Earth's Future

RESEARCH ARTICLE
10.1029/2020EF001674

Key Points:
- Terrestrial ecosystems only slowly adapt to environmental changes
- Most of the modeled future (2015–2099) carbon uptake can be attributed to historical (1850–2015) rather than future environmental changes
- Legacy effects are mostly a result of CO_2 fertilization and also due to historical nitrogen deposition, land use change, and wood harvest

Supporting Information:
- Supporting Information S1

Correspondence to:
A. Krause,
andy.krause@tum.de

Citation:
Krause, A., Arneth, A., Anthoni, P., & Rammig, A. (2020). Legacy effects from historical environmental changes dominate future terrestrial carbon uptake. *Earth's Future*, *8*, e2020EF001674. https://doi.org/10.1029/2020EF001674

Received 19 JUN 2020
Accepted 28 SEP 2020
Accepted article online 5 OCT 2020

Legacy Effects from Historical Environmental Changes Dominate Future Terrestrial Carbon Uptake

A. Krause[1], A. Arneth[2], P. Anthoni[2], and A. Rammig[1]

[1]TUM School of Life Sciences Weihenstephan, Technical University of Munich, Freising, Germany, [2]Institute of Meteorology and Climate Research, Atmospheric Environmental Research, Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany

Abstract Ecosystems continuously adapt to interacting environmental drivers that change over time. Consequently, the carbon balance of terrestrial ecosystem may presently still be affected by past anthropogenic disturbances (e.g., deforestation) and other environmental changes (e.g., climate change). However, even though such so-called "legacy effects" are implicitly included in many carbon cycle modeling studies, they are typically not explicitly quantified and therefore scientists might not be aware of their long-term importance. Here, we use the ecosystem model LPJ-GUESS to quantify legacy effects for the 21st century and the respective contributions of the following environmental drivers: climate change, CO_2 fertilization, land use change, wood harvest, nitrogen deposition, and nitrogen fertilization. According to our simulations, the combined legacy effects of historical (1850–2015) environmental changes result in a land carbon uptake of +126 Gt C over the future (2015–2099) period. This by far exceeds the impacts of future environmental changes (range −53 Gt C to +16 Gt C for three scenarios) and is comparable in magnitude to historical carbon losses (−154 Gt C). Legacy effects can mainly be attributed to ecosystems still adapting to historical increases in atmospheric CO_2 (+65 Gt C) and nitrogen deposition (+33 Gt C), but long-term vegetation regrowth following agricultural abandonment (+8 Gt C) and wood harvest (+19 Gt C) also play a role. The response of the biosphere to historical environmental changes dominates future terrestrial carbon cycling at least until midcentury. Legacy effects persist many decades after environmental changes occurred and need to be considered when interpreting changes and estimating terrestrial carbon uptake potentials.

1. Introduction

Terrestrial ecosystems and the atmosphere constantly exchange carbon via photosynthesis, respiration, and disturbances. The direction and magnitude of these fluxes are regulated by environmental drivers, which interact with each other and change over time. For instance, until around the 1970s the land represented a net carbon source to the atmosphere (Friedlingstein et al., 2019) because emissions from land use change (i.e., agricultural expansion), wood harvest, and negative climate change impacts (e.g., droughts) exceeded enhanced carbon sequestration via positive climate change impacts (e.g., longer-growing seasons in high latitudes), forest area expansion (especially in temperate regions), carbon dioxide (CO_2) fertilization, and increased nitrogen input to ecosystems. However, since then the land acted as a net carbon sink and the terrestrial biosphere currently takes up around 30% of total anthropogenic CO_2 emissions, thereby reducing the growth rate of atmospheric CO_2 concentration (Friedlingstein et al., 2019). The interplay of changing environmental drivers will determine the fate of the land carbon sink in the future, but the relative importance of individual drivers is still under debate.

Process-based ecosystem models simulate the terrestrial carbon cycle as a function of changing environmental conditions. Accordingly, several modeling studies aimed to quantify the effects of specific environmental drivers on historical or future terrestrial carbon cycling (e.g., Friedlingstein et al., 2019; Huntzinger et al., 2017; McGuire et al., 2001; Tagesson et al., 2020). A review of recent modeling studies can be found in Tharammal, Bala, Devaraju, and Nemani (2019), who reported continued land carbon uptake in the 21st century across most scenarios and models, mainly due to CO_2 fertilization. However, the review of Tharammal, Bala, Devaraju, and Nemani (2019) also highlighted that often only the effects of one or two environmental drivers on the carbon cycle were investigated, making comprehensive assessments of the interplay of different drivers difficult. In addition, studies often do not separate the isolated effects of climate change versus CO_2 or distinguish between effects from wood harvest (if included) and other aspects of land use change, and contributions from nitrogen deposition or nitrogen fertilization are usually ignored. The individual contributions of all relevant drivers and their direct and, in particular, delayed (i.e., legacy) effects on the carbon cycle have to our knowledge so far not been investigated within a consistent modeling framework. Furthermore, a previous study (Krause et al., 2019) with three dynamic global vegetation models (DGVMs) found a large residual carbon uptake (~135 Gt C between 2006–2025 and 2080–2099) which could not be explained by future climate change (including CO_2 fertilization) and land use change (including wood harvest). While Krause et al. (2019) assumed that future nitrogen input may have played a role, a large fraction of this residual carbon uptake was likely caused by legacy effects from past environmental changes to which ecosystems presently still adapt. Legacy effects are typically included as an implicit flux in carbon cycle model experiments that capture transient changes through time. However, model experiments typically are not designed to quantify and write out these fluxes specifically and therefore scientists might not be aware of their long-term importance. While a recent study attributed 65.5% of the terrestrial carbon sink from 1981 to 2016 to environmental changes prior to 1981 (Chen et al., 2019), the relative contributions of individual drivers to legacy effects are still unknown. This leads to the question whether the future terrestrial carbon balance is primarily controlled by historical rather than future environmental changes—and if so, for how long?

Here, we perform factorial simulations with the LPJ-GUESS DGVM in which we keep isolated environmental drivers constant for specific time periods (1850–2099, 1850–2015, 2015–2099). This enables us to (a) investigate both historical and future changes in terrestrial carbon stocks; (b) quantify the individual contributions of a large number of environmental drivers, namely climate change, CO_2, land use change (including shifting cultivation), wood harvest, nitrogen deposition, and nitrogen fertilization; and (c) distinguish legacy effects from the effects of future environmental changes on future carbon cycling. We show that legacy effects are substantial, by far exceeding the net impacts of future environmental changes.

2. Materials and Methods

2.1. The LPJ-GUESS Ecosystem Model

We use the dynamic ecosystem model LPJ-GUESS (B. Smith et al., 2014) to investigate the impacts of historical and future environmental changes on historical and future carbon cycling. Model inputs include monthly temperature, short-wave radiation, and precipitation, and annual atmospheric CO_2 concentration, nitrogen deposition, and land use changes. The diversity of worldwide plant species is consolidated by the simulation of 10 tree and two grass (C3 and C4) plant functional types (PFTs), which are distinguished by their growth form, access to and demand for light and nutrients, and climatic preferences. Vegetation dynamics arise from simulated plant growth, competition, and mortality, influenced by environmental conditions and land management. Stochastic disturbance with an average return interval of 100 years (the default LPJ-GUESS value for global simulations) are simulated for a number of patches (here: 10) in each grid cell. LPJ-GUESS has a detailed representation of forest demography, allowing the explicit simulation of subgrid-scale land use dynamics like deforestation and forest regrowth in shifting cultivation systems (Bayer et al., 2017) or after wood harvest. Cropland and pasture PFTs and their management (e.g., harvest or nitrogen fertilization) are also simulated (Lindeskog et al., 2013; Olin et al., 2015).

2.2. Simulation Setup

We use the same model version and simulation setup as in Krause et al. (2019) where we forced LPJ-GUESS by three combinations of global land use change scenarios from the Land Use Harmonization project (LUH2, https://luh.umd.edu/) and bias-corrected climate projections from the IPSL-CM5A-LR climate model (Dufresne et al., 2013; Hempel et al., 2013) to investigate climate change + CO_2 and land use change + wood harvest impacts on terrestrial carbon stocks. The bias correction was done using observations from ERA-40 (daily) and CRU TS2.1 (monthly) for the reference period 1960–1999 and preserving absolute changes in monthly temperature and relative changes in monthly precipitation (Hempel et al., 2013). IPSL-CM5A-LR climate was chosen as LPJ-GUESS input because the simulated climate changes are quite representative of the ISI-MIP ensemble mean (Warszawski et al., 2014). We conduct a large number of factorial experiments (see Table S1 in the supporting information) and due to computational limitations only investigate in detail (i.e., separating effects from individual drivers) the high-emission/moderate

10.1029/2020EF001674

deforestation SSP5-8.5 scenario exemplarily for the future period. However, in section 4 we also compare legacy effects to the combined impacts of future environmental changes for two other scenarios, SSP1-2.6 and SSP3-6.0. In the baseline simulation (Simulation 1 in Table S1) future climate change (as simulated by IPSL-CM5A-LR), CO_2 concentration, and nitrogen deposition follow RCP8.5 (Riahi et al., 2011), while future land use change (including nitrogen fertilization) and wood harvest are taken from the LUH2 SSP5-8.5 scenario (https://luh.umd.edu/). The total simulation period is 1850–2099, with a prior 500-year spin-up to bring carbon pools into equilibrium with preindustrial environmental conditions (i.e., no vegetation nor soil carbon pools exists at the start of the spin-up; these are built up dynamically in the spin-up simulation period). While a constant land cover map is used during the spin-up, land cover transitions (including gross transitions) and wood harvest only take place after the spin-up. This leads to moderate reductions in carbon stocks directly after the spin-up, but long-term effects (i.e., after year 2015) are very small. Similarly, legacy effects from environmental changes before 1850 are assumed to be negligible.

2.3. Factorial Simulations

We carry out factorial simulations in which we keep either climate or atmospheric CO_2 constant from year 2015 on (rather than both as in Krause et al., 2019) while all other drivers follow RCP8.5/SSP5-8.5 (Simulations 2 + 3 in Table S1). Similarly, we investigate impacts of increased nitrogen input to ecosystems by keeping nitrogen deposition or nitrogen fertilization constant from year 2015 on (Simulations 4 + 5). In addition, we perform factorial simulations to quantify the isolated effects of land use change and wood harvest. Constant wood harvest is implemented as in Krause et al. (2019) by fixing harvest rates at average 1996–2014 rates from year 2015 on (but keeping land use change transient, Simulation 6). A minimum forest age of 15 years is assumed for harvesting from secondary young forests as provided by LUH2. To isolate the land use change effect, net land cover transitions (i.e., transitions that modify land cover fractions within a grid cell) are stopped in year 2015, while gross transitions (subgrid-scale transitions that modify forest age structure but not land cover fractions, e.g., shifting cultivation) are continued at the average rate of the last 20 years (analogous to wood harvest, Simulation 7). We note that this implementation of "constant land use" is different than in Krause et al. (2019) as in our previous study we stopped both net and gross transitions. While this might have been a technically valid interpretation of "constant land use," we here use the implementation described above because stopping gross transitions completely represents an unlikely scenario in which undisturbed forest regrowth in shifting cultivation systems likely contributed to the large residual carbon uptake found in Krause et al. (2019).

To allow for quantifying not only the impacts of future environmental changes on future carbon cycling but also the effects of historical environmental changes on historical carbon cycling, we repeat all factorial experiments with individual environmental drivers (climate change, CO_2, land use change, wood harvest, nitrogen deposition, nitrogen fertilization) kept constant at year 1850 levels directly after the spin-up (keeping other drivers transient; Simulations 8–13 in Table S1). Additionally, for each environmental driver we perform a third simulation in which we keep the driver constant at year 2015 levels from the start of the simulation (i.e., the start of the spin-up) until year 2015 (keeping other drivers transient) before applying transient changes for the 2015–2099 period (Simulations 14–19 in Table S1). In this way, we can estimate the legacy effects from historical environmental changes on future carbon uptake (calculation see below), assuming that carbon stocks in year 2015 are in equilibrium with the respective driver in these simulations (and thus different than in the transient simulations). Lastly, we perform two simulations in which we keep all environmental drivers constant from/until year 2015 (Simulations 20 + 21 in Table S1) to estimate the net impact of all environmental drivers combined and thus identify potential synergy effects (i.e., the net effect of all drivers being different from the sum of the individual effects; see also, e.g., Calvo & Prentice, 2015; Warlind et al., 2014).

2.4. Calculation of Effects From Individual Environmental Drivers

Figure 1 shows an example of how we calculate the effects of historical and future changes in atmospheric CO_2 concentration on historical and future carbon uptake. The impact of historical changes in atmospheric CO_2 on historical carbon cycling is calculated as the year 2015 difference between the baseline simulation (all drivers transient, gray line, Simulation 1 in Table S1) and the simulation in which we fix CO_2 at year 1850 levels (other drivers transient, orange line, Simulation 9 in Table S1). Similarly, the effect of future environmental changes on future carbon cycling is calculated as the year 2099 difference between the

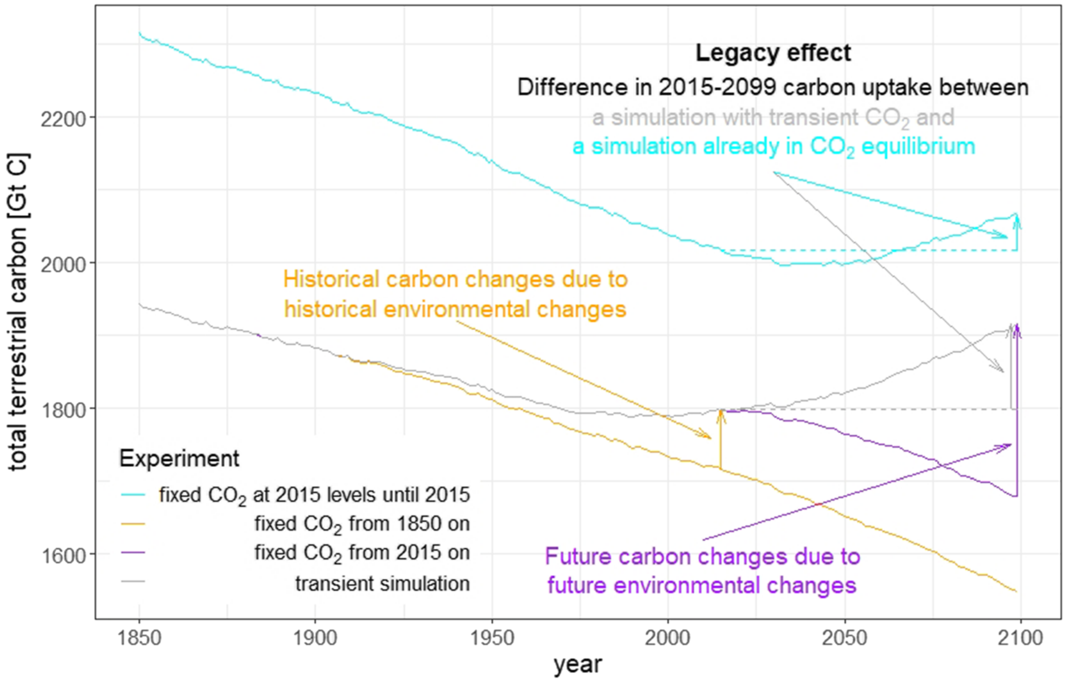

Figure 1. Example of how we calculate the effects of historical and future changes in atmospheric CO_2 on historical and future carbon cycling using our factorial simulations. The legacy effect is calculated as the difference in future (2015–2099) carbon uptake between a simulation in which ecosystems still adapt to present-day CO_2 levels (the baseline simulation, gray line; Simulation 1 in Table S1) and a simulation in equilibrium with year 2015 CO_2 levels (cyan line, Simulation 15). Environmental drivers other than CO_2 (climate change, land use change, wood harvest, nitrogen deposition, and nitrogen fertilization) are transient in all simulations shown in this figure. The individual effects of these other drivers are calculated the same way as for CO_2.

baseline simulation and the simulation in which atmospheric CO_2 is held constant from year 2015 on (purple line, Simulation 3 in Table S1). Finally, the impact of historical CO_2 on future carbon cycling (the legacy effect) is calculated by subtracting the 2015–2099 carbon uptake in a simulation in which ecosystems are already in equilibrium with present-day CO_2 levels (cyan line, Simulation 15 in Table S1) from the 2015–2099 carbon uptake in the baseline simulation (in which the system still adapts to present-day CO_2 levels; gray line). We thus assume that the additional carbon uptake in the nonequilibrium baseline simulation can be attributed to ecosystems still adapting to present-day CO_2 levels. The effects are calculated the same way for the other environmental drivers (climate change, land use change, wood harvest, nitrogen deposition, nitrogen fertilization).

3. Results

3.1. Historical Carbon Cycling

Historical (1850–2015) net land carbon release (−154 Gt C; Figure 2) is a result of land use change (−167 Gt C), wood harvest (−33 Gt C), climate change (−32 Gt C), and synergies between drivers (−29 Gt C; termed "residual" in Figure 2) exceeding positive impacts from CO_2 fertilization (+80 Gt C), nitrogen deposition (+25 Gt C), and nitrogen fertilization (+3 Gt C). Spatially, historical land use change and wood harvest emissions are concentrated in temperate regions, while CO_2 effects are mostly found in tropical and boreal forests (Figures 3 and S1). Notably, LPJ-GUESS simulates a smaller net land flux over the last decades (Figure 1, gray line) than the TRENDY ensemble, but within the 90% confidence interval of constraints by global atmospheric and oceanic observations (Friedlingstein et al., 2019).

3.2. The Importance of Legacy Effects for Future Carbon Cycling

Historical environmental changes continue to affect ecosystem carbon storage in the future. These legacy effects cause a net land carbon uptake of +126 Gt C from 2015 to 2099, which is substantially larger than

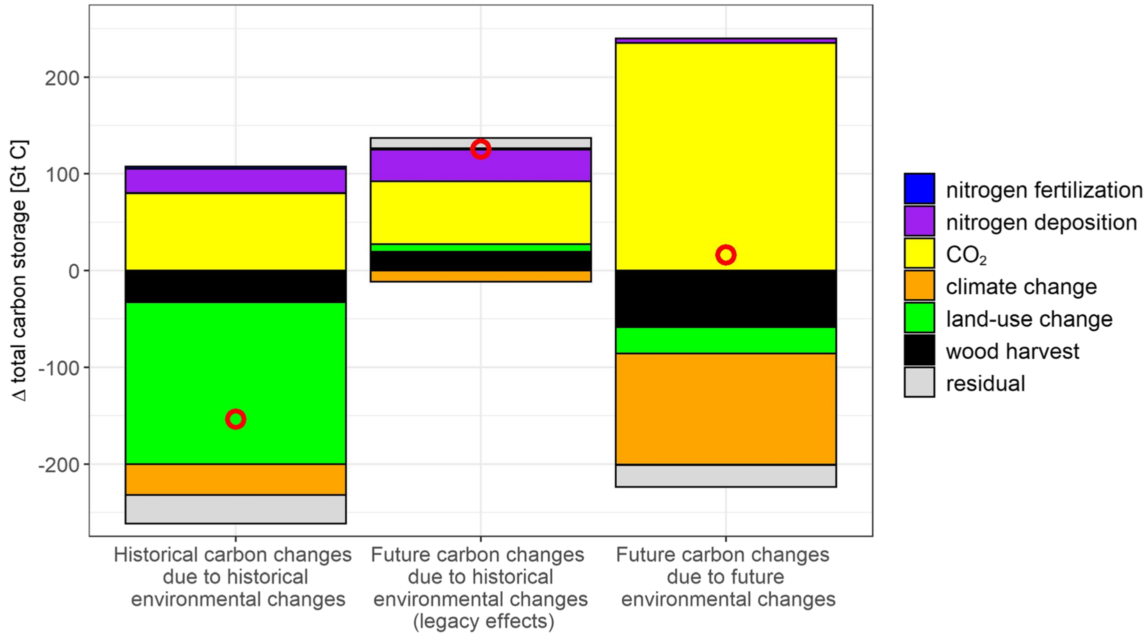

Figure 2. Individual contributions of historical (1850–2015) and future (2015–2099) changes in environmental drivers on historical and future carbon cycling. Red circles indicate the combined effect of all drivers, including synergies ("residual") between drivers.

the combined impacts from future environmental changes (+16 Gt C) and, despite the shorter time period, comparable in magnitude to historical losses (Figure 2). This can largely be explained by ecosystems still adapting to present-day CO_2 levels (+65 Gt C), but, maybe more surprisingly, also by ecosystems not yet being in equilibrium with present-day nitrogen deposition levels (+33 Gt C). In addition, despite having triggered carbon losses over the historical period, wood harvest and land use change also cause positive legacy effects (+19 and +8 Gt C, respectively) due to slow vegetation regrowth in managed forests and abandoned agricultural fields (mostly located in temperate and boreal regions, Figure 3). Legacy effects from historical climate change cause a net carbon release to the atmosphere (−11 Gt C) which is a result of enhanced soil carbon decomposition in the nowadays warmer climate (Figure S2b). However, in tundra regions concurrent tree growth, in response to historical warming, results in carbon gains (Figure 3). Individual legacy effects do not add up to the total net legacy effect derived from the simulation in which all drivers are kept constant until year 2015, indicating that synergies between environmental drivers trigger an additional small carbon uptake (+11 Gt C).

Even though the combined impact of future environmental changes on future carbon cycling is much smaller than the combined legacy effect, contributions of individual drivers tend to be larger (Figure 2). Future CO_2 increase is by far the most important positive driver (+235 Gt C) but is largely canceled by carbon losses from future climate change (−115 Gt C, mostly soil carbon emissions see Figure S2), land use change (−27 Gt C), and wood harvest (−58 Gt C). Future nitrogen deposition and fertilization have only small impacts (+5 and −0 Gt C, respectively). Residual effects from synergies between drivers occur mostly regionally (Figure 3).

3.3. Legacy Effects Versus Future Environmental Changes Over the Next Decades

We also compare the relevance of legacy effects versus future environmental changes on near-term carbon sequestration (Figure 4). Even though future environmental changes trigger substantial carbon losses until around 2050, the net impact is still a carbon uptake due to strong positive legacy effects. Residual effects (in this case the difference between carbon uptake in the baseline simulation and the sum of legacy effects and future environmental changes effects) trigger a small carbon loss throughout the century. The strength of legacy carbon uptake slowly diminishes over time, but as future environmental changes start to trigger carbon accumulation after 2050, the land carbon sink persists and even intensifies in the second half of the

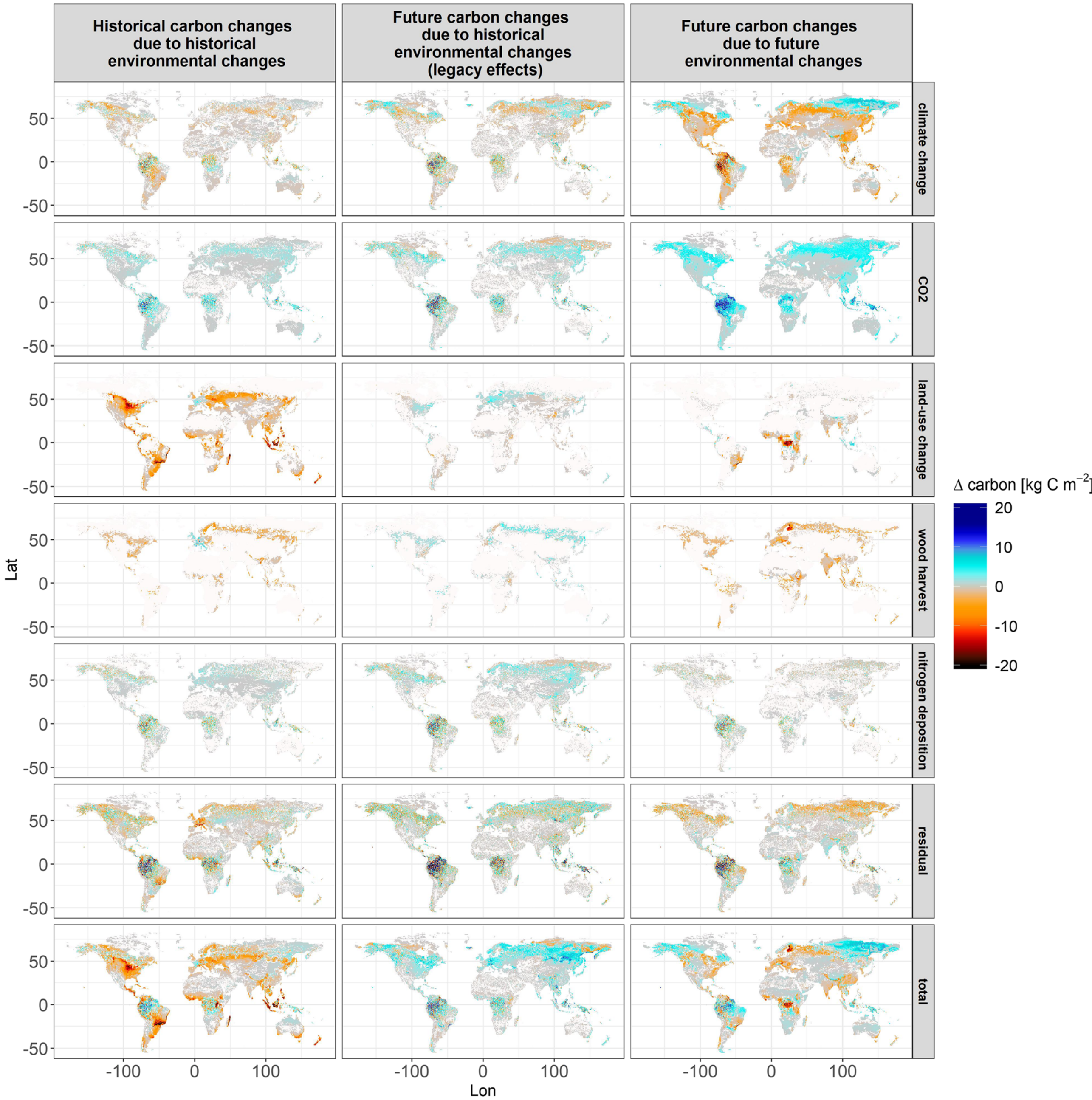

Figure 3. Maps of individual contributions of historical (1850–2015) and future (2015–2099) changes in environmental drivers on historical and future carbon cycling. Nitrogen fertilization is not shown because effects are too small to be visible. Regions where carbon changes are smaller than the year-to-year natural variability (1 σ over the 1950–2015 period) in the constant forcing Simulation 21 are masked in very light gray, while small but significant changes are displayed in dark gray.

century. Nevertheless, legacy effects will dominate the net ecosystem carbon balance for at least the next three decades.

4. Discussion

The main outcome of our analysis is that legacy effects from historical environmental changes affect ecosystem carbon cycling long after these changes occurred and might at least for some decades be far more important (+126 Gt C over the 2015–2099 period) than the net impact of future environmental changes according to the SSP5-8.5 scenario (+16 Gt C).

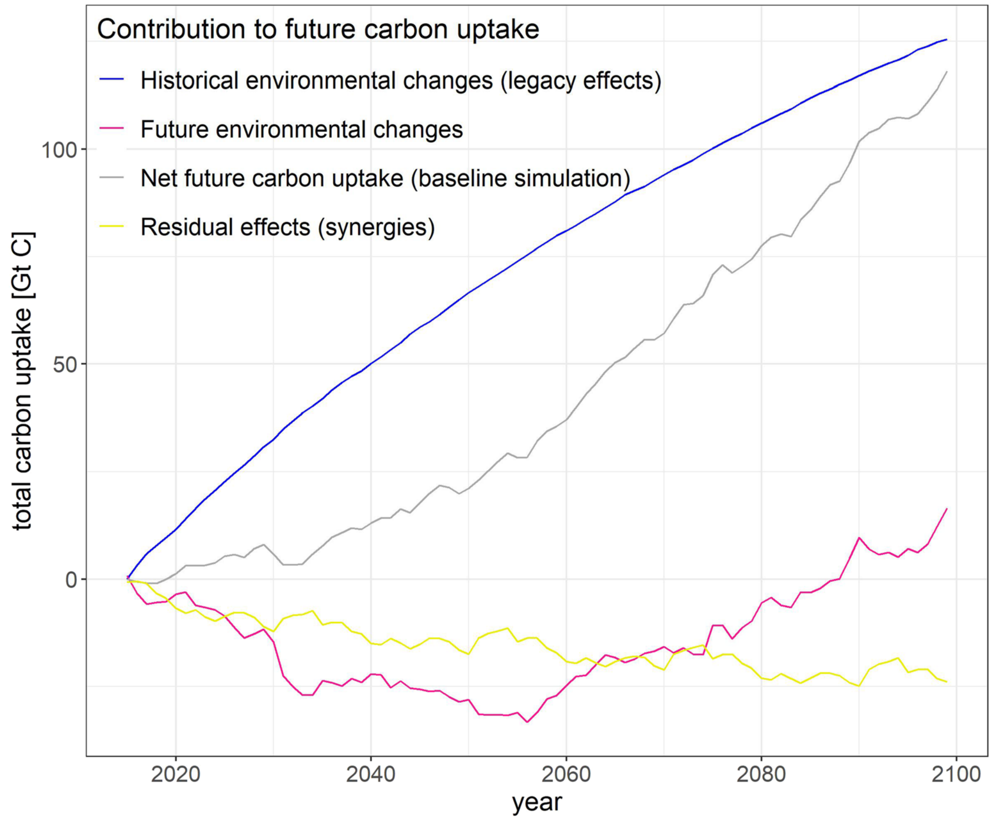

Figure 4. Time series of the contributions of historical and future environmental changes on cumulative future terrestrial carbon uptake. While legacy effects cause carbon uptake throughout the entire future period (blue line), future environmental changes (according to the SSP5-8.5 scenario) result in carbon release until around midcentury (pink line) due to negative impacts, for example, from agricultural expansion exceeding positive impacts, for example, from CO_2 fertilization. The blue line is calculated as the difference in carbon uptake between the baseline simulation (gray line) and a simulation in which all drivers are held constant at 2015 levels until 2015 (i.e., ecosystems are in equilibrium with present-day conditions; Simulation 21 in Table S1). The pink line is calculated as the difference in carbon uptake between the baseline simulation and a simulation in which all drivers are held constant at 2015 levels from 2015 on (Simulation 20 in Table S1). Residual effects (yellow line) are calculated as the difference in carbon uptake between the baseline simulation and the sum of legacy effects and effects of future environmental changes.

4.1. Are Our Findings Scenario-, Model- or Setup-Dependent?

Even though the effects of future environmental changes are computed for only one scenario, similar findings would likely emerge for other pathways. For instance, subtracting the carbon uptake in Simulation 20 (the simulation with all drivers constant from year 2015 on) from the carbon uptake in the transient simulations analyzed in Krause et al. (2019) reveals negative impacts of future environmental changes for SSP1-2.6 (−16 Gt C) and SSP3-6.0 (−53 Gt C) (Figure S3), despite a net carbon uptake of +88 and +47 Gt C, respectively. For SSP1-2.6 this can be mainly explained by very little additional CO_2 fertilization, while for SSP3-6.0 this is a result of large-scale deforestation. On the other hand, as all scenarios share the same historical forcing we can assume legacy effects to be the same as in SSP5-8.5 (+126 Gt C, even though synergies might be different), which is confirmed by the large net carbon uptake in both scenarios.

Results, however, may be highly model-dependent due to the very different representations of forest dynamics, soil nutrients, and land use processes in DGVMs. For instance, models with an implemented carbon-nitrogen-phosphorus cycle (phosphorus cycle is not implemented in LPJ-GUESS) simulate around 50% less biomass growth from CO_2 fertilization in tropical forests compared to carbon-only and carbon-nitrogen models (Fleischer et al., 2019), while a more detailed representation of land management (implemented in LPJ-GUESS) substantially increases historical land use emissions (Arneth et al., 2017). However, the large residual carbon uptake for two other DGVMs reported by Krause et al. (2019)

indicates that the substantial legacy effects found in the present study are not only occurring in LPJ-GUESS simulations.

Furthermore, a study that compared long-term (time horizon of several centuries) impacts of legacy effects (termed "committed change") with transient simulations found a total carbon uptake between preindustrial and 2100 ranging from +87 to +464 Gt C, and an additional 205–329 Gt C until the carbon cycle reached equilibrium (Pugh et al., 2018). For LPJ-GUESS, the corresponding values were +87 Gt C for the transient effect (i.e., the smallest transient effect of all models) and +253 Gt C for the committed effect (which is close to the model average). This indicates that the transient effects from future environmental changes might be relatively more pronounced in other DGVMs than in LPJ-GUESS. However, as the equilibrium stage was only reached 150–200 years after fixing the forcing, the committed effect in Pugh et al. (2018) is not directly comparable to our combined legacy effects calculated over 85 years, even though the magnitudes of carbon uptake seem reasonable in comparison.

We here identify contributions from individual environmental drivers on terrestrial carbon cycling by comparing simulations where we keep the driver constant from/until a specific year (other drivers transient) with a baseline simulation in which all drivers are transient. We also considered the reverse option (individual driver transient while keeping all other drivers constant and compare to a simulation with all drivers constant). However, test simulations for future CO_2 reveal an almost identical global effect (+235 Gt C in both cases), suggesting that findings are not sensitive to the selected approach.

4.2. What Are the Drivers of Legacy Effects?

While a strong legacy effect has been previously found in other ecosystem models (Chen et al., 2019; Krause et al., 2019), the role of individual drivers for such effect has so far not been quantified. The legacy effect reported by Chen et al. (2019) for the 1981–2016 period is smaller (+62 Gt C) than in our study, but comparable when adjusting for equivalent time intervals (e.g., 2015–2050 in our study: +67 Gt C; Figure 4). Our simulations suggest that around half of this uptake is due to ecosystems still adapting to present-day atmospheric CO_2 concentration. Even though CO_2 fertilization has been identified in many models as a key driver of increasing terrestrial carbon stocks over recent decades (Chen et al., 2019; Devaraju et al., 2016; Huntzinger et al., 2017), substantial uncertainties remain about the strength and persistence of this effect, not only because of large model disagreement (e.g., between carbon-only and carbon-nitrogen models, see Huntzinger et al., 2017) but also because Free Air Carbon Dioxide Enrichment (FACE) experiments, atmospheric inversion data, tree ring data, and satellite-derived productivity analyses do not yet reveal a coherent picture (e.g., Fernandez-Martinez et al., 2019; Hararuk et al., 2019; Schimel et al., 2015; W. K. Smith et al., 2016). In particular, large uncertainties about a possible CO_2 fertilization effect exist in tropical forests where phosphorous limitation could substantially reduce the CO_2 effect (Fleischer et al., 2019; Terrer et al., 2019).

Besides CO_2 fertilization, the second-largest contributor to legacy effects is nitrogen deposition. Interestingly, this effect is even larger than the impact of historical nitrogen deposition on historical carbon uptake. The effect of nitrogen deposition on cumulative carbon uptake over the 1850–2099 period in our study is comparable to an earlier LPJ-GUESS version with only potential natural vegetation (62 Gt C vs. 55 Gt C) (Warlind et al., 2014). Warlind et al. (2014) note that nitrogen limitation in middle/high latitudes might be overestimated in LPJ-GUESS (and most other models) due to the lack of a dynamic representation of organic nitrogen uptake and/or a process-based representation of biological nitrogen fixation. Moreover, while the strength of the CO_2 effect in Warlind et al. (2014) is also in agreement with our study (381 Gt C vs. 361 Gt C), our climate change impacts are substantially smaller (−158 Gt C vs. 320 Gt C), possibly because the input climate was derived from a different climate model (both RCP8.5 though).

In addition, carbon uptake via legacy effects is triggered by historical land conversion and wood harvest, which is a result of vegetation regrowth proceeding over many decades (Krause et al., 2016) outweighing ongoing soil carbon depletions in recently established croplands (Pugh et al., 2015). The combined legacy effect from land use change and wood harvest in our study is smaller (+27 Gt C) than the +69 Gt C forest regrowth potential calculated by Pugh et al. (2019). Potential reasons for this mismatch are differences in investigated variables (total carbon vs. biomass), time frames (2015–2099 vs. equilibrium stage) and processes included besides vegetation regrowth after agricultural abandonment (e.g., soil carbon emissions in croplands vs. forest recovery from natural disturbances). Nevertheless, both Pugh et al. (2019) and our study emphasize the need to represent forest management in ecosystem models projecting future terrestrial carbon stocks (as do other studies, e.g., Pongratz et al., 2018).

4.3. Implications for Interpreting Carbon Cycle Alterations

The existence of strong legacy effects has important implications for interpretation of changes in the terrestrial carbon cycle. We can now reason that legacy effects were responsible for ~76% (+103 Gt C) of the residual carbon uptake (i.e., not explained by future climate change, CO_2, land use change, and wood harvest) reported in Krause et al. (2019). Future nitrogen deposition (3% or +5 Gt C, respectively), nitrogen fertilization (−0%), and the arguably unrealistic implementation of "constant land use" (i.e., allowing unlimited forest regrowth in shifting cultivation regions; 20% or +27 Gt C, respectively) played only minor roles. Our simulations also show that caution is needed when impacts from future land use change are determined by fixing all other environmental drivers constant at present-day levels (Tharammal, Bala, Narayanappa, & Nemani, 2019) because the carbon uptake will be a result not only of future land use change but also—maybe more important—historical environmental changes.

5. Conclusions

Legacy effects from environmental changes still impact ecosystems many decades after these changes took place. Even though this mechanism is generally included in simulations of the future carbon cycle (by starting the simulations decades or centuries before the period of interest), legacy effects are usually not calculated separately. Consequently, scientists might not be aware of the strength of legacy effects in the long-term and erroneously attribute most or all of the residual carbon uptake to future changes in environmental drivers not investigated in their study (e.g., CO_2 and climate change if the study focuses on land use changes). In fact, however, legacy effects over the 21st century can be assumed to be much larger than the transient effects of future environmental changes. The fact that ecosystems are presently not yet in equilibrium with their environment needs to be considered when interpreting changes in the terrestrial carbon cycle.

Conflict of Interest

The authors declare no conflict of interest.

Data Availability Statement

Data underlying the analyses are available online (https://figshare.com/articles/dataset/Krause_et_al_2020_Earth_s_Future/13041977).

Acknowledgments

We thank the anonymous reviewers for their helpful and constructive comments which improved the manuscript. We are also grateful to the LSAI group for fruitful discussions and ISI-MIP and LUH2 for making the input data to LPJ-GUESS available. LPJ-GUESS simulations were performed on the Linux cluster of the Leibniz Supercomputing Centre (LRZ). All figures were produced using the tidyverse/ggplot2 package of the R programming language (https://www.r-project.org/). Open access funding enabled and organized by Projekt DEAL.

References

Arneth, A., Sitch, S., Pongratz, J., Stocker, B. D., Ciais, P., Poulter, B., et al. (2017). Historical carbon dioxide emissions caused by land-use changes are possibly larger than assumed. *Nature Geoscience*, *10*, 79–84. https://doi.org/10.1038/Ngeo2882

Bayer, A. D., Lindeskog, M., Pugh, T. A. M., Anthoni, P. M., Fuchs, R., & Arneth, A. (2017). Uncertainties in the land-use flux resulting from land-use change reconstructions and gross land transitions. *Earth System Dynamics*, *8*, 91–111. https://doi.org/10.5194/esd-8-91-2017

Calvo, M. M., & Prentice, I. C. (2015). Effects of fire and CO_2 on biogeography and primary production in glacial and modern climates. *New Phytologist*, *208*, 987–994. https://doi.org/10.1111/nph.13485

Chen, J. M., Ju, W. M., Ciais, P., Viovy, N., Liu, R. G., Liu, Y., & Lu, X. H. (2019). Vegetation structural change since 1981 significantly enhanced the terrestrial carbon sink. *Nature Communications*, *10*, 1–7. https://doi.org/10.1038/s41467-019-12,257-8

Devaraju, N., Bala, G., Caldeira, K., & Nemani, R. (2016). A model based investigation of the relative importance of CO_2-fertilization, climate warming, nitrogen deposition and land use change on the global terrestrial carbon uptake in the historical period. *Climate Dynamics*, *47*, 173–190. https://doi.org/10.1007/s00382-015-2830-8

Dufresne, J. L., Foujols, M. A., Denvil, S., Caubel, A., Marti, O., Aumont, O., et al. (2013). Climate change projections using the IPSL-CM5 Earth System Model: from CMIP3 to CMIP5. *Climate Dynamics*, *40*, 2123–2165. https://doi.org/10.1007/s00382-012-1636-1

Fernandez-Martinez, M., Sardans, J., Chevallier, F., Ciais, P., Obersteiner, M., Vicca, S., et al. (2019). Global trends in carbon sinks and their relationships with CO_2 and temperature. *Nature Climate Change*, *9*, 73–79. https://doi.org/10.1038/s41558-018-0367-7

Fleischer, K., Rammig, A., De Kauwe, M. G., Walker, A. P., Domingues, T. F., Fuchslueger, L., et al. (2019). Amazon forest response to CO_2 fertilization dependent on plant phosphorus acquisition. *Nature Geoscience*, *12*, 736–741. https://doi.org/10.1038/s41561-019-0404-9

Friedlingstein, P., Jones, M. W., O'Sullivan, M., Andrew, R. M., Hauck, J., Peters, G. P., et al. (2019). Global Carbon Budget 2019. *Earth System Science Data*, *11*, 1783–1838. https://doi.org/10.5194/essd-11-1783-2019

Hararuk, O., Campbell, E. M., Antos, J. A., & Parish, R. (2019). Tree rings provide no evidence of a CO_2 fertilization effect in old-growth subalpine forests of western Canada. *Global Change Biology*, *25*, 1222–1234. https://doi.org/10.1111/gcb.14561

Hempel, S., Frieler, K., Warszawski, L., Schewe, J., & Piontek, F. (2013). A trend-preserving bias correction – the ISI-MIP approach. *Earth System Dynamics*, *4*, 219–236. https://doi.org/10.5194/esd-4-219-2013

Huntzinger, D. N., Michalak, A. M., Schwalm, C., Ciais, P., King, A. W., Fang, Y., et al. (2017). Uncertainty in the response of terrestrial carbon sink to environmental drivers undermines carbon-climate feedback predictions. *Scientific Reports*, *7*, 4765. https://doi.org/10.1038/s41598-017-03818-2

Krause, A., Haverd, V., Poulter, B., Anthoni, P., Quesada, B., Rammig, A., & Arneth, A. (2019). Multi-model analysis of future land-use and climate change impacts on ecosystem functioning. *Earth's Future*, *7*, 833–851. https://doi.org/10.1029/2018EF001123

Krause, A., Pugh, T. A. M., Bayer, A. D., Lindeskog, M., & Arneth, A. (2016). Impacts of land-use history on the recovery of ecosystems after agricultural abandonment. *Earth System Dynamics*, *7*, 745–766. https://doi.org/10.5194/esd-7-745-2016

Lindeskog, M., Arneth, A., Bondeau, A., Waha, K., Seaquist, J., Olin, S., & Smith, B. (2013). Implications of accounting for land use in simulations of ecosystem carbon cycling in Africa. *Earth System Dynamics*, *4*, 385–407. https://doi.org/10.5194/esd-4-385-2013

McGuire, A. D., Sitch, S., Clein, J. S., Dargaville, R., Esser, G., Foley, J., et al. (2001). Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO_2, climate and land use effects with four process-based ecosystem models. *Global Biogeochemical Cycles*, *15*(1), 183–206. https://doi.org/10.1029/2000gb001298

Olin, S., Schurgers, G., Lindeskog, M., Warlind, D., Smith, B., Bodin, P., et al. (2015). Modeling the response of yields and tissue C: N to changes in atmospheric CO_2 and N management in the main wheat regions of western Europe. *Biogeosciences*, *12*, 2489–2515. https://doi.org/10.5194/bg-12-2489-2015

Pongratz, J., Dolman, H., Don, A., Erb, K. H., Fuchs, R., Herold, M., et al. (2018). Models meet data: Challenges and opportunities in implementing land management in Earth system models. *Global Change Biology*, *24*, 1470–1487. https://doi.org/10.1111/gcb.13988

Pugh, T. A. M., Arneth, A., Olin, S., Ahlstrom, A., Bayer, A. D., Goldewijk, K. K., et al. (2015). Simulated carbon emissions from land-use change are substantially enhanced by accounting for agricultural management. *Environmental Research Letters*, *10*, 124008. https://doi.org/10.1088/1748-9326/10/12/124008

Pugh, T. A. M., Jones, C. D., Huntingford, C., Burton, C., Arneth, A., Brovkin, V., et al. (2018). A large committed long-term sink of carbon due to vegetation dynamics. *Earth's Future*, *6*, 1413–1432. https://doi.org/10.1029/2018ef000935

Pugh, T. A. M., Lindeskog, M., Smith, B., Poulter, B., Arneth, A., Haverd, V., & Calle, L. (2019). Role of forest regrowth in global carbon sink dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 4382–4387. https://doi.org/10.1073/pnas.1810512116

Riahi, K., Rao, S., Krey, V., Cho, C. H., Chirkov, V., Fischer, G., et al. (2011). RCP 8.5-A scenario of comparatively high greenhouse gas emissions. *Climatic Change*, *109*(1–2), 33–57. https://doi.org/10.1007/s10584-011-0149-y

Schimel, D., Stephens, B. B., & Fisher, J. B. (2015). Effect of increasing CO_2 on the terrestrial carbon cycle. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 436–441. https://doi.org/10.1073/pnas.1407302112

Smith, B., Warlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., & Zaehle, S. (2014). Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences*, *11*, 2027–2054. https://doi.org/10.5194/bg-11-2027-2014

Smith, W. K., Reed, S. C., Cleveland, C. C., Ballantyne, A. P., Anderegg, W. R. L., Wieder, W. R., et al. (2016). Large divergence of satellite and Earth system model estimates of global terrestrial CO_2 fertilization. *Nature Climate Change*, *6*, 306–310. https://doi.org/10.1038/Nclimate2879

Tagesson, T., Schurgers, G., Horion, S., Ciais, P., Tian, F., Brandt, M., et al. (2020). Recent divergence in the contributions of tropical and boreal forests to the terrestrial carbon sink. *Nature Ecology & Evolution*, *4*, 202–209. https://doi.org/10.1038/s41559-019-1090-0

Terrer, C., Jackson, R. B., Prentice, I. C., Keenan, T. F., Kaiser, C., Vicca, S., et al. (2019). Nitrogen and phosphorus constrain the CO_2 fertilization of global plant biomass. *Nature Climate Change*, *9*, 684–689. https://doi.org/10.1038/s41558-019-0545-2

Tharammal, T., Bala, G., Devaraju, N., & Nemani, R. (2019). A review of the major drivers of the terrestrial carbon uptake: Model-based assessments, consensus, and uncertainties. *Environmental Research Letters*, *14*, 093005. https://doi.org/10.1088/1748-9326/ab3012

Tharammal, T., Bala, G., Narayanappa, D., & Nemani, R. (2019). Potential roles of CO_2 fertilization, nitrogen deposition, climate change, and land use and land cover change on the global terrestrial carbon uptake in the twenty-first century. *Climate Dynamics*, *52*, 4393–4406. https://doi.org/10.1007/s00382-018-4388-8

Warlind, D., Smith, B., Hickler, T., & Arneth, A. (2014). Nitrogen feedbacks increase future terrestrial ecosystem carbon uptake in an individual-based dynamic vegetation model. *Biogeosciences*, *11*, 6131–6146. https://doi.org/10.5194/bg-11-6131-2014

Warszawski, L., Frieler, K., Huber, V., Piontek, F., Serdeczny, O., & Schewe, J. (2014). The Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP): Project framework. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 3228–3232. https://doi.org/10.1073/pnas.1312330110