









BRIEF REPORT

Not just semantics: CO₂ fertilization can be a disturbance leading to worldwide forest degradation

David M. Lapola¹  | Carolina C. Blanco¹  | Barbara R. Cardeli¹  |
 Adriane Esquivel-Muelbert^{2,3}  | João V. Martinelli¹  | Carlos A. N. Quesada⁴  |
 Bianca F. Rius¹  | Celso H. L. Silva-Junior⁵ 

¹Laboratório de Ciência do Sistema Terrestre – LabTerra, Centro de Pesquisas Meteorológicas e Climáticas Aplicadas à Agricultura – CEPAGRI, Universidade Estadual de Campinas – UNICAMP, Campinas, São Paulo, Brazil

²School of Geography, University of Birmingham, Birmingham, UK

³Birmingham Institute of Forest Research (BIFoR), Birmingham, UK

⁴Coordenação de Dinâmica Ambiental, Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, Amazonas, Brazil

⁵Instituto de Pesquisa Ambiental da Amazônia – IPAM, Brasília, Federal District, Brazil

Correspondence

David M. Lapola, Laboratório de Ciência do Sistema Terrestre – LabTerra, Centro de Pesquisas Meteorológicas e Climáticas Aplicadas à Agricultura – CEPAGRI, Universidade Estadual de Campinas – UNICAMP, 13083-886 Campinas, São Paulo, Brazil.
 Email: dmlapola@unicamp.br

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Societal Impact Statement

The physiological effects of increased atmospheric CO₂ (CO₂ fertilization) on intact forests are generally seen as a process that might buffer them against the impacts of climate change. However, CO₂ fertilization can also cause adverse changes in forest conditions, such as alterations in species composition and reduced ecosystem moisture availability. Because of this, we argue that the effect of CO₂ fertilization is a disturbance that leads to changes in the functioning of worldwide forests and causes low-intensity degradation of these ecosystems. This demonstrates that even the most remote forests in the world have been altered by human action via CO₂ fertilization, and the responsibility for their integrity must be shared globally.

KEYWORDS

Amazon, degradation, rainfall, transpiration, tree community shifts, tropical carbon sink

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1 | INTRODUCTION

The direct physiological effect of increased atmospheric CO₂ concentration, also known as CO₂ fertilization effect, is long known to potentially enhance carbon assimilation and lead to increased water-use efficiency by plants, as revealed by a number of laboratory studies with potted plants, field-based open-top chambers, ecosystem-scale experiments using free-air CO₂ enrichment (FACE) technology and remote sensing (Ainsworth & Long, 2005; Fortirer et al., 2023; Walker et al., 2021). One of the possible cascading effects of increased carbon assimilation is the accumulation of that additional carbon in plant biomass, particularly wood and derived litter, which can increase ecosystem carbon storage due to their longer residence times.

Forests worldwide have sequestered carbon at constant rate over the last three decades ($3.6 \pm 0.4 \text{ PgC year}^{-1}$) (Pan et al., 2024). Statistical analyses on long-term field plots indicate CO₂ fertilization as the most likely explanation for that carbon sink observed for several decades in worldwide forests (Hubau et al., 2020; Pan et al., 2024; Walker et al., 2021). Nevertheless, the effects of CO₂ fertilization on net primary productivity and carbon uptake are, in general, stronger in tropical rather than in boreal forests due the temperature dependence of Rubisco kinetics (Hickler et al., 2008). The strength of the carbon sink in intact tropical forests has been reduced by 31% since the 1990s apparently due to increased temperature, more frequent droughts, and losses in intact forest area (Hubau et al., 2020; Pan et al., 2024). European boreal forests have also been supposedly affected by CO₂ fertilization effect, as well as longer growing seasons (Kauppi et al., 2022; Pan et al., 2024). The same seems to hold true also for forests in eastern United States, where climatic changes, namely droughts, have not been severe (Davis et al., 2022; Hogan et al., 2024).

Such an enhanced carbon sink caused by CO₂ fertilization effect has been observed, although temporarily, in planted temperate forest FACE experiments (Norby et al., 2010), in a mature temperate forest FACE (Norby et al., 2024), but not in a savanna woodland in Australia (Yang et al., 2020). No direct experiment-based evidence of such enhanced carbon storage driven by CO₂ fertilization exists for tropical or boreal forests yet (Norby et al., 2016).

The balance between tree recruitment/growth and tree mortality/turnover is determinant for the evolution of that carbon sink. Tree recruitment/growth is consistently rising in Amazon and Central African forests, apparently due to CO₂ fertilization, but in the Amazon, it is increasingly being outpaced by tree mortality/turnover supposedly as a reaction to increasing temperature (Hubau et al., 2020). Also, CO₂ fertilization has long been suggested—though not properly proved—as the cause of increased tree turnover in tropical forests (Phillips & Gentry, 1994), as well as favoring the occurrence of lianas in these ecosystems (Phillips et al., 2002). Indirect (radiative) effects of increased CO₂ such as increased temperature and more frequent droughts may also play a role in such altered turnover.

Inventory data and model data integration show that enhanced growth driven by CO₂ fertilization might be offset by decreased longevity in temperate forest trees (Bugmann & Bigler, 2011; Büntgen

et al., 2019), though exceptions to that tradeoff are common across all forest types (Cailleret et al., 2017; Rüger et al., 2020). More recent and robust observational evidence suggest that CO₂ fertilization is driving a shift within Amazonian tree communities to large-statured species, even though such large-statured species tend to be the most affected by droughts (i.e., CO₂ fertilization effects are apparently overwhelming the effects of more frequent droughts in the region in that specific ecological process) (Esquivel-Muelbert et al., 2019).

All in all, the role of CO₂ fertilization on forest tree mortality, turnover, and the growth–survivorship tradeoff is still uncertain (Maschler et al., 2022; Walker et al., 2021), with the indirect (radiative) effects of increased atmospheric CO₂ likely playing an important role too (Hubau et al., 2020). Because of that, the attribution of the long-term observed carbon sink in worldwide forests majorly to CO₂ fertilization (Pan et al., 2024) is permeated by uncertainties as well, especially given the discrepancies found so far in ecosystem-scale FACE experiments and long-term inventories, tree rings, and remote sensing data (Maschler et al., 2022). Notwithstanding, taking the available evidence into account, it seems reasonable to at least hypothesize that CO₂ fertilization can have a key role in altering carbon fluxes, community dynamics, and the structure of tropical, temperate, and boreal forests (Bugmann & Bigler, 2011; Esquivel-Muelbert et al., 2019; Hubau et al., 2020; Laurance et al., 2004; Pan et al., 2024).

On the other hand, the increased water-use efficiency usually resulting from CO₂ fertilization is related to reductions in stomatal conductance (De Kauwe et al., 2013; Gimeno et al., 2016; Norby & Zak, 2011) and to potential decrease in canopy-level transpiration of forests (De Kauwe et al., 2013). Such an increased water-use efficiency is highly variable among different experiments in temperate forests, sometimes species-specific, smaller in needle-leaf trees, and can potentially be offset by increases in total leaf area (Norby & Zak, 2011; Ward et al., 2018). Modeling exercises indicate that such a potential reduction in the flux of moisture from the vegetation to the atmosphere over large expanses of tropical forests, namely the Amazon forest, can substantially modify the hydrological cycle and cascade into basin-wide reduced precipitation totals (Kooperman et al., 2018; Langenbrunner et al., 2019; Sampaio et al., 2021). In fact, the physiological effects of increased CO₂ (CO₂ fertilization) on tree transpiration dominate multimodel mean precipitation projections over the Amazon in the future (Richardson et al., 2018).

Reduced precipitation is long known to have low-intensity but a large-scale effect on tree mortality and carbon emissions to the atmosphere (Lewis et al., 2011). Long-term reductions in soil water, such as represented in the above-mentioned modelling exercises could potentially, have an even worse effect on forest functions and structure, increasing the mortality of selected functional groups of trees, especially large trees (Rowland et al., 2015). This sort of widespread changes in forest community composition is already being observed in several sites in the Amazon forest, a process that is attributed to CO₂ fertilization and the concomitant lengthening of the dry season, with dry-affiliated taxa replacing wet-affiliated taxa (Esquivel-Muelbert et al., 2019).

The body of evidence so far suggests that CO₂ fertilization is a process that can possibly lead to considerable alteration of forest water cycle. In the case explored above, CO₂ fertilization leads to reduced moisture flux from the vegetation to the atmosphere, with consequent reduction in large-scale precipitation, which feeds back to the forest in the form of selective mortality of certain functional groups of trees, ultimately leading to changes in tree community composition (Esquivel-Muelbert et al., 2019).

In that sense, the CO₂ fertilization effect could be considered a low-intensity disturbance leading to degradation of worldwide forests, namely due to its impacts on the water cycle and likely on carbon balance and community composition of these ecosystems. A recent review paper on Amazon forest degradation defines degradation as:

(...) a transitory or long-term (10 to 1000-year time scale) deleterious change in forest condition. Condition includes functions, properties, or services such as, but not restricted to, carbon storage, biological productivity, species composition, forest structure, local atmospheric moisture or uses or values of the forest to humans.

(Lapola et al., 2023).

Other definitions are similar to that and include:

(...) a negative trend in land condition, caused by direct or indirect human-induced processes including anthropogenic climate change, expressed as long-term reduction or loss of at least one of the following: biological productivity, ecological integrity or value to humans

(Olsson et al., 2019).

Degradation implies a persistent reduction of some attribute relative to a preferred (nondegraded) condition. (...) forest degradation involves changes in the structure, composition, or function of a forest. The outcomes of these changes are subject to alternative interpretations and values, which might be based on productive functions (e.g., goods), biodiversity, carbon storage, or other ecosystem services. The preferred condition might reflect a desire to return to some perceived historical condition, often assumed to be relatively undisturbed by humans. Perceptions of degradation and recovery are, however, social constructs subject to cultural and ethical norms

(Ghazoul & Chazdon, 2017).

Whether such human-driven ecological changes linked to forest degradation are “deleterious” or “negative” is therefore a matter of “social constructs subject to cultural and ethical norms”. In this analysis, we follow a conservationist perspective, considering the pre-industrial state of these forests, when they were little affected by the direct and indirect effects of increased atmospheric CO₂. Surely some of these changes, like large-scale intentional shifts in species composition, are

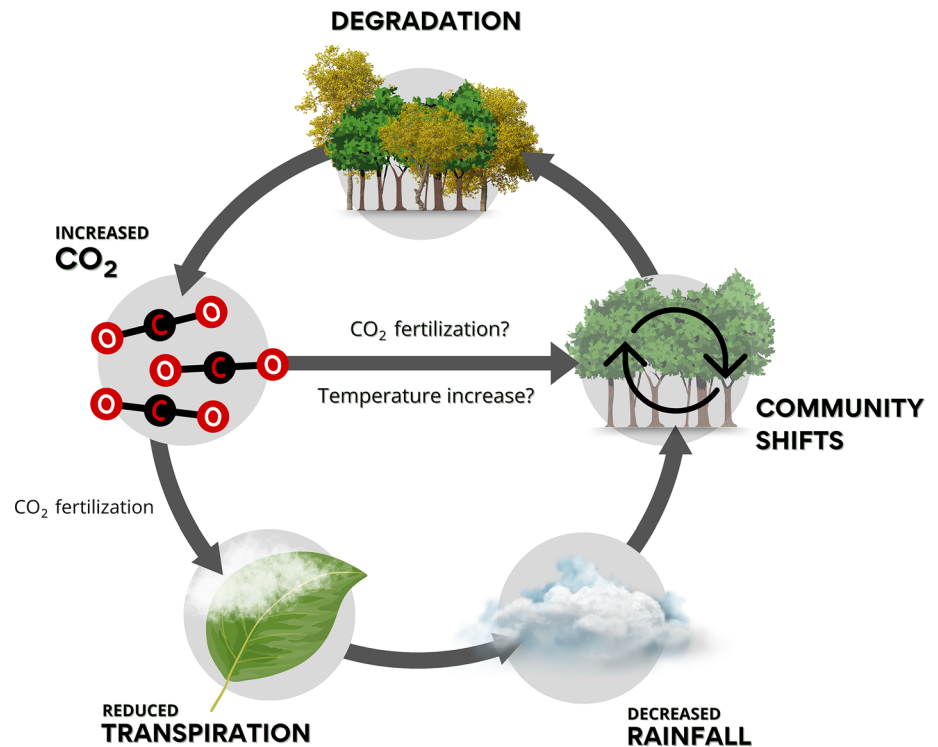
not seen as deleterious or negative by some actors such as indigenous people (Clement et al., 2015). The latter interpretation however should not be extended to actors undertaking illegal activities like as timber extraction.

Following the aforementioned conservationist perspective, CO₂ fertilization is a potential disturbance and its ultimate effect on the water cycle is the negative change in forest function, compared to a pre-industrial condition (when atmospheric CO₂ levels were relatively stable). The same potentially applies to other changes driven at least partially by CO₂ fertilization, such as the probable changes in community composition referred above and its cascading effects on the forest carbon balance (Esquivel-Muelbert et al., 2019; Hubau et al., 2020; Laurance et al., 2004). CO₂ fertilization has a lower intensity of impacts compared to fire or edge effects (Lapola et al., 2023). But it induces a feedback loop by enhancing carbon emissions to the atmosphere (which opposes the negative feedback normally associated with CO₂ fertilization; Friedlingstein, 2015), increasing the CO₂ fertilization disturbance over these forests (Figure 1). Moreover, such changes in forest properties have the potential to also alter the provision of ecosystem services such as food, wood, and fiber, thus making it possible that forest inhabitants themselves classify the forest as “degraded,” as predicted in the definitions of degradation given above.

One can argue that the press of CO₂ over tropical forest is not short-lived and that formal definitions account that (ecological) disturbance is relatively discrete in time (Newman, 2019). However, we understand that it can indeed be called a disturbance given that it disrupts certain aspects of the functioning of tropical forests in a time horizon that is relatively short in ecological terms, i.e., a few to several decades, which is way shorter than the upper time limit (1000 years) used in the definition of degradation above. Moreover, as a process causing a permanent disturbance, it has the potential to lead the system to a steady state different from the original (Rykiel, 1985). And, of course, the CO₂ fertilization effect is undoubtedly human-caused.

The effects of CO₂ fertilization on worldwide forests are, nevertheless, still permeated by uncertainties (Maschler et al., 2022; Walker et al., 2021). For example, short-term experimental evidence suggests that leaf-level reductions in transpiration in tropical forest understory can be compensated by an increase in leaf area index (Damasceno et al., 2024), resulting in potentially no changes in the integrated flux of moisture from the forest canopy to the atmosphere. The attribution of the causes of the worldwide forests carbon sink, increased turnover and tree mortality, and compositional changes to CO₂ fertilization is so far the result of probabilistic analyses, still lacking mechanistic explanations and more direct evidence (Esquivel-Muelbert et al., 2019; Hubau et al., 2020; Pan et al., 2024). One logical way of obtaining such direct evidence would be through FACE experiments run over meaningful ecological scales (>80 years) that could properly capture tree recruitment and mortality dynamics and potential community shifts, but seems financially impractical today and certainly too long for guiding short-term policy.

FIGURE 1 The effects of CO₂ fertilization as a disturbance that leads to alteration of key ecosystem properties such as reduced plant transpiration, which in turn leads to decreased regional rainfall and thereafter to tree community shifts (favoring drought affiliated species), ultimately configuring a degradation of tropical forests. Increased CO₂ as well as temperature increase (caused by the radiative effect of increasing atmospheric CO₂) can possibly also have a direct effect on community shifts.



But in case we can indeed call CO₂ fertilization a disturbance and its impacts—for example on the water cycle or on community composition—as changes attributable to forest degradation; then, it is reasonable to think that something close to 100% of the Amazon forest is somehow degraded, and not the 38% previously estimated analyzing other disturbances (fire, edge effects, logging, and extreme droughts) (Lapola et al., 2023). The same line or argument applies to other “intact” forests and raises the question whether the “wild woodlands” anthrome category is appropriate (Ellis et al., 2021). While on the one hand this seems only a matter of semantics, it has a key relevance from the political perspective. Defining CO₂ fertilization as a disturbance leading to forest degradation (in addition to the already recognized impacts of the indirect effects of increased CO₂ on forest degradation; Lewis et al., 2011) puts in evidence the shared responsibility of other countries (other than forest countries), namely top emitters, over the integrity of worldwide forests. Curbing deforestation and certain disturbances (e.g. forest fires or illegal timber extraction) that lead to forest degradation is certainly a major task for the countries hosting these forests. But the curbing of others disturbances that lead to degradation and which are related to global climate change, like extreme droughts (Lapola et al., 2023) or CO₂ fertilization, is something that forest countries cannot attain alone, but depends on a concerted effort of other countries in curbing greenhouse gas emissions.

AUTHOR CONTRIBUTIONS

David M. Lapola was responsible for the conceptualization of this manuscript. All authors wrote the original draft, revised subsequent drafts and contributed additional ideas. Barbara R. Cardeli produced the manuscript figure. David M. Lapola and Carlos A. N. Quesada acquired funding that made this study possible.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

David M. Lapola  <https://orcid.org/0000-0002-2654-7835>
 Carolina C. Blanco  <https://orcid.org/0000-0002-8959-2633>
 Barbara R. Cardeli  <https://orcid.org/0000-0001-7551-4768>
 Adriane Esquivel-Muelbert  <https://orcid.org/0000-0001-5335-1259>
 João V. Martinelli  <https://orcid.org/0000-0001-7296-8676>
 Carlos A. N. Quesada  <https://orcid.org/0000-0001-7178-9713>
 Bianca F. Rius  <https://orcid.org/0000-0002-7623-9152>
 Celso H. L. Silva-Junior  <https://orcid.org/0000-0002-1052-5551>

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