stand | 3.75 | 107 |

| | | | | |
|---|---|---|---|---|
| Nevada Desert FACE | FACE | Shrubland | 10 | 108,109 |
| BangorFACE - alnus | FACE | Tree Stand | 4 | 99,110 |
| BangorFACE - betula | FACE | Tree Stand | 4 | 99,110 |
| BangorFACE - fagus | FACE | Tree Stand | 4 | 99,110 |
| Tas FACE | FACE | Grassland | 6 | 111 |
| Ginninderra | Chamber | Grassland | 2 | 42 |
| Sky Oaks | Chamber | Shrubland | 6 | 112 |
| Antwerp OTC | OTC | Tree Stand | 3.75 | 113 |
| Lancaster - Abies alba | Chamber | Tree Stand | 1.25 | 114 |
| Lancaster - Abies alba | Chamber | Tree Stand | 1.25 | 114 |
| Lancaster - Betula pendula | Chamber | Tree Stand | 1.25 | 114 |
| Lancaster - Betula pendula | Chamber | Tree Stand | 1.25 | 114 |
| Lancaster - Carpinus betulus | Chamber | Tree Stand | 1.25 | 114 |
| Lancaster - Carpinus betulus | Chamber | Tree Stand | 1.25 | 114 |
| Lancaster - Fagus sylvatica | Chamber | Tree Stand | 1.25 | 114 |
| Lancaster - Fagus sylvatica | Chamber | Tree Stand | 1.25 | 114 |
| Lancaster - Pinus sylvestris | Chamber | Tree Stand | 1.25 | 114 |
| Lancaster - Pinus sylvestris | Chamber | Tree Stand | 1.25 | 114 |
| Lancaster - Quercus robur | Chamber | Tree Stand | 1.25 | 114 |
| Lancaster - Quercus robur | Chamber | Tree Stand | 1.25 | 114 |
| BioCON - Low N | FACE | Grassland | 10 | http://www.cedarcreek.umn.edu |
| BioCON - High N | FACE | Grassland | 10 | http://www.cedarcreek.umn.edu |
| BioCON - legumes - Low N | FACE | Grassland | 10 | http://www.cedarcreek.umn.edu |

| | | | | |
|---|---|---|---|---|
| BioCON - legumes - High N | FACE | Grassland | 10 | http://www.cedarcreek.umn.edu |
| Gainesville - Arachis glabrata | Chamber | Agricultural | 6 | [115] |
| Gainesville - Paspalum notatum | Chamber | Agricultural | 6 | [115] |
| Swiss Central Alps | OTC | Grassland | 3.17 | [116] |
| Swiss Central Alps F | OTC | Grassland | 3.17 | [116] |
| Swiss Jura | Chamber | Grassland | 6 | [117] |
| CLIMAITE | FACE | Shrubland | 8 | [118] |
| CLIMAITE D | FACE | Shrubland | 8 | [119] |
| CLIMAITE T | FACE | Shrubland | 8 | [119] |
| CLIMAITE TD | FACE | Shrubland | 8 | [119] |
| MBS - low N | OTC | Tree Stand | 1.5 | [120] |
| MBS - high N | OTC | Tree Stand | 1.5 | [120] |
| PHACE - ambient T | FACE | Grassland | 8 | [65] |
| PHACE - elevated T | FACE | Grassland | 8 | [65] |
| Rice-FACE - LN | FACE | Agricultural | 2 | [121,122] |
| Rice-FACE - HN | FACE | Agricultural | 2 | [121,122] |
| Rice-FACE2 - LN | FACE | Agricultural | 7 | [123,124] |
| Rice-FACE2 - HN | FACE | Agricultural | 10 | [123,124] |
| Rice-FACE3 | FACE | Agricultural | 5 | [125] |
| T-FACE - ambient T | FACE | Agricultural | 3 | [126,127] |
| T-FACE - elevated T | FACE | Agricultural | 3 | [126,127] |
| OTC Changbai Mountain Research | OTC | Tree Stand | 10 | [128,129] |
| Maoxian Field China | Chamber | Tree Stand | 6 | [130] |
| SoilFACE4 - LN | FACE | Agricultural | 0.5 | [131] |

| | | | | |
|---|---|---|---|---|
| SoilFACE4 - HN | FACE | Agricultural | 0.5 | [131] |
| SoilFACE4 - LN | FACE | Agricultural | 0.5 | [131] |
| SoilFACE4 - HN | FACE | Agricultural | 0.5 | [131] |
| OTC New Delhi | OTC | Agricultural | 2 | [132] |
| FACE NBRI - teak | FACE | Tree Stand | 3.83 | [133] |
| FACE NBRI - butea | FACE | Tree Stand | 3.83 | [133] |
| OTC Hyperaba India - 550ppm - C4 | OTC | Agricultural | 5 | [134] |
| OTC Hyperaba India - 700ppm - C4 | OTC | Agricultural | 5 | |
| OTC Hyperaba India - 550ppm - C3 | OTC | Agricultural | 5 | [134] |
| OTC Hyperaba India - 700ppm - C3 | OTC | Agricultural | 5 | [134] |
| OTC CRRI Cuttack India | OTC | Agricultural | 3 | [135] |
| FACE Sapporo - brown soil | FACE | Tree Stand | 10 | [136], pers.comm |
| FACE Sapporo - volcanic ash | FACE | Tree Stand | 10 | [137], pers.comm |
| Glasshouse University of Paris XI | Chamber | Agricultural | 0.67 | [138] |
| SAWFACE Spain | FACE | Wetland | 2 | [139] |

Myc: mycorrhizal type (AM: arbuscular mycorrhizae, ECM: ectomycorrhizae), F: nitrogen-fertilization treatment, W: high water treatment, T: high temperature treatment, D: drought treatment, P: phosphorus treatment, FACE: Free Air Carbon Dioxide Enrichment, G: Greenhouse/Growth chamber, OTC = Open Top Chamber