Partitioning direct and indirect effects reveals the response of water limited ecosystems to elevated CO$_2$

Simone Fatichi[a,1], **Sebastian Leuzinger**[b], **Athanasios Paschalis**[c,d], **J. Adam Langley**[e], **Alicia Donnellan Barraclough**[b], and **Mark Hovenden**[f]

[a]Institute of Environmental Engineering, ETH Zurich, Stefano Franscini-Platz 5, 8093 Zurich, Switzerland; [b]Applied Ecology New Zealand, School of Applied Sciences, Auckland University of Technology, Auckland, New Zealand; [c]Faculty of Engineering and the Environment, University of Southampton, Southampton, UK; [d]Nicholas School of the Environment, Duke University, Durham, NC, USA; [e]Department of Biology, Villanova University, Villanova, PA, USA; [f]School of Biological Sciences, University of Tasmania, Hobart, Tasmania, Australia

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Increasing concentrations of atmospheric carbon dioxide are expected to affect carbon assimilation and evapotranspiration (ET), ultimately driving changes in plant growth, hydrology and the global carbon balance. Direct leaf biochemical effects have been widely investigated, while indirect effects, although documented, elude explicit quantification in experiments. Here, we used a mechanistic model to investigate the relative contributions of direct (through carbon assimilation) and indirect (via soil moisture savings due to stomatal closure, and changes in leaf area index, LAI) effects of elevated CO$_2$ across a variety of ecosystems. We specifically determined which ecosystems and climatic conditions maximise the indirect effects of elevated CO$_2$. The simulations suggest that the indirect effects of elevated CO$_2$ on net primary productivity are large and variable, ranging from less than 10% to more than 100% of the size of direct effects. For ET, indirect effects were on average 65% of the size of direct effects. Indirect effects tended to be considerably larger in water-limited ecosystems. As a consequence, the total CO$_2$ effect had a significant, inverse relationship with the wetness index and was directly related to vapor pressure deficit. These results have major implications for our understanding of the CO$_2$-response of ecosystems and for global projections of CO$_2$ fertilization because, while direct effects are typically understood and easily reproducible in models, simulations of indirect effects are far more challenging and difficult to constrain. Our findings also provide an explanation for the discrepancies between experiments in the total CO$_2$ effect on net primary productivity.

Carbon dioxide | Modeling | FACE | Soil moisture | Evapotranspiration

The leaf-level response to elevated CO$_2$ (eCO$_2$) is well known: at current CO$_2$ levels photosynthesis of C3 plants is not saturated, while for C4 plants it is close to saturation [e.g., 1–4]. If acclimation is limited, leaf-level carbon assimilation of C3 plants will increase as the CO$_2$ concentration increases, as shown, among others, by observations in FACE (Free-Air CO$_2$ Enrichment) experiments [5–7]. Concurrently, stomatal conductance decreases consistently with eCO$_2$ in most species [8–11]. Even though the leaf-level responses are well characterized and quantifiable, the ecosystem response to eCO$_2$ remains considerably more uncertain and difficult to predict [12–17]. This discrepancy is not simply a consequence of the uncertainty in scaling up from leaf to canopy and ecosystem but derives from indirect effects and feedbacks that may lead to an amplification or dampening of the direct leaf-level response to eCO$_2$.

Indirect effects may be related to (i) modifications of plant water status through changes in soil moisture within the root zone, which occur as a consequence of stomatal closure; (ii) changes in Leaf Area Index (LAI), root biomass and depth, and canopy structure; (iii) limitations due to soil nutrient scarcity or plant incapability to take up nutrients at a rate sufficient to support enhanced carbon assimilation; (iv) changes in ecosystem composition and biodiversity; and (v) higher order interactions of the above indirect effects. Changes in soil moisture due to the reduction in stomatal conductance with eCO$_2$ (water saving effects) have been observed in a series of studies, most commonly in grasslands [18–21], but also in other ecosystems [22, 23]. Water saving effects have been hypothesized to stimulate vegetation productivity by a magnitude comparable or larger than the direct eCO$_2$ effect [21, 24], but no study has quantitatively partitioned direct and indirect effects. For instance, the water-saving effects of eCO$_2$ can even lead to an increase in C4 plant abundance over that of C3 plants, despite the absence of substantial direct effects on C4 plant growth [25, 26]. Such strong indirect effects mediated by hydrology have led to the hypothesis that the response of vegetation to eCO$_2$ may be more an issue of water than carbon [27]. Despite evidence from individual studies for a considerable stimulation of plant productivity through eCO$_2$-

Significance Statement

Elevated levels of atmospheric carbon dioxide affect plants directly by stimulating photosynthesis and reducing stomatal aperture. These direct effects trigger several more subtle, indirect effects via changes in soil moisture and plant structure. While such effects have been acknowledged, they have never been assessed quantitatively, partly due to the fact they are inseparable in field experiments. Here we show that the indirect effects of elevated CO$_2$ explain on average 28% of the total plant productivity response, and are almost equal to the size of direct effects on evapotranspiration. This finding has major implications for our mechanistic understanding of plant response to elevated CO$_2$, forcing us to revisit the interpretation of experimental results as well as simulations of future productivity.

S.F., S.L. and M. H. designed the study and methodology. S.F. performed model simulations. All authors contributed to simulation analysis and interpretation. S.F. drafted the manuscript with input from all authors. All authors commented on and approved the final manuscript.

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[1] To whom correspondence should be addressed. E-mail: simone.fatichi ifu.baug.ethz.ch

derived water savings, a meta-analysis of vegetation responses to eCO_2 showed no strong relationship between the effect size of CO_2 stimulation (elevated over ambient, E/A) and annual precipitation [28]. Considering sites independently showed a larger CO_2 effect with decreasing precipitation, but the authors also hypothesized that the sign could be reversed approaching very dry conditions, based on observations from a desert study [29]. Other indirect effects through LAI and nutrient limitations are interlinked with changes in soil moisture [e.g., 30, 31]. A more favorable water status can increase LAI, but such an increase in LAI can also lead to more rapid depletion of soil moisture. Altered soil moisture may also influence soil microbial activity and soil organic matter turnover rates, ultimately modifying nutrient availability [32].

While it is essential to improve our understanding of ecosystem response to climate change, a detailed quantification of indirect effects of eCO_2 and the comparison with direct physiological effects is fundamentally impossible in field experiments such as FACE [3, 5, 15, 33]. Field experiments can only estimate the total response to a given external treatment or combination of treatments. The different components of the total response cannot be quantitatively separated in most cases, rendering the discussion of indirect effects speculative [e.g., 20, 21, 24, 29, 34, 35]. A precise separation of the various effects is possible, however, using terrestrial biosphere models. Despite numerous limitations, these tools are capable of shedding light onto complex environmental issues with multiple interacting feedbacks [e.g., 36, 37]. Here, for the first time, we employ the state-of-the-art ecohydrological model Tethys-Chloris, T&C [38, 39] to disentangle direct from indirect CO_2 effects on productivity and evapotranspiration. The model was used to simulate the response to an eCO_2 treatment in a series of ecosystems spanning a wide range of climates and biomes (see Method section). The specific questions addressed here are: (i) What are the relative contributions of direct and indirect effects to the total productivity and evapotranspiration response to elevated CO_2 and do these depend on ecosystem water availability? (ii) In which biomes should we expect the strongest response? (iii) Does the total response to eCO_2 correlate with wetness? We hypothesize that indirect effects will be generally significant and potentially comparable to direct effects in water limited grassland ecosystems, especially in sites containing C4 species. We further expect a negative correlation between indirect effects on net primary productivity and wetness index for wet and mesic sites [28].

While quantifying direct leaf-level effects is relatively easy, untangling the indirect effects at the ecosystem scale is far more difficult and requires a dedicated approach as presented here. Quantitative knowledge of the role of indirect effects is expected to shed light on the observed differences between sites in the response to eCO_2 and to improve our understanding of the interannual variability of the eCO_2 effects. A mechanistic explanation of indirect effects also suggests avenues for improvement of global terrestrial biosphere models, which have limitations in capturing ecosystem level responses to eCO_2 [40].

Results

Effect partitioning. We identified four principal effects, which are the main determinants of the total ecosystem response to eCO_2. The first effect (E1) is the well-known, direct physiological effect, where a higher partial pressure of CO_2 stimulates photosynthesis in C3 plants and reduces stomatal conductance in both C3 and C4 plants. This effect is always positive because it increases Gross Primary Production (GPP) and Net Primary Production (NPP). The second effect (E2) is almost always positive and is the indirect effect mediated by reduced stomatal conductance, which leads to soil moisture savings. Reduced stomatal conductance may, in rare cases, suppress plant growth when soil water savings exacerbate anoxia in frequently waterlogged soils. The third effect (E3) is related to a potential increase in LAI, which by itself may lead to an additional increase in carbon assimilation because of greater leaf area. This effect is always positive for GPP but can be negative in terms of NPP in specific situations of stress because greater LAI implies greater respiration rates. The fourth effect (E4) is typically negative and is related to the higher evapotranspiration rates associated with an increase in LAI. Higher evapotranspiration tends to decrease soil moisture, which may increase plant water deficit, reducing productivity. In reality, all effects occur simultaneously, and the water mass budget must be preserved. Therefore, E4 acts mostly by offsetting the positive effect of E2. The total response is finally given by $E1 + E2 + E3 + E4$, which corresponds to what can be typically observed in a CO_2 manipulation experiment. Note that the above partitioning does not include indirect effects acting through nutrients, increases in root depth or changes in species composition. While it is incontrovertible that these factors play important roles in regulating ecosystem response to eCO_2 [e.g., 41–44], they remain poorly simulated by current terrestrial biosphere models [45–48]. Therefore, we purposefully excluded such effects to avoid introducing further levels of uncertainty related to the specific model structure.

The combination of six numerical simulations, which were used to separate E1, E2, E3, and E4, is described in the methods section. Two atmospheric CO_2 concentration levels, 375 and 550 ppm, were used in the simulations representing the ambient CO_2 concentration at the beginning of this century and the level used in several FACE experiments, respectively. The treatment corresponded to an overall step increase in CO_2 of +46%. Boundary conditions in terms of soil properties and depth, biome parameterizations, as well as hourly meteorological inputs were taken from 44 sites corresponding to locations where observations from flux towers, manipulation experiments or experimental stations were available to force and test the model (Suppl. Table S1). Importantly, biomes were not parameterized with generic plant functional types, but for each site we identified a parameter set able to provide satisfactory results in terms of vegetation productivity, leaf area index, soil moisture, energy and water fluxes, and local phenology acting on the most sensitive parameters [49]. The capability of the T&C model to reproduce the observed response to eCO_2 was evaluated against observations of total effects at three FACE experiments [50, 51]: Duke-FACE, ORNL-FACE and TasFACE (Suppl. Figures S1, S2 and S3), and has been previously tested for the Swiss Canopy Crane FACE experiment [52]. Results were satisfactory when compared to current capabilities of ecosystem models [e.g., 40] especially at the Duke-FACE site. Simulations at ORNL-FACE were less satisfactory especially in the period when nutrient limitation became significant. However, the overall consistency in simulated and observed average effects for different variables (NPP, ET, water use efficiency) was adequate for the investigation of the questions posed here.

NPP response. The total effect of the eCO_2 treatment on NPP, computed as (eCO_2-aCO_2)/aCO_2, was a function of the wetness index, W_I, i.e., the ratio between annual precipitation and annual potential evapotranspiration (Fig. 1). Decomposing the response between direct and indirect effects shows that the direct effect was unrelated ($R^2 = 0.02$, p-value=0.35) to W_I, while indirect effects increased exponentially with decreasing W_I, thus driving an increase in the total response (Fig. 1b). The direct effect was positively correlated with annual and growing season air temperature ($R^2 = 0.78$, p-value < 0.001), suggesting that the strongest direct physiological response should be expected at warmer sites where photosynthesis is not temperature limited during most of the growing season (Fig. S4). Further sub-division of the three analyzed indirect effects showed that the indirect effect through soil moisture savings, E2, increased exponentially with dryness, reaching values of 20-40% of the ambient NPP for $W_I < 0.5$ (Fig. 1c). The indirect effect due to carbon assimilation stimulation through a larger LAI, E3, also increased for very dry conditions but at lower W_I values than E2, and was rarely larger than 20% of the ambient NPP (Fig. 1c). This pattern occurred because at drier sites, LAI is generally lower, so that even a small increase in LAI due to eCO_2 may cause significant stimulation of GPP, as the negative feedback of self-shading is minimal. Finally, E4 reached large negative values at dry sites (-40% of ambient NPP) and counteracted the combined positive effects of E2 and E3 (Fig. 1c). In other words, the increased LAI generated by eCO_2 was typically sufficient to deplete a large fraction of the soil moisture savings, which would otherwise occur because of the reduction in stomatal conductance. However, the sum $E2 + E3 + E4$ almost always yielded a positive value as testified by Figure 1b. The ratio between indirect and direct effects (R_{id}) supports the idea that indirect effects can be comparable ($R_{id} > 0.25$) to the direct effect at many sites and much larger ($R_{id} > 1$) for dry sites with C4 species (Fig. S5). Only wet tropical forest sites, a groundwater fed ecosystem, and a grassland in Scotland showed a total predominance of direct effects ($R_{id} < 0.1$). On average and across all sites, indirect effects accounted for 28% of the NPP response to eCO_2.

In terms of total eCO_2 treatment effect, the 46% increase in CO_2 led to greater variation in NPP among sites, but the overall effect on NPP was positive, ranging between 11 and 45% of ambient NPP. The eCO_2 effect was most variable when wetness conditions were intermediate ($0.75 < W_I < 1.25$) (Fig. 1a). Despite this scatter, a significant negative relationship ($R^2 = 0.20$, p-value $= 0.0021$) between NPP effect size and W_I was evident, with the driest sites having the strongest NPP response to eCO_2. This pattern was also apparent for sites with a considerable fraction of C4 species (Fig. 1a). The total NPP effect was even more strongly correlated ($R^2 = 0.51$, p-value < 0.001) with the growing season average vapor pressure deficit (VPD) (Fig. S4).

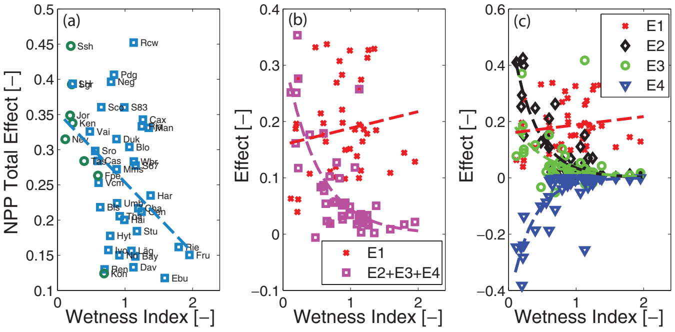

Fig. 1. (a) Scatter plot between the wetness index and the total effect on NPP (E1+E2+E3+E4), sites with a considerable fraction of C4 grass are indicated with circles ($R^2 = 0.20$, p-value=0.0021). (b) Scatter plot between wetness index and direct effect, E1 (crosses) and indirect effects, E2+E3+E4 (squares), ($R^2 = 0.55$). (c) Scatter plot between wetness index and four different effects, E1 ($R^2 = 0.02$) (crosses), E2 ($R^2 = 0.73$) (diamonds), E3 ($R^2 = 0.27$) (circles), E4 ($R^2 = 0.68$) (triangles). All the effects were computed as: (eCO_2-aCO_2)/aCO_2. Site acronyms in (a) are detailed in the Supporting Material.

Whether or not eCO_2 stimulates LAI is a matter of debate, because responses differ among experiments [53, 54], and there is contention as to whether nutrient limitation or direct environmental controls limit growth regardless of carbon assimilation rates [12, 44, 55–58]. Hence, we examined the impact of eCO_2 on NPP while holding LAI constant. In this case, the only mechanisms leading to eCO_2 effects on NPP were direct physiological and indirect soil moisture impacts ($E1 + E2$) (Fig. 2). Despite some site-to-site variability, removing eCO_2 effects on LAI had contrasting consequences in dry and wet sites (Fig. 2). In dry sites, the stimulation of LAI by eCO_2 resulted in increased water use, more than offsetting the beneficial effects of LAI on photosynthesis. Therefore, removing the impact of eCO_2 on LAI substantially increased the overall stimulation of NPP in dry sites (Fig. 2). In contrast, in wet sites, preventing eCO_2 from stimulating NPP via increased LAI had no effect or reduced the eCO_2 effect since water was clearly not limiting at these sites. Hence, the impact of changes in LAI in response to eCO_2 depends upon whether the ecosystem has the necessary water availability to support greater LAI.

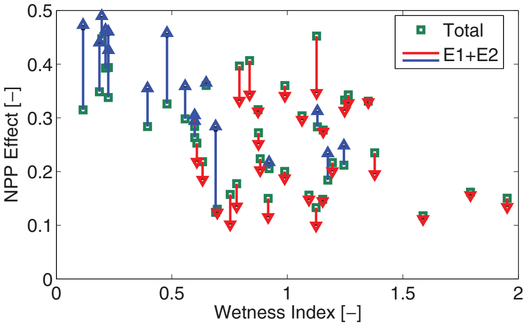

Fig. 2. Effect of removing indirect effects due to LAI on the scatter plot between wetness index and total effect on NPP (E1+E2+E3+E4), the directions and magnitudes of the arrows indicate the change in total response when LAI mediated effects (E3 and E4) are removed for each site, i.e., only E1 and E2 effects are left. The red color indicates a decrease in the NPP effect, while a blue color indicates an increase in the NPP effect.

ET response. Enrichment of CO_2 influenced ET in a manner even more tightly controlled by W_I than for NPP (Fig. 3). On average the ratio of indirect-to-direct effects was 65%, pointing to a large significance of indirect eCO_2 effects on ET. Indirect effects on ET through soil moisture savings (E2) and increased LAI (E3) were positive and similar in magnitude, with an exponential increase evident for $W_I < 1$ (Fig 3c). Both E2 and E3 led to higher ET but for different reasons: E2 alleviated water stress thereby supporting continued ET, whereas E3 simply increased the transpiring leaf area. These theoretical increments in ET cannot be physically sustained as they would violate the water mass budget, or in other words, an increase in ET must imply a decrease in soil moisture. Therefore, E4 was strongly negative and offset partially, or almost entirely in the most xeric sites, the sum of E2 and E3. The direct effect reached -15% and was positively and linearly correlated ($R^2 = 0.41$ p-value < 0.001) with W_I (Fig. 3b). This pattern was related to the fact that ET during periods of high water availability in drier sites can be larger than in wetter sites due to higher radiation loads and temperature. In these locations, allowing only the direct effect of stomatal conductance reduction (E1) to occur can lead to more pronounced responses (proportionally lower ET) than in wetter sites. However, the combined indirect effects increased ET in a manner that was negatively and exponentially related ($R^2 = 0.70$) to W_I. Further, this trend largely offset the direct effect for $W_I < 0.5$.

The total effect eCO_2 on ET was generally negative, ranging between -8% and +2% and approaching zero under arid conditions (Fig. 3a). This result was not surprising because long-term ET at dry sites is almost equal to long-term precipitation with only a marginal influence of other factors such as CO_2 concentration, climate variability or vegetation composition [39, 59, 60].

Ecosystem Water Use Efficiency (EWUE), defined as the ratio between GPP and evapotranspiration, also responded positively to eCO_2 following general expectations [40, 61–63], with a total increase between 14% and 39%, less than proportional to the 46% increase in CO_2. The scatter in the EWUE response was considerable, the response was mostly driven by the direct effect but was enhanced by the sum of indirect effects at the driest sites (Fig. S6).

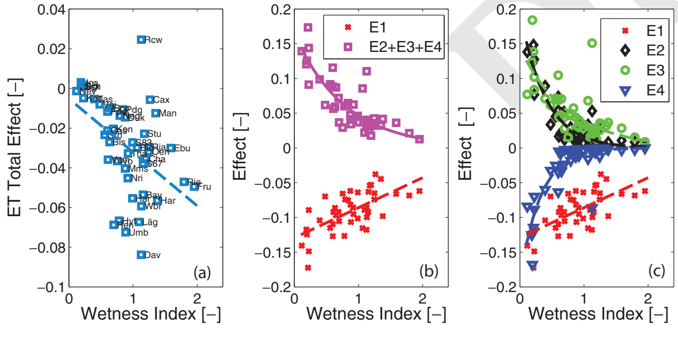

Fig. 3. (a) Scatter plot between wetness index and total effect on ET (E1+E2+E3+E4) ($R^2 = 0.22$, p-value=0.0012). (b) Scatter plot between wetness index and direct effect, E1 (crosses) and indirect effects, E2+E3+E4 (squares), ($R^2 = 0.70$). (c) Scatter plot between wetness index and four different effects, E1 ($R^2 = 0.41$) (crosses), E2 ($R^2 = 0.84$) (diamonds), E3 ($R^2 = 0.51$) (circles), E4 ($R^2 = 0.73$) (triangles). Site acronyms in (a) are detailed in the Supporting Material.

Discussion

This study aimed to investigate the relative importance of direct and indirect effects of eCO_2 on ecosystem NPP and ET. Our results suggest that in xeric environments, indirect effects can be comparable to or even larger than the direct, photosynthetic effect of eCO_2 on NPP. On average, indirect effects accounted for 28% of the total stimulation of NPP. The indirect/direct effect ratio ranged from less than 0.1 for tropical and moist sites to more than 1 for semiarid C4 grasslands. The hypothesized decrease of effect size with extremely dry conditions [28] was not supported by our simulations, which represent integrated responses across multiple years. However, our results should be regarded as potential responses in the absence of nutrient limitations. Suppression of eCO_2 effects on NPP by severe water deficit remains a possibility for explaining interannual variation in response within sites. Note that for arid or semi-arid sites characterized by herbaceous species and relatively fast biomass turnovers, eCO_2 stimulation of NPP does not necessarily translate in an increase in standing biomass even after several years [64, 65], but may be detected in an increase in soil organic carbon [66]. This result is only partially captured in model simulations that still shows a positive effect on biomass also in the most arid ecosystems, even though the effect is considerably smaller than for NPP. Limitations in nutrient uptake exacerbated by water stress can also dampen the biomass response of the most arid sites. Additionally, eCO_2 may stimulate rhizodeposition, potentially explaining the discrepancy between NPP and biomass responses.

We found that changes in ET due to eCO_2 were smaller than what a pure, direct response of stomatal conductance would suggest even at the ecosystem level (i.e., direct effect of -5 to -15%), because indirect effects tend to compensate partially or totally for the direct effect. Further, water "saved" via reduced stomatal conductance is likely to be consumed in water limited systems, either immediately via increased LAI or by extension of the growing period if LAI is unaffected by eCO_2 (Fig. 2). Some of the effects might be due to changes in root biomass, which were included in the model, however, changes in rooting depth in response to eCO_2 were not considered, therefore it is possible that indirect effects of eCO_2 may increase beyond those simulated here, if development of deeper roots were able to access water not otherwise available. The overall difference between the two CO_2 scenarios (375 vs 550 ppm) in terms of water fluxes (ET) was typically less than 8% and mostly constrained between -5% and 0. Changes in water use of this magnitude would rarely be observable due to a combination of measurement uncertainty [e.g., 67] and interannual variability [e.g., 39].

Over the large number of sites we simulated, the total change in NPP with the increase in CO_2 concentration was mostly in the order of 20-35%. These values are very similar or slightly larger than observations in FACE experiments when nutrient limitations do not play a role [28, 68]. In fact, our results should be considered as the potential response of NPP to eCO_2 in the absence of sink limitations [e.g., 58]. The variation in the NPP response as a function of the wetness index is quite impressive since these are numerical simulations from a mechanistic model rather than observations from real experiments. The large scatter in intermediate wetness conditions suggests that differences in phenology, temperature, short-term meteorological variability, biome and soil type, all of which were accounted for in the simulations, play a significant role in the NPP response to eCO_2. Contrary to the situation with ET, the total sum of indirect effects tends to enhance the response of NPP to eCO_2 because it adds to the direct physiological response. This is especially evident in semi-arid sites, which are responsive to eCO$_2$ even when C4 species are predominant, as supported from observations [25].

Our results demonstrate that mechanistic models of terrestrial ecosystems, despite known limitations [e.g., 46, 58, 69, 70], do provide substantial insights on ecosystem response to eCO$_2$ that are impossible to obtain with field experiments alone. Model limitations and structure may affect the magnitude of some of the estimates but are unlikely to change the prevailing patterns, with the important exception of nutrient limitation. Furthermore, T&C generated total responses to eCO$_2$ that closely matched observations. For instance, the average modeled eCO$_2$ effect size of NPP, ET, and WUE is consistent for the Duke-FACE and for the first seven years of the ORNL-FACE experiments.

Regardless of inherent shortcomings of simulation models, ecosystems at the dry-end of the climate spectrum, which experience repeated water stress, are expected to be the most responsive to eCO$_2$ in terms of productivity. When indirect LAI effects are removed, mimicking a lack of stimulation in LAI growth (Fig. 2), productivity in these sites responds more strongly to eCO$_2$. Further, the significant positive relationships between VPD, a measure of atmospheric dryness, and total NPP response to eCO$_2$ (Fig. S4b) reinforces the idea that the drier sites are where the most significant effects of eCO$_2$ on NPP should be expected. This agrees with modeling studies based on optimality principles [71, 72] and is supported by global patterns of positive response of semi-arid ecosystems to CO$_2$ fertilization [73, 74], forcing the re-evaluation of the role of semi-arid ecosystems in the land carbon sink [75, 76]. All this evidence corroborates our results and suggests that projections of eCO$_2$ effects at local and global scale are substantially affected by mechanisms and feedbacks contributing to indirect effects, which are inherently more challenging to reproduce than the direct effect on carbon assimilation. Information on indirect effects derivable from conventional field experiments is necessarily limited. This issue demands both novel experiments specifically designed to target indirect effects and mechanistic solutions in models that do not strongly depend on empirical results. In this context, particular focus should be devoted to addressing the representation of water stress effects on the response of ecosystem productivity.

Materials and Methods

Partitioning direct and indirect effects of elevated CO$_2$. The contributions of the four identified effects (E1, E2, E3, and E4) were quantified by running a series of six simulations with the T&C model [38, 39, 49, 52, 77] (Suppl. Text S1). The first two simulations were used to compute the total eCO$_2$ effect ($E1 + E2 + E3 + E4$) and simply represent a simulation with CO$_2$ concentration prescribed at ambient level (375 ppm) and one with elevated CO$_2$ (550 ppm), where all the identified effects co-occur as in reality. The effect magnitude was computed as (eCO$_2$-aCO$_2$)/aCO$_2$. Other three simulations were then necessary to partition the four effects (since there were four unknowns in four equations). In these simulations, atmospheric CO$_2$ concentration was kept at 550 ppm and either soil moisture or LAI or both were externally prescribed to be the same as obtained from the ambient or eCO$_2$ simulations, rather than being prognostic variables. We ran four additional simulations to have redundancy on the estimate and keep the simulation with the total eCO$_2$ effect as a counterproof. These were: (i) a simulation with eCO$_2$ and prescribed ambient LAI and soil moisture, where the direct effect only remained (i.e. only E1); (ii) a simulation with eCO$_2$ but prescribed ambient LAI, where all the indirect effects mediated by LAI were absent (i.e. $E1 + E2$ occurred); (iii) a simulation with eCO$_2$ and prescribed ambient soil moisture and eCO$_2$-LAI, where all the indirect effects related to soil moisture were eliminated (i.e. $E1 + E3$ occurred); (iv) a simulation with eCO$_2$ and prescribed eCO$_2$ soil moisture and ambient LAI, where only the E3 effect was eliminated (i.e. $E1 + E2 + E4$ occurred). Opportune combinations of the two basic simulations with the four additional simulations with prescribed soil moisture or LAI were able to provide a distinct estimate of the quantitative contributions of the four effects (E1, E2, E3, and E4) to the total (combined) effect. Note that prescribing either soil moisture or LAI externally rather than allowing its prognostic computation in the model violates to some extent the water and/or carbon budget in the specific simulation. However, this was the only way to separate the four effects. As a final check, the sum of the four effects estimated with the additional simulations corresponded almost perfectly to the total eCO$_2$ effect ($E1 + E2 + E3 + E4$) testifying the correctness of the procedure (Fig. S7). An example of the results obtained with the adopted methodology is illustrated by the time series of NPP simulated imposing ambient CO$_2$ concentration (aCO2), eCO$_2$ concentration, and a case with eCO$_2$ but with LAI and soil moisture fixed to ambient values (Fig. S8 and Text S2). In the article, only long-term averaged responses over the entire simulation period (Suppl. Table S1) are shown, which are the results of effects occurring from the hourly to the multi-annual scale.

Climate forcing and vegetation. We selected 44 locations corresponding to sites of flux towers, manipulation experiments and experimental stations covering different climates and biomes across the globe (Table S1). For each site, the six described simulations were used to partition the four effects at an hourly scale. Values averaged over the entire length of the simulation were then reported in the results. The length of meteorological time series depended on the length of the available, good quality hourly data for each location and ranged from a minimum of 2 years to a maximum of 31.7 years with a median of 7.8 years (Table S1). Eight sites were also characterized by a non-negligible fraction of C4 species. The broad range of climate and vegetation types allowed for robustness in the investigation of eCO$_2$ effect and how it is partitioned, minimizing the risk of idiosyncratic results related to parametrization of a given biome or climate in a single location. At the same time, running the model locally rather than globally allowed us to avoid generic PFT parameterizations and large-scale climate forcing that may lead to large biases in the ecosystem response at a given site [49, 60, 78, 79].

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