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Nitrogen and phosphorus constrain the CO₂ fertilization of global plant biomass

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The CO₂ fertilization effect on global plant biomass

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Supplementary information

1. Supplementary Discussion

1.1 Causes of the CO₂ fertilization effect. Several mechanisms have been suggested to explain the magnitude of the CO₂ fertilization effect. Nitrogen (N), or phosphorus (P) availability limit plant growth in most ecosystems^{27,55}, and have been shown to limit the magnitude of the CO₂ fertilization effect at local scales, especially for N^{1,4,26,56}, and also for P⁵. Previous work (e.g. ⁴) studied the role of N availability on the CO₂ fertilization of plant biomass using a qualitative assessment (i.e. either high or low N availability), but this categorical approach to N limitation cannot readily be applied to scale CO₂ effects from experiments to the globe. Therefore, we assessed different soil parameters readily available at the global scale that can quantitatively determine the role of nutrients on CO₂ fertilization, including soil C:N ratio⁵⁷, soil N content (%), P retention potential, P amount, cation exchange capacity (CEC), soil clay content (%) and pH, which is a critical determinant of phosphorus availability⁵⁸ and microbial diversity⁵⁹. A full list of the potential predictors we examined is available in Supplementary Table 2.

In addition to the direct effect of eCO₂ on photosynthesis⁶, eCO₂ lowers stomatal conductance⁶⁰, potentially reducing plant water use^{61,62}. This indirect effect of eCO₂ on water use has therefore been hypothesized to cause relatively greater growth and biomass responses to eCO₂ in drier environments⁶³. The hypothesis is supported by some grassland experiments from drier regions that have shown greater biomass responses to eCO₂ in drier than wetter years^{64,65}. However, a recent study suggests these larger eCO₂ effects in drier than wet years might have been driven by the negative effect of wet-season precipitation on N availability, and not by total precipitation⁶⁶. A meta-analysis of widely distributed grasslands found no relationship between mean annual precipitation (MAP) and eCO₂-driven biomass increase⁶⁷, and many studies have shown low growth enhancements by eCO₂ when water supply is reduced^{3,68}. Thus, no general support for this hypothesis has to our knowledge been found. Here, we study the role of MAP, aridity, soil moisture, Annual Average Water Limitation and other factors as potential predictors of the eCO₂ effect on biomass (Supplementary Table 2).

Predictors other than soil nutrient and water availability have also been invoked as modulators of the magnitude of the CO₂ fertilization effect. Some of these factors are associated with vegetation and climate attributes, including biome type (e.g. tropical, boreal, temperate forest, grassland, cropland, shrubland), the age of the vegetation, with potentially

relatively smaller responses in mature than younger plants⁶⁹, temperature³², and the type of mycorrhizal fungi associated with the plants⁴—which impacts plant nutrient availability⁷⁰—. Attributes of the experimental system can also influence results, including the type of eCO₂ experiment⁷¹ -which may increase the availability of nutrients to plants in chambers as compared to Free Air Carbon Dioxide Enrichment (FACE) designs⁷², and the duration of the experiment -as the magnitude of the effect may decrease over time due to a progressive reduction in N-availability^{1,73}.

We thus considered predictors of four different categories: climatic, nutritional, vegetative and experimental (Supplementary Table 2) and run a random-forest approach in the context of meta-analysis for the selection of the important predictors of the eCO₂ effect. As a sensitivity test, we also used likelihood model fitting with model selection guided by information criteria (specifically, Akaike's Information Criterion corrected for small sample sizes, AICc). Model selection through AICc, though robust, is slow, and cannot be used to test interactions when the number of predictors is large and also assumes all relationships are linear. We thus i) used random-meta-forest as preferred approach to rank predictors by their importance, identify the best predictors and visualize the shape of the regressions; and ii) used AICc model selection fitting all possible models containing only the most important predictors and their interactions, including transformations for nonlinear variables, in order to obtain the best AICc final model.

Map-based predictors on soil P and climate were correlated. We thus used principal component analysis (PCA) to extract individual components before including them in model selection. PCA suggested one component for soil P measurements extracted from gridded datasets (*P_pca*) and two components for climate predictors extracted from gridded datasets (*clima_pca1*, *clima_pca2*). We included all field-based predictors, together with PCA map-based predictors in a bootstrapped random-forest meta-analysis recursive preselection. We trained a random-forest meta-analysis with preselected predictors and calculated variable importance (Supplementary Fig. 3). Based on Partial Dependence plots (Supplementary Fig. 5), we used reciprocal transformations for nonlinear predictors showing ceiling/floor effects (1/variable). We included the 10 most important predictors in a mixed-effects meta-regression model, including reciprocal transformations for soil C:N, P, MAP, MAT and *P_pca*. Finally, we pruned the model once (Supplementary Table 5) keeping only significant predictors. The final model was $y \sim Myc \times C:N + Myc \times P + Fumigation.type$ (pseudo-R² = 0.9385), with *Myc* as mycorrhizal status (AM or ECM). As a sensitivity test, we run model-selection using maximum likelihood estimation. The best AICc-model confirmed the results from the meta-forest analysis.

The larger CO₂ effect on aboveground biomass in OTC than FACE was already found in previous meta-analyses^{71,74,75}. de Graaff et al.⁷¹ argued these differences could be potentially driven by i) the higher CO₂ concentrations, and ii) younger age in OTC than FACE. However, these multiple effects and their interactions were not statistically quantified. We have simultaneously quantified the effects of multiple potential predictors by random-forest and multiple meta-regression, and found that even after accounting for the effect of [CO₂] and age, fumigation type still significantly ($p\text{-value} < 0.0001$) influences biomass responses

to CO₂. We hypothesise that the larger responses found in OTC than FACE are driven by differences in microenvironment, edge effects and hidden design effects:

- Microenvironment. Chambers affect temperature and precipitation, but these effects are accounted for in the model through MAT and MAP. Chambers can also affect relative humidity, air circulation and boundary layer. However, these factors are less likely to significantly affect the magnitude of CO₂ effects systematically.
- Edge effects. OTC and chambers are smaller than FACE plots, so there is greater potential for edge effects in OTC and chamber plots. However, we hypothesise that edge effects could have both positive and negative effects, determined by the balance between the inputs of nutrients and water from lateral flow, and the outputs extracted by plants from outside the plots.
- Hidden design effects. Experiments using chambers are more likely to be in ecosystems in earlier stages of development, with planted rather than intact systems, and with disturbed rather than intact soils. As a result, plants in OTC may experience greater resource supply and less competition (fewer neighbours and less canopy density). These differences are likely to play an important role⁷², and thus we extrapolated the response found in FACE experiments only.

We conducted a sensitivity analysis to ensure that the relationships we found were consistent across our full dataset of 205 studies. Using estimates of soil N and P, we inferred missing data in the studies that were initially excluded (Supplementary Table 3) due to data missingness (Methods). This sensitivity analysis confirmed that the CO₂ stimulation of biomass was best described by soil C:N (p -value<0.001), P (p -value<0.001), Fumigation type (p -value<0.001) and Mycorrhizal type (p -value= 0.0085), although using approximated C:N and P data reduced the variability explained by the model ($pseudo-R^2=0.52$).

None of the climate predictors included in the analysis were important in predicting the CO₂ effect on biomass (Supplementary Figs. 3-5), and thus were not included in the final model. When excluding nutrient-related predictors, MAT and MAP alone had very low predictive power ($y \sim MAP + MAT + Fumigation.type$, $R^2=0.05$, AICc = -107.54, p -value = 0.9779 and 0.5377 for MAT and MAP, respectively). Indeed, once the effects of mycorrhizal type, C:N and P were accounted for, MAT and MAP did not significantly influence the outcome ($y \sim Myc \times C:N + Myc \times P + MAP + MAT + Fumigation.type$), as illustrated in Supplementary Fig. 4c-f. Actually, including MAT and MAP in the final model reduced the quality of the model (AICc from -168.52 to -159.00), and were thus excluded as initially suggested by our model selection analysis.

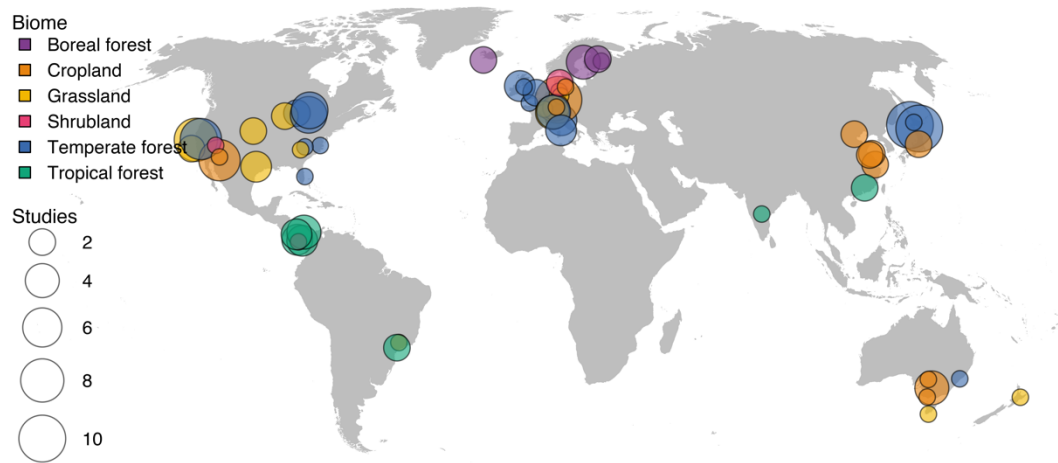
In a recent paper, Hovenden *et al.*⁷⁶ synthesized biomass production responses to eCO₂ across 19 temperate grassland experiments, and found positive effects associated with mean spring precipitation and negative effects associated with mean precipitation in seasons other than spring. Some of the climate proxies associated with precipitation seasonality in our study are statistically significant for grasslands (n=26), consistent with the findings by Hovenden *et al.*⁷⁶ (Supplementary Fig. 8). In other ecosystems (n=138), however, climate proxies could

not explain any (additional) variation (Supplementary Fig. 8), and nutrient-related predictors were clearly better at predicting the CO₂ fertilization effect (Supplementary Fig. 3)". Our model selection approach accounted for interactions between climate and e.g. ecosystem type, suggesting that nutrients better describe variation in the dataset than interactions between ecosystems and climate.

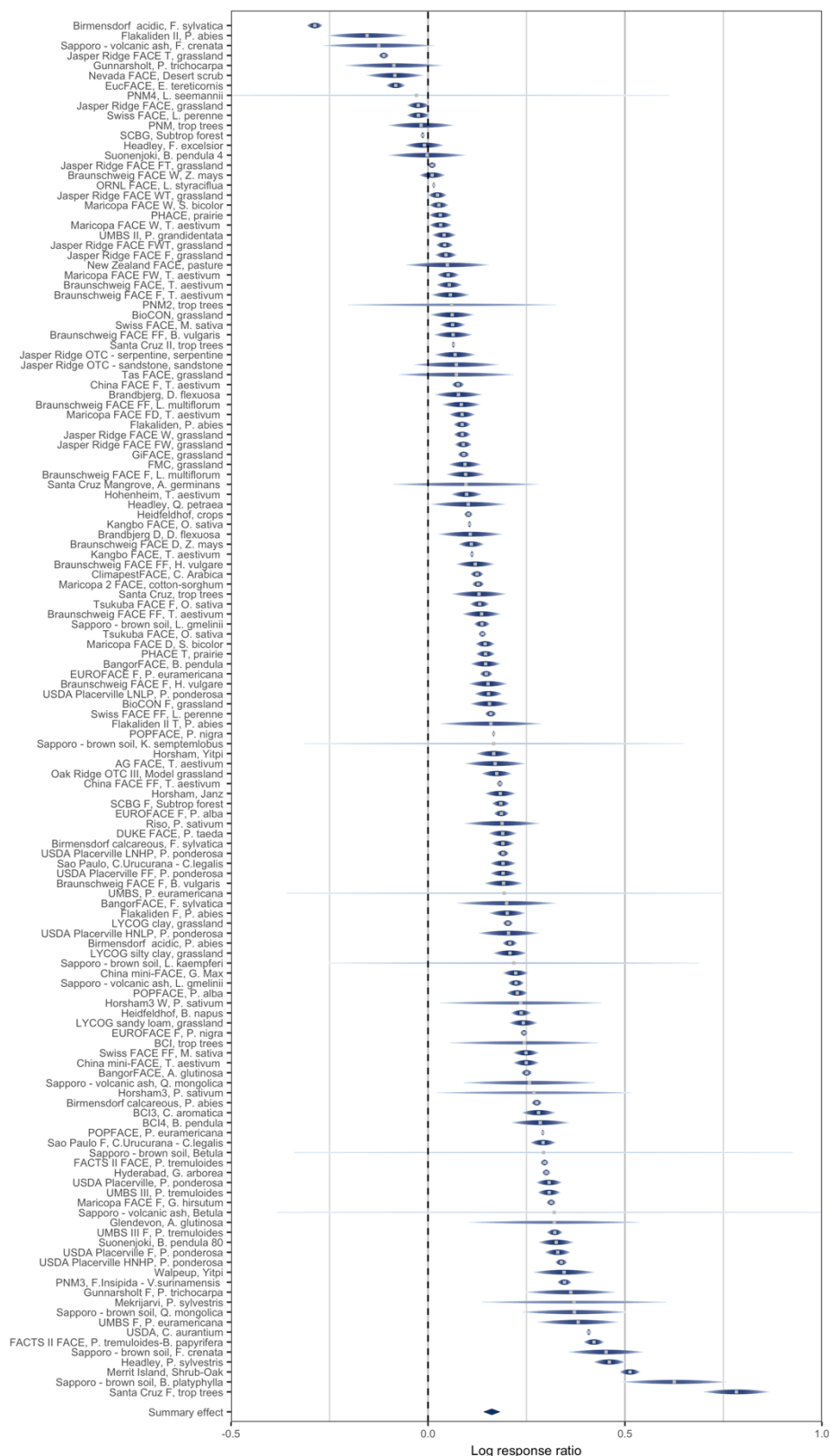
Model selection indicated that ΔCO_2 was not among the most important predictors (Supplementary Figs. 3,5). As a result, ΔCO_2 was not included as a covariate in the model, and the model results were not standardized for a particular ΔCO_2 value. We thus assumed that the results derived from this model represent an increase in atmospheric CO₂ of 250 ppm, from an average [CO₂] of 375 ppm in ambient plots, to an average [CO₂] of 625 ppm in elevated CO₂ plots.

The sensitivity of photosynthesis and productivity to CO₂ is not linear, with a higher sensitivity for e.g. over a 200-300 ppm range than over a 400-500 ppm range, thus resulting in a saturating effect as CO₂ concentration increases²⁸. For the saturating response in biomass, however, much less is known. Biomass lags productivity, and is influenced by the turnover times of various carbon pools within plants, precluding a direct assumption about the saturating effect on biomass. Our results do not provide any statistical evidence for a relationship between the magnitude of eCO₂ and the biomass response (Supplementary Figs. 3,5), so imposing a saturating response when none is present in our data would bias the results. Consequently, when we standardized our model results for a 100 ppm increase in CO₂ (Fig. 3a), we assumed that the sensitivity of biomass to CO₂ is linear within the experimental range.

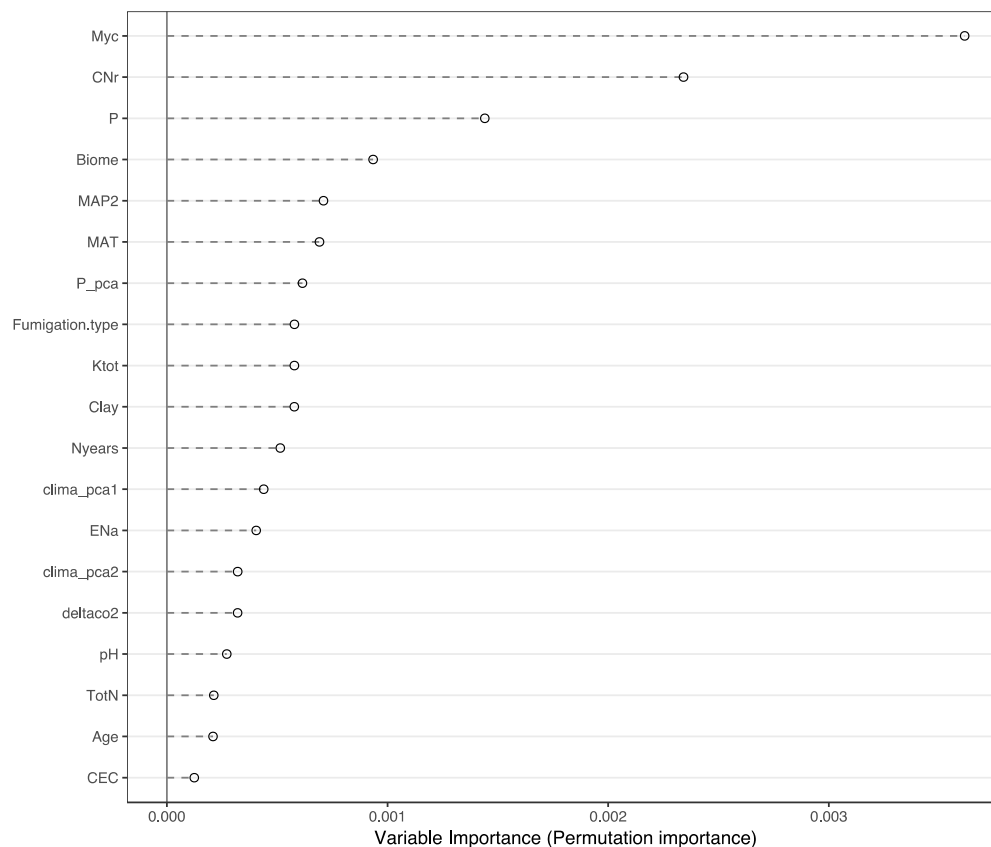
2. Supplementary Figures



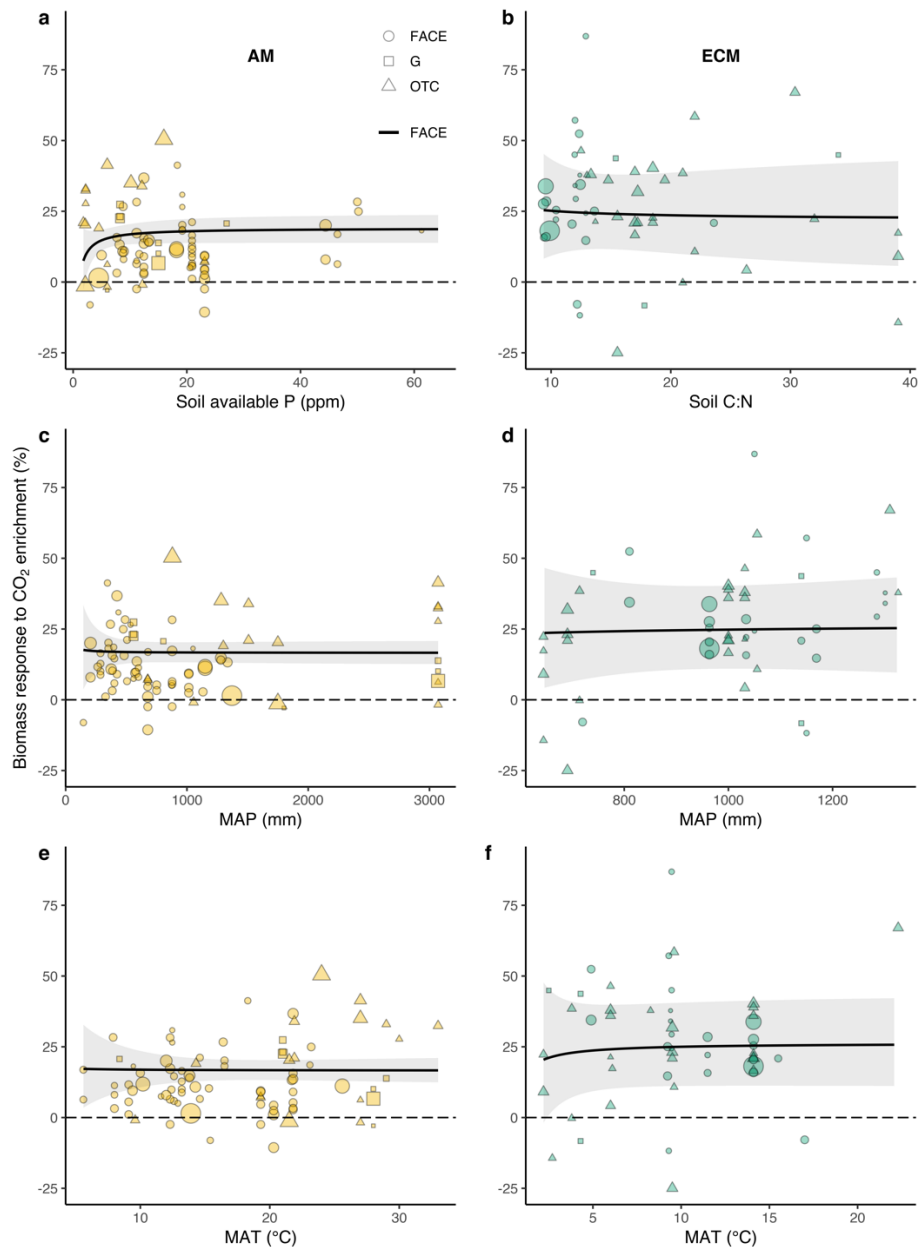
Supplementary Fig. 1. Geographical distribution of the 138 elevated CO₂ experiments included in the analysis. Colours indicate the type of biome and sizes indicate the number of studies at the same location to avoid overlap.



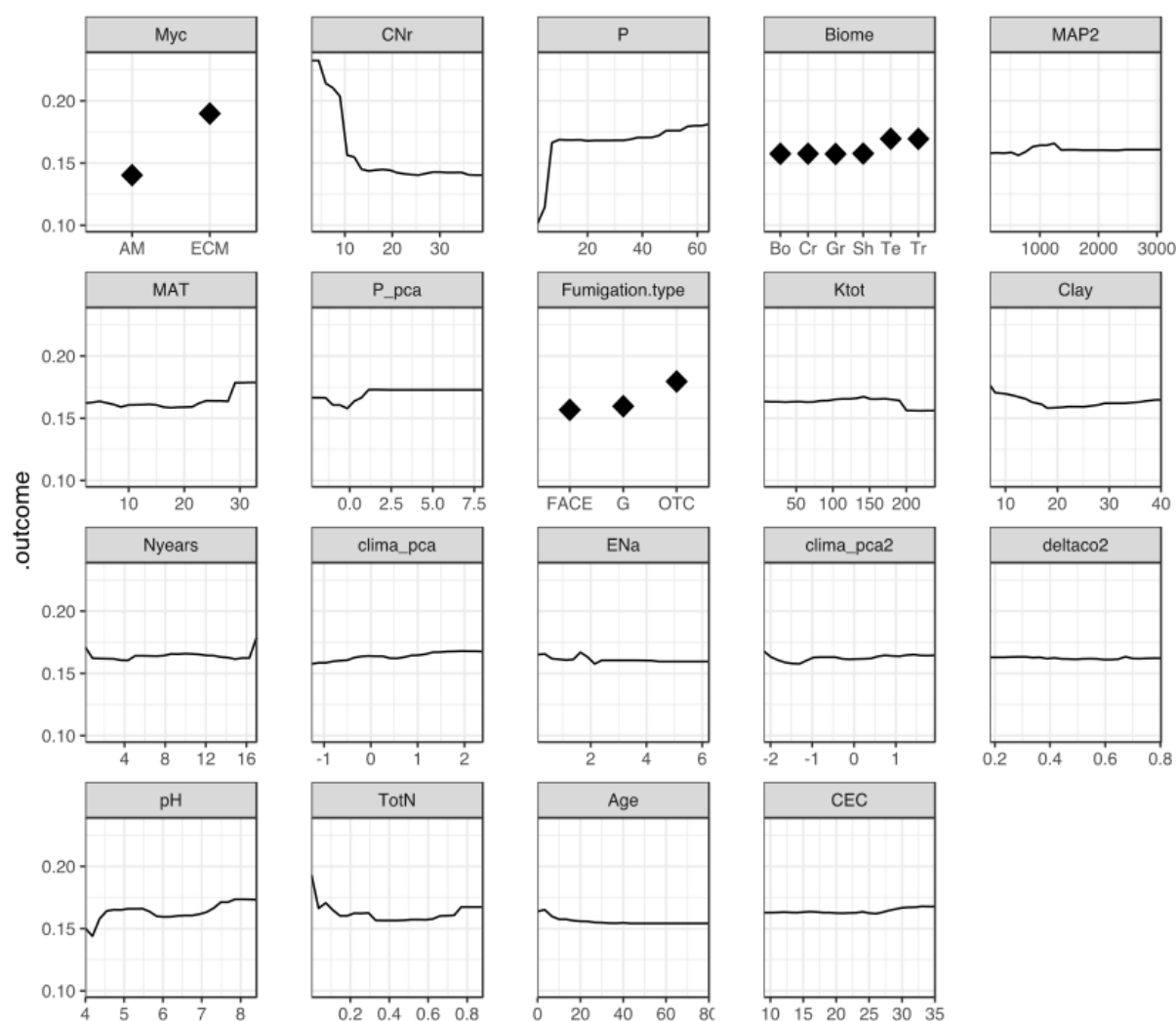
Supplementary Fig. 2. CO₂ effects on aboveground biomass included in the meta-analysis. More information can be found in Supplementary Table 1.



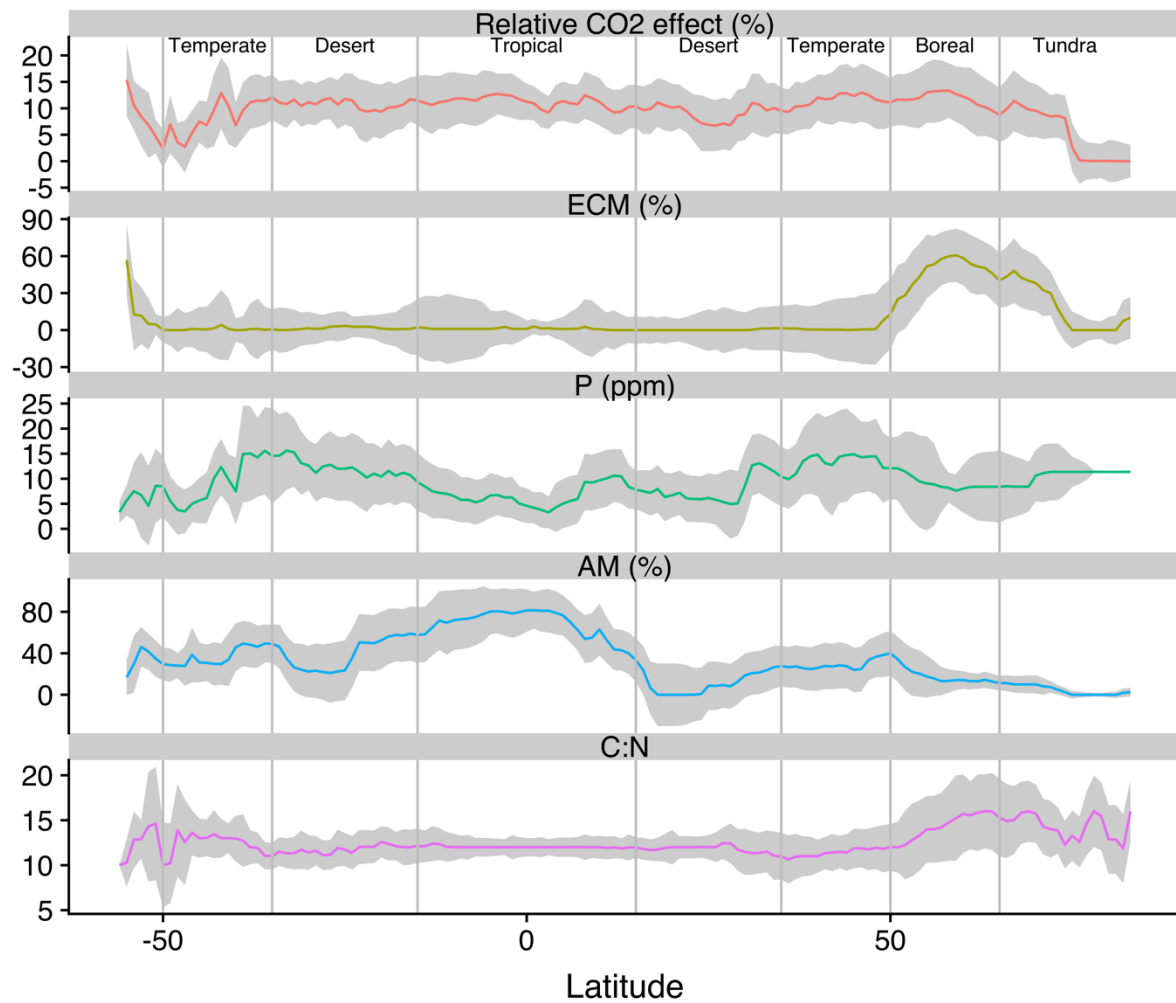
Supplementary Fig. 3. Variable importance of predictors of the effect of CO₂ on aboveground biomass. Variable importance values are derived from a weighted random-forest analysis including predictors as moderators in the model. More details about the different predictors in Supplementary Table 2. P_pca, clima_pca1 and clima_pca2 are the principal components of the redundant map-derived predictors for phosphorus availability and climate.



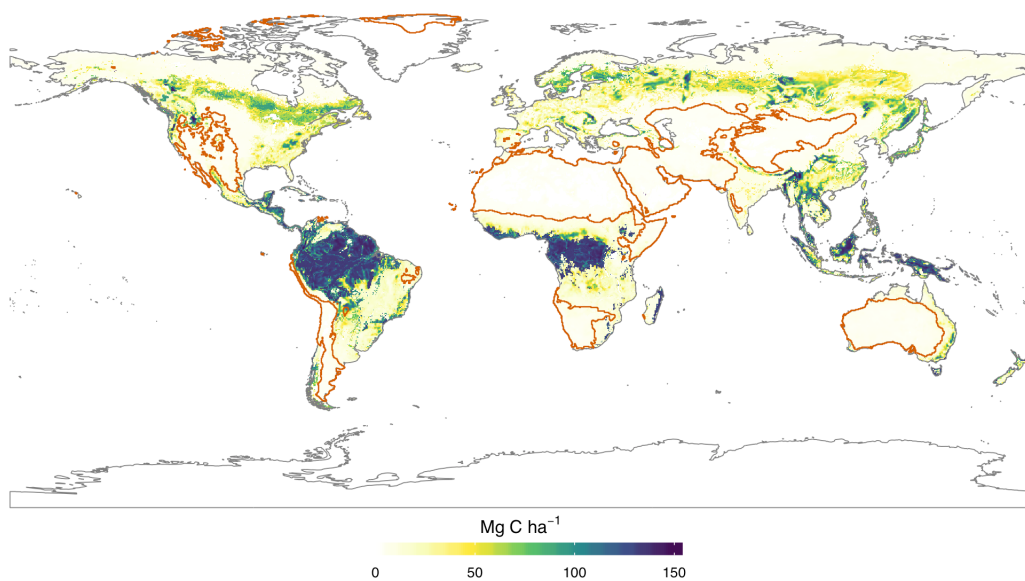
Supplementary Fig. 4. Regression plots of the CO₂ effect on aboveground biomass with soil C:N, soil phosphorus, mean annual precipitation (MAP) and mean annual temperature (MAT) in arbuscular (AM) (a,c,e) and ectomycorrhizal (ECM) (b,d,f) plants. (a,b) represent nonsignificant relationships in the final model ($y \sim \text{Myc} * \text{C:N} + \text{Myc} * \text{P} + \text{Fumigation.type}$). (c-f) represent the relationships $y \sim \text{MAP}$ and $y \sim \text{MAT}$ in the model ($y \sim \text{Myc} * \text{MAP} + \text{Myc} * \text{MAT} + \text{Myc} * \text{C:N} + \text{Myc} * \text{P} + \text{Fumigation.type}$) while keeping the rest of variables constant at their average values, here illustrating the lack of a significant relationship between MAP and MAT and the CO₂ effect once the main effects in the final model are accounted for. Regressions are based on a non-linear mixed-effects meta-regression model. Data points represent the individual studies in the dataset, with the size of the dots drawn proportional to the weights in the model. Point shapes represent the type of experiment, with regression lines representing the effect in FACE studies.



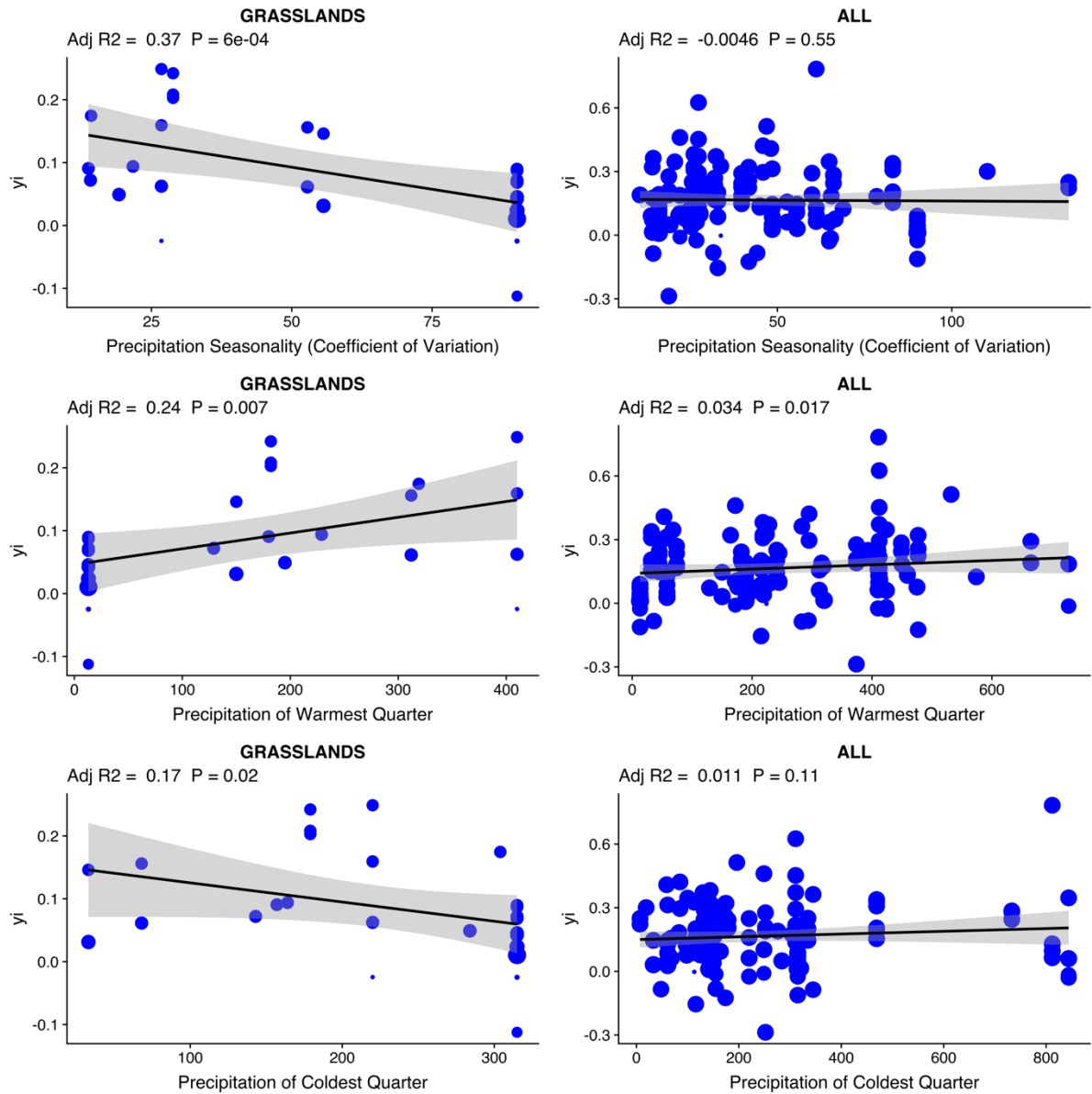
Supplementary Fig. 5. Partial dependence plots of the predictors of the elevated CO₂ effect on biomass. The figure shows the predicted CO₂ effect (y_i) as a function of the value of each predictor variable in a random-forest meta-analysis. Partial regression plots give a graphical depiction of the marginal effect of a variable on the response and the shape and direction of the relationship. Little variation in y_i across the values of a predictor reflects the low predictive power of the predictor for y_i . More details about the different predictors in Supplementary Table 2. P_pca, clima_pca1 and clima_pca2 are the principal components of the redundant map-derived predictors for phosphorus availability and climate.



Supplementary Fig. 6. latitudinal distribution of the relative effect of elevated CO₂ on aboveground biomass derived from 138 CO₂ experiments and its drivers: relative abundance of ectomycorrhizal (ECM) plant biomass, soil available phosphorus (P) by Bray1 method, relative abundance of arbuscular mycorrhizal (AM) plant biomass, and soil C:N ratio. Latitudinal distributions were computed as the average value of all pixels contained within 1° latitude. Error bands represent one standard deviation above and below the mean, and thus represent the geographical variability of the pixels contained within 1° latitude. Data sources and further details in Supplementary Table 2.



Supplementary Fig. 7. “Current” aboveground biomass in 2012 (ref¹⁸) from satellite passive microwave observations. Areas shaded in red have aridity index < 0.32.



Supplementary Fig. 8. Effect of seasonal precipitation on plant biomass responses to elevated CO₂. Regressions (and 95% confidence intervals) represent variation in the effect of elevated CO₂ on biomass with precipitation seasonality, precipitation of the warmest quarter and precipitation of the coldest quarter for grasslands (n=26) and all ecosystems (n=138) in the dataset. Data points represent the individual studies, with the size of the dots drawn proportional to the weights in the model.

3. Supplementary Tables

Supplementary Table 1. Overview of CO₂ enrichment experiments included in the main analysis. Abbreviations: Myc: mycorrhizal type (AM: arbuscular mycorrhizae, ECM: ectomycorrhizae), aC: CO₂ concentration in ambient (control) plots, eC: CO₂ concentration in elevated CO₂ plots, 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.

Study name	Species	System	Country	Myc	Facility	aC	eC	Ref.
AG FACE	<i>Triticum aestivum</i> , Yitpi	Agricultural	Australia	AM	FACE	365	550	77
BangorFACE	<i>Alnus glutinosa</i>	Tree Stand	UK	ECM	FACE	380	580	78
BangorFACE	<i>Betula pendula</i>	Tree Stand	UK	ECM	FACE	380	580	78
BangorFACE	<i>Fagus sylvatica</i>	Tree Stand	UK	ECM	FACE	380	580	79
BCI	Mixed tropical trees	Tree Stand	Panama	AM	OTC	380	720	80
BCI3	<i>Copaifera aromatica</i>	Tree Stand	Panama	AM	OTC	386	861	81
BCI4	<i>Beilschmiedia pendula</i>	Tree Stand	Panama	AM	OTC	380	790	82
BioCON	perennial grassland, legumes excluded	Grassland	USA	AM	FACE	360	560	56
BioCON F	perennial grassland, legumes excluded	Grassland	USA	AM	FACE	360	560	56
Birmensdorf acidic	<i>Fagus sylvatica</i>	Tree Stand	Switzerland	ECM	OTC	370	570	83
Birmensdorf acidic	<i>Picea abies</i>	Tree Stand	Switzerland	ECM	OTC	370	570	83
Birmensdorf calcareous	<i>Fagus sylvatica</i>	Tree Stand	Switzerland	ECM	OTC	370	570	83
Birmensdorf calcareous	<i>Picea abies</i>	Tree Stand	Switzerland	ECM	OTC	370	570	83
Brandbjerg	<i>Deschampsia flexuosa</i>	Scrubland	Denmark	AM	FACE	380	510	84
Brandbjerg D	<i>Deschampsia flexuosa</i>	Scrubland	Denmark	AM	FACE	380	510	84
Braunschweig FACE	<i>Triticum aestivum</i>	Agricultural	Germany	AM	FACE	400	600	85
Braunschweig FACE D	<i>Zea mays</i>	Agricultural	Germany	AM	FACE	400	600	86
Braunschweig FACE F	<i>Hordeum vulgare</i>	Agricultural	Germany	AM	FACE	400	600	87
Braunschweig FACE F	<i>Beta vulgaris</i>	Agricultural	Germany	AM	FACE	400	600	87
Braunschweig FACE F	<i>Lolium multiflorum</i>	Agricultural	Germany	AM	FACE	400	600	87
Braunschweig FACE F	<i>Triticum aestivum</i>	Agricultural	Germany	AM	FACE	400	600	87
Braunschweig FACE FF	<i>Hordeum vulgare</i>	Agricultural	Germany	AM	FACE	400	600	87
Braunschweig FACE FF	<i>Beta vulgaris</i>	Agricultural	Germany	AM	FACE	400	600	87
Braunschweig FACE FF	<i>Lolium multiflorum</i>	Agricultural	Germany	AM	FACE	400	600	87
Braunschweig FACE FF	<i>Triticum aestivum</i>	Agricultural	Germany	AM	FACE	400	600	87

Braunschweig FACE W	<i>Zea mays</i>	Agricultural	Germany	AM	FACE	400	600	86
China FACE F	<i>Triticum aestivum</i>	Agricultural	China	AM	FACE	380	580	88
China FACE FF	<i>Triticum aestivum</i>	Agricultural	China	AM	FACE	380	580	88
China mini- FACE	<i>Glycine max</i>	Agricultural	China	AM	FACE	415	550	89
China mini- FACE	<i>Triticum aestivum</i>	Agricultural	China	AM	FACE	415	550	90
ClimapestFAC E	<i>Coffea arabica</i>	Agricultural	Brazil	AM	FACE	390	550	91
DUKE FACE	<i>Pinus taeda</i>	Tree Stand	USA	ECM	FACE	380	570	2
EucFACE	<i>Eucalyptus tereticornis</i>	Tree Stand	Australia	ECM	FACE	400	550	5
EUROFACE F	<i>Populus alba</i>	Tree Stand	Italy	ECM	FACE	370	550	92
EUROFACE F	<i>Populus euramericana</i>	Tree Stand	Italy	ECM	FACE	370	550	92
EUROFACE F	<i>Populus nigra</i>	Tree Stand	Italy	ECM	FACE	370	550	92
FACTS II FACE	<i>Populus tremuloides</i>	Tree Stand	USA	ECM	FACE	370	532	93
FACTS II FACE	<i>Populus tremuloides-Betula papyrifera</i>	Tree Stand	USA	ECM	FACE	370	532	93
Flakaliden	<i>Picea abies</i>	Tree Stand	Sweden	ECM	OTC	365	700	94
Flakaliden F	<i>Picea abies</i>	Tree Stand	Sweden	ECM	OTC	365	700	94
Flakaliden II	<i>Picea abies</i>	Tree Stand	Sweden	ECM	OTC	365	700	94
Flakaliden II T	<i>Picea abies</i>	Tree Stand	Sweden	ECM	OTC	365	700	94
FMC	grassland	Grassland	France	AM	FACE	395	588	95
GiFACE	grassland	Grassland	Germany	AM	FACE	380	456	96
Glendevon	<i>Alnus glutinosa</i>	Tree Stand	UK	ECM	OTC	350	700	31
Gunnarsholt	<i>Populus trichocarpa</i>	Tree Stand	Iceland	ECM	G	350	700	97
Gunnarsholt F	<i>Populus trichocarpa</i>	Tree Stand	Iceland	ECM	G	350	700	97
Headley	<i>Fraxinus excelsior</i>	Tree Stand	UK	AM	OTC	350	700	98
Headley	<i>Pinus sylvestris</i>	Tree Stand	UK	ECM	OTC	350	700	98
Headley	<i>Quercus petraea</i>	Tree Stand	UK	ECM	OTC	350	700	98
Heidfeldhof	<i>Brassica napus</i>	Agricultural	Germany	AM	FACE	380	530	99
Heidfeldhof	Mixed crops	Agricultural	Germany	AM	FACE	380	530	100
Hohenheim	<i>Triticum aestivum</i>	Agricultural	Germany	AM	FACE	409	537	101
Horsham	<i>Triticum aestivum, Janz</i>	Agricultural	Australia	AM	FACE	366	550	102
Horsham	<i>Triticum aestivum, Yitpi</i>	Agricultural	Australia	AM	FACE	366	550	102
Horsham3	<i>Pisum sativum</i>	Agricultural	Australia	AM	FACE	366	550	103
Horsham3 W	<i>Pisum sativum</i>	Agricultural	Australia	AM	FACE	366	550	103
Hyderabad	<i>Gmelina arborea</i>	Tree Stand	India	AM	OTC	360	460	104
Jasper Ridge FACE	annual grassland	Grassland	USA	AM	FACE	380	680	105
Jasper Ridge FACE F	annual grassland	Grassland	USA	AM	FACE	380	680	105
Jasper Ridge FACE FT	annual grassland	Grassland	USA	AM	FACE	380	680	105
Jasper Ridge FACE FW	annual grassland	Grassland	USA	AM	FACE	380	680	105

Jasper Ridge FACE FWT	annual grassland	Grassland	USA	AM	FACE	380	680	105
Jasper Ridge FACE T	annual grassland	Grassland	USA	AM	FACE	380	680	105
Jasper Ridge FACE W	annual grassland	Grassland	USA	AM	FACE	380	680	105
Jasper Ridge FACE WT	annual grassland	Grassland	USA	AM	FACE	380	680	105
Jasper Ridge OTC - sandstone	Sandstone grassland	Grassland	USA	AM	OTC	360	720	106
Jasper Ridge OTC - serpentine	Serpentine grassland	Grassland	USA	AM	OTC	360	720	107
Kangbo FACE	<i>Oryza sativa</i>	Agricultural	China	AM	FACE	400	511	108
Kangbo FACE	<i>Triticum aestivum</i>	Agricultural	China	AM	FACE	400	490	108
LYCOG clay	Grassland	Grassland	USA	AM	G	350	475	109
LYCOG sandy loam	Grassland	Grassland	USA	AM	G	350	475	109
LYCOG silty clay	Grassland	Grassland	USA	AM	G	350	475	109
Maricopa 2 FACE	<i>Gossypium hirsutum-Sorghum bicolor</i>	Agricultural	USA	AM	FACE	370	550	110
Maricopa FACE D	<i>Sorghum bicolor</i>	Agricultural	USA	AM	FACE	370	550	111
Maricopa FACE F	<i>Gossypium hirsutum</i>	Agricultural	USA	AM	FACE	370	550	112
Maricopa FACE FD	<i>Triticum aestivum</i>	Agricultural	USA	AM	FACE	370	550	113
Maricopa FACE FW	<i>Triticum aestivum</i>	Agricultural	USA	AM	FACE	370	550	113
Maricopa FACE W	<i>Sorghum bicolor</i>	Agricultural	USA	AM	FACE	370	550	111
Maricopa FACE W	<i>Triticum aestivum</i>	Agricultural	USA	AM	FACE	370	550	113
Mekrijarvi	<i>Pinus sylvestris</i>	Tree Stand	Finland	ECM	G	380	700	114
Merrit Island	Shrub Oak system	Tree Stand	USA	ECM	OTC	370	720	115
Nevada FACE	Desert scrub	Scrubland	USA	AM	FACE	380	550	53
New Zealand FACE	temperate pasture	Grassland	New Zealand	AM	FACE	366	470	116
Oak Ridge OTC III	Model grassland	Grassland	USA	AM	OTC	380	680	117
ORNL FACE	<i>Liquidambar styraciflua</i>	Tree Stand	USA	AM	FACE	380	550	1
PHACE	Mixed-grass prairie	Grassland	USA	AM	FACE	385	600	118
PHACE T	Mixed-grass prairie	Grassland	USA	AM	FACE	385	600	118
PNM	Mixed tropical trees	Tree Stand	Panama	AM	OTC	350	700	119
PNM2	Mixed tropical trees	Tree Stand	Panama	AM	OTC	380	700	120
PNM3	<i>Ficus insipida, Virola surinamensis</i>	Tree Stand	Panama	AM	OTC	380	730	121
PNM4	<i>Luehea seemannii</i>	Tree Stand	Panama	AM	G	360	754	122
POPFACE	<i>Populus alba</i>	Tree Stand	Italy	ECM	FACE	385	550	123
POPFACE	<i>Populus euramericana</i>	Tree Stand	Italy	ECM	FACE	385	550	123
POPFACE	<i>Populus nigra</i>	Tree Stand	Italy	ECM	FACE	385	550	123

Riso	<i>Pisum sativum</i> and field fungi	Agricultural	Denmark	AM	G	368	688	124
Santa Cruz	Mixed tropical trees	Tree Stand	Panama	AM	G	400	700	21
Santa Cruz F	Mixed tropical trees	Tree Stand	Panama	AM	G	400	700	21
Santa Cruz II	<i>Araucaria, Tabebuia, Chrysophyllum and Podocarpus</i>	Tree Stand	Panama	AM	G	400	800	125
Santa Cruz Mangrove	<i>Avicennia germinans</i>	Shrubland	Panama	AM	G	400	800	126
Sao Paulo	<i>Croton urucurana, Cariniana legalis</i>	Tree Stand	Brazil	AM	OTC	380	660	127
Sao Paulo F	<i>Croton urucurana, Cariniana legalis</i>	Tree Stand	Brazil	AM	OTC	380	660	127
Sapporo - brown soil	<i>Betula sp.</i>	Tree Stand	Japan	ECM	FACE	370	500	128
Sapporo - brown soil	<i>Larix gmelinii</i>	Tree Stand	Japan	ECM	FACE	370	500	128
Sapporo - brown soil	<i>Betula platyphylla</i>	Tree Stand	Japan	ECM	FACE	370	500	129
Sapporo - brown soil	<i>Fagus crenata</i>	Tree Stand	Japan	ECM	FACE	370	500	128
Sapporo - brown soil	<i>Kalopanax septemlobus</i>	Tree Stand	Japan	AM	FACE	370	500	129
Sapporo - brown soil	<i>Larix kaempferi</i>	Tree Stand	Japan	ECM	FACE	370	500	128
Sapporo - brown soil	<i>Quercus mongolica</i>	Tree Stand	Japan	ECM	FACE	370	500	128
Sapporo - volcanic ash	<i>Betula sp.</i>	Tree Stand	Japan	ECM	FACE	370	500	128
Sapporo - volcanic ash	<i>Larix gmelinii</i>	Tree Stand	Japan	ECM	FACE	370	500	129
Sapporo - volcanic ash	<i>Fagus crenata</i>	Tree Stand	Japan	ECM	FACE	370	500	128
Sapporo - volcanic ash	<i>Quercus mongolica</i>	Tree Stand	Japan	ECM	FACE	370	500	128
SCBG	Subtrop forest	Tree Stand	China	AM	OTC	380	700	130
SCBG F	Subtrop forest	Tree Stand	China	AM	OTC	380	700	130
Suonenjoki	<i>Betula pendula</i> clone4	Tree Stand	Finland	ECM	OTC	360	720	131
Suonenjoki	<i>Betula pendula</i> clone80	Tree Stand	Finland	ECM	OTC	360	720	131
Swiss FACE	<i>Lolium perenne</i>	Grassland	Switzerland	AM	FACE	350	600	132
Swiss FACE	<i>Medicago sativa</i>	Grassland	Switzerland	AM	FACE	350	600	133
Swiss FACE FF	<i>Lolium perenne</i>	Grassland	Switzerland	AM	FACE	350	600	132
Swiss FACE FF	<i>Medicago sativa</i>	Grassland	Switzerland	AM	FACE	350	600	133
Tas FACE	Temperate grassland	Grassland	Australia	AM	FACE	372	550	66
Tsukuba FACE	<i>Oryza sativa</i>	Agricultural	Japan	AM	FACE	385	585	134
Tsukuba FACE F	<i>Oryza sativa</i>	Agricultural	Japan	AM	FACE	385	585	135
UMBS	<i>Populus euramericana</i>	Tree Stand	USA	ECM	OTC	345	690	136
UMBS F	<i>Populus euramericana</i>	Tree Stand	USA	ECM	OTC	345	690	136
UMBS II	<i>Populus grandidentata</i>	Tree Stand	USA	ECM	OTC	342	692	137

UMBS III	<i>Populus tremuloides</i>	Tree Stand	USA	ECM	OTC	367	715	138
UMBS III F	<i>Populus tremuloides</i>	Tree Stand	USA	ECM	OTC	367	715	138
USDA	<i>Citrus aurantium</i>	Tree Stand	USA	AM	OTC	380	680	139
USDA Placerville	<i>Pinus ponderosa</i>	Tree Stand	USA	ECM	OTC	352	700	140
USDA Placerville F	<i>Pinus ponderosa</i>	Tree Stand	USA	ECM	OTC	352	700	140
USDA Placerville FF	<i>Pinus ponderosa</i>	Tree Stand	USA	ECM	OTC	352	700	140
USDA Placerville HNHP	<i>Pinus ponderosa</i>	Tree Stand	USA	ECM	OTC	352	700	141
USDA Placerville HNLP	<i>Pinus ponderosa</i>	Tree Stand	USA	ECM	OTC	352	700	141
USDA Placerville LNHP	<i>Pinus ponderosa</i>	Tree Stand	USA	ECM	OTC	352	700	141
USDA Placerville LNLP	<i>Pinus ponderosa</i>	Tree Stand	USA	ECM	OTC	352	700	141
Walpeup	<i>Triticum aestivum</i> , <i>Yitpi</i>	Agricultural	Australia	AM	FACE	366	550	102

Supplementary Table 2. List of predictors used to examine the effects of elevated CO₂ on aboveground biomass.

Predictor	Type	Source	Reference
Mean annual temperature (MAT)	Climatic	reported in papers	scaled from ref ³⁴
Mean annual precipitation (MAP)	Climatic	reported in papers	scaled from ref ³⁴
Potential evapotranspiration (PET)	Climatic	SPLASH, 0.5° 1982-2016	142
Aridity index	Climatic	CGIAR-CSI Global-Aridity, 30 arcsec	51
Growing season temperature 5°C	Climatic	mean temp months > 5°C, CRU TS v. 4.00, 2010-2015, 0.5°	calculated from ref ³⁴
Growing season temperature 0°C	Climatic	mean temp months > 0°C, CRU TS v. 4.00, 2010-2015, 0.5°	calculated from ref ³⁴
Annual Growing Degree Days	Climatic	degree days accumulated with temp > 5°C, CRU TS v. 4.00, 2010-2015, 0.5°	calculated from ref ³⁴
Actual Evapotranspiration (AET)	Climatic	SPLASH, 0.5° 1982-2016	142
Annual Average Water Limitation	Climatic	Mean daily AET/PET	calculated
Moisture Index	Climatic	MAP/PET	calculated
Solar Radiation	Climatic	WORLDCLIM V2 30 arcsec	143
Mean Diurnal Range	Climatic	WORLDCLIM V2 30 arcsec	143
Isothermality	Climatic	WORLDCLIM V2 30 arcsec	143
Temperature Seasonality (standard deviation *100)	Climatic	WORLDCLIM V2 30 arcsec	143
Max Temperature of Warmest Month	Climatic	WORLDCLIM V2 30 arcsec	143
Min Temperature of Coldest Month	Climatic	WORLDCLIM V2 30 arcsec	143
Temperature Annual Range	Climatic	WORLDCLIM V2 30 arcsec	143
Mean Temperature of Wettest Quarter	Climatic	WORLDCLIM V2 30 arcsec	143
Mean Temperature of Driest Quarter	Climatic	WORLDCLIM V2 30 arcsec	143
Mean Temperature of Warmest Quarter	Climatic	WORLDCLIM V2 30 arcsec	143
Mean Temperature of Coldest Quarter	Climatic	WORLDCLIM V2 30 arcsec	143
Precipitation of Wettest Month	Climatic	WORLDCLIM V2 30 arcsec	143
Precipitation of Driest Month	Climatic	WORLDCLIM V2 30 arcsec	143
Precipitation Seasonality (Coefficient of Variation)	Climatic	WORLDCLIM V2 30 arcsec	143
Precipitation of Wettest Quarter	Climatic	WORLDCLIM V2 30 arcsec	143
Precipitation of Driest Quarter	Climatic	WORLDCLIM V2 30 arcsec	143
Precipitation of Warmest Quarter	Climatic	WORLDCLIM V2 30 arcsec	143
Precipitation of Coldest Quarter	Climatic	WORLDCLIM V2 30 arcsec	143
Gaussen index	Climatic	MAP/2*MAT	calculated from reported data
Soil C:N ratio	Nutritional	reported in papers	scaled from ref ⁴⁷
Soil pH	Nutritional	reported in papers	
Soil nitrogen content (%)	Nutritional	reported in papers	
Mycorrhizal type	Nutritional	reported in papers	scaled from ref ²⁴
Soil phosphorus (P) retention potential	Nutritional	ISRIC, 5 arcmin	144

Soil P amount by Bray1 method	Nutritional	reported in papers	scaled from ref ¹⁴⁵
Soil P amount by Olsen method	Nutritional	GSDE, 30 arcsec	145
Soil P amount by Mehlich method	Nutritional	GSDE, 30 arcsec	145
Total P	Nutritional	GSDE, 30 arcsec	145
The amount of water soluble P	Nutritional	GSDE, 30 arcsec	145
Exchangeable sodium percentage (ENa)	Nutritional	GSDE, 30 arcsec	145
Total potassium (Ktot)	Nutritional	GSDE, 30 arcsec	145
Total P	Nutritional	Global Gridded Soil Phosphorus Distribution Maps, 0.5°	146
Labile Inorganic P	Nutritional	Global Gridded Soil Phosphorus Distribution Maps, 0.5°	146
Organic P	Nutritional	Global Gridded Soil Phosphorus Distribution Maps, 0.5°	146
Occluded P	Nutritional	Global Gridded Soil Phosphorus Distribution Maps, 0.5°	146
Secondary Mineral P	Nutritional	Global Gridded Soil Phosphorus Distribution Maps, 0.5°	146
Apatite P	Nutritional	Global Gridded Soil Phosphorus Distribution Maps, 0.5°	146
Carbon exchange capacity (CEC)	Nutritional	ISRIC-WISE, 30 arcse	47
Soil clay content (%)	Nutritional	ISRIC-WISE, 30 arcse	47
Duration of the experiment (Nyears)	Experimental	reported in papers	
Experiment type	Experimental	reported in papers	
ΔCO_2 [$\log(\text{ambCO}_2/\text{elevCO}_2)$]	Experimental	reported in papers	
Age of the vegetation	Vegetative	reported in papers	
Biome type	Vegetative	reported in papers	

Supplementary Table 3. Overview of CO₂ enrichment experiments excluded in the main analysis due to data missingness, but included in a sensitivity test after estimating missing data from proxies. Abbreviations: FACE: Free Air Carbon Dioxide Enrichment, G: Greenhouse/Growth chamber, OTC = Open Top Chamber.

Study name	Species	System	Facility	Ref.
Duke Prototype F	<i>Pinus taeda</i>	Tree Stand	FACE	2
Antwerp OTC	<i>Pinus sylvestris</i>	Tree Stand	OTC	147
BCI2	<i>Pharus latifolius</i>	Grassland	G	148
BCI2	<i>Piper cordulatum, Psychotria limonensis</i>	Shrubland	G	148
BCI2	<i>Beilschmiedia pendula, Tachigalia versicolor</i>	Tree Stand	G	148
Bungendore 2	<i>Eucalyptus pauciflora</i>	Tree Stand	OTC	149
Ginninderra	<i>Phalaris aquatica</i>	Grassland	G	150
Guelph	<i>Artemisia tridentata</i>	Grassland	G	151
Oak Ridge OTC III D	Model grassland	Grassland	OTC	117
Oak Ridge OTC III W	Model grassland	Grassland	OTC	117
PNM5 F	<i>Ficus insipida</i>	Tree Stand	OTC	121
PNM5	<i>Ficus insipida</i>	Tree Stand	OTC	121
Santa Cruz Mangrove F	<i>Avicennia germinans</i>	Shrubland	G	126
Basel spruce F	<i>Picea abies</i>	Tree Stand	G	152
Basel spruce	<i>Picea abies</i>	Tree Stand	G	152
Basel tropical	Trop forest	Tree Stand	G	153
Basel tropical II	Trop forest	Tree Stand	G	154
Birmensdorf acidic F	<i>Fagus sylvatica</i>	Tree Stand	OTC	83
Birmensdorf acidic F	<i>Picea abies</i>	Tree Stand	OTC	83
Birmensdorf calcareous F	<i>Fagus sylvatica</i>	Tree Stand	OTC	83
Birmensdorf calcareous F	<i>Picea abies</i>	Tree Stand	OTC	83
Bungendore 3	<i>Eucalyptus pauciflora</i>	Tree Stand	OTC	155
Bungendore	<i>Eucalyptus pauciflora</i>	Tree Stand	OTC	156
Brandbjerg T	<i>Deschampsia flexuosa</i>	Scrubland	FACE	84
Brandbjerg DT	<i>Deschampsia flexuosa</i>	Scrubland	FACE	84
Darwin CTC	<i>Mangifera indica</i>	Tree Stand	OTC	157
Davos	<i>Larix decidua</i>	Tree Stand	FACE	158
Davos	<i>Pinus mugo</i>	Tree Stand	FACE	158
DUKE Phytotron F	<i>Pinus taeda</i>	Tree Stand	G	159
DUKE Phytotron	<i>Pinus taeda</i>	Tree Stand	G	159
Glendevon F	<i>Alnus glutinosa</i>	Tree Stand	OTC	31
Harvard II	<i>Betula alleghaniensis</i>	Tree Stand	G	160
HFE	<i>Eucalyptus globulus</i>	Tree Stand	OTC	161
Jasper Ridge mesocosm F	Sandstone grassland	Grassland	G	162
Jasper Ridge mesocosm	Sandstone grassland	Grassland	G	162
Jasper Ridge mesocosm F	Serpentine grassland	Grassland	G	162
Jasper Ridge mesocosm	Serpentine grassland	Grassland	G	162
Lancaster Solardomes	<i>Abies alba</i>	Tree Stand	G	163
Lancaster Solardomes	<i>Betula pendula</i>	Tree Stand	G	163

Lancaster Solardomes	<i>Carpinus betulus</i>	Tree Stand	G	163
Lancaster Solardomes	<i>Fagus sylvatica</i>	Tree Stand	G	163
Lancaster Solardomes	<i>Pinus sylvestris</i>	Tree Stand	G	163
Lancaster Solardomes	<i>Quercus robur</i>	Tree Stand	G	163
Lancaster Solardomes F	<i>Abies alba</i>	Tree Stand	G	163
Lancaster Solardomes F	<i>Betula pendula</i>	Tree Stand	G	163
Lancaster Solardomes F	<i>Carpinus betulus</i>	Tree Stand	G	163
Lancaster Solardomes F	<i>Fagus sylvatica</i>	Tree Stand	G	163
Lancaster Solardomes F	<i>Pinus sylvestris</i>	Tree Stand	G	163
Lancaster Solardomes F	<i>Quercus robur</i>	Tree Stand	G	163
UMBS_alnus	<i>Alnus glutinosa</i>	Tree Stand	OTC	164
ORNL OTC highC	<i>Liriodendron tulipifera</i>	Tree Stand	OTC	165
ORNL OTC highC	<i>Quercus alba</i>	Tree Stand	OTC	166
ORNL OTC lowC	<i>Liriodendron tulipifera</i>	Tree Stand	OTC	165
ORNL OTC lowC	<i>Quercus alba</i>	Tree Stand	OTC	166
ORNL OTC	<i>Acer rubrum</i>	Tree Stand	OTC	167
ORNL OTC	<i>Acer saccharum</i>	Tree Stand	OTC	167
ORNL OTC T	<i>Acer saccharum</i>	Tree Stand	OTC	167
ORNL OTC T	<i>Acer rubrum</i>	Tree Stand	OTC	167
Phoenix OTC highC	<i>Pinus eldarica</i>	Tree Stand	OTC	168
Phoenix OTC lowC	<i>Pinus eldarica</i>	Tree Stand	OTC	168
Phoenix OTC midC	<i>Pinus eldarica</i>	Tree Stand	OTC	168
Swiss Jura	<i>Bromus erectus</i>	Grassland	G	169
Swiss Central Alps F	Alpine grassland	Grassland	OTC	170
Swiss Central Alps	Alpine grassland	Grassland	OTC	170
USEPA	<i>Pseudotsuga menziesii</i>	Tree Stand	G	171

Supplementary Table 4. The effects of elevated CO₂ on total plant biomass. Total biomass (TB) increment for an increase in atmospheric CO₂ of +250 ppm, estimated from aboveground biomass (AGB) using biome-specific TB/AGB conversion ratios based on published inventory data (references in table). Biome classification was based on MODIS IGBP land cover map, with forests further divided by regions following the classification by Pan *et al.* (ref^{ref 54}). For example, “boreal forests” include all IGBP forests in Asian Russia, Canada, European Russia, Norway, Sweden and Finland. Areas labelled as “no data/other countries” in Pan *et al.* (2011) appear as “other” here. In some cases, TB/AGB ratios were calculated based on FAO statistics¹⁷² for specific countries. More details about TB/AGB conversion ratios in refs^{18,54}.

Biome	Region	TB/AGB	Reference	TB (PgC)
Boreal forest	Asian Russia	1.19	¹⁷³	2.71
	Canada	1.27	¹⁷⁴	3.49
	European Russia	1.28	¹⁷³	1.05
	European boreal	1.20	FAO: Sweden, Norway and Finland	0.34
Cropland		1.25	¹⁷⁵	3.4
Grassland		3.45	¹⁷⁵	2.28
Other		1.56	Table average	2.52
Savanna		2.38	¹⁷⁵	3.78
Shrubland		2.78	¹⁷⁵	1.5
Temperate forest	Australia	1.42	FAO: Australia	0.62
	China	1.32	FAO: China	1.37
	Europe	1.28	FAO: Germany, France, Belarus, Italy, Poland and Romania	0.63
	Japan	1.24	¹⁷⁶	0.45
	Korea	1.35	FAO: South Korea	0.08
	New Zealand	1.25	¹⁷⁷	0.14
	US	1.20	¹⁷⁸	2.05
Tropical forest	Africa	1.48	¹⁷⁹	5.85
	Americas	1.30	¹⁸⁰	13.78
	Asia	1.28	¹⁸⁰	6.46
Woody savanna		1.82	¹⁷⁵	8.48

Supplementary Table 5. Coefficients of retained terms in best multivariate meta-regression model.

	estimate	se	z-val	p-val	ci.lb	ci.ub
intercept	0.0608	0.0394	1.5415	0.1232	-0.0165	0.138
AM-ECM	0.1586	0.0478	3.3137	0.0009	0.0648	0.2523
1/CN	2.1623	0.4495	4.8105	0	1.2813	3.0432
1/P	-0.4776	0.0992	-4.8166	0	-0.672	-0.2833
Fumigation.type FACE-OTC	0.0257	0.0115	2.2351	0.0254	0.0032	0.0483
Fumigation.type FACE-G	0.0524	0.0195	2.6843	0.0073	0.0141	0.0907
AM-ECM:1/CN	-0.8772	0.484	-1.8124	0.0699	-1.8259	0.0714
AM-ECM:1/P	-0.348	0.095	-3.6643	0.0002	-0.5341	-0.1619

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