## A temperate climate with low atmospheric CO<sub>2</sub> and high O<sub>2</sub> levels before the emergence of forested ecosystems

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Traditionally, the evolution of trees and the establishment of the first forests during the Devonian (419-359 Ma) have been linked to an enhancement of terrestrial weathering processes and a subsequent reduction of atmospheric CO<sub>2</sub> levels by one order of magnitude. However, empirical estimates of early-Devonian CO<sub>2</sub> concentrations are sparse and carry large error bars. We have calibrated a gas exchange model in modern lycophytes that has allowed us to estimate atmospheric CO<sub>2</sub> levels 410-380 million years ago from leaf carbon isotopes, stomata density, and stomata pore length measurements of fossilized lycophytes. We find that Earth's atmosphere contained about 525-715 ppm of CO<sub>2</sub> before the emergence of forested ecosystems, far less than previously thought [1]. Using a coupled climate model, we show that Earth was partially glaciated at these moderate CO2 levels and that this cool climate state is in good agreement with available climate proxies and fossil evidence for the distribution of terrestrial vegetation. Finally, we revise a process-based biogeochemical model (COPSE reloaded) to demonstrate that our results are consistent with a scenario in which enhanced weathering and climate cooling is associated with the earlier emergence of shallow-rooted vascular ecosystems rather than the appearance of the first forests. Also, volcanic outgassing from Earth's interior is primarily linked to the amount of subducted carbonate platforms rather than global volcanic activity, as was previously thought. From this, we establish a new hypothesis for the evolution of atmospheric O<sub>2</sub> and CO<sub>2</sub> in which the Silurian appearance of vascular plants play a key role in transforming Earth's surface environment to modern-like climate and redox state.

 [1] Dahl et al. "Low atmospheric CO2 levels before the rise of forested ecosystems". *Nature Communications* 13, 1–10 (2022) https://doi.org/10.1038/s41467-022-35085-9