

Biogeosciences Discuss., referee comment RC2
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Comment on bg-2021-139

Anonymous Referee #2

Referee comment on "The Cretaceous physiological adaptation of angiosperms to a declining $p\text{CO}_2$: a modeling approach emulating paleo-traits" by Julia Bres et al., Biogeosciences Discuss., <https://doi.org/10.5194/bg-2021-139-RC2>, 2021

The authors present a three-parameter sensitivity study involving atmospheric CO_2 concentration, maximum upper stomatal conductance constraint (physiological constraint on dynamic stomatal conductance), and photosynthetic capacity via adjustment of V_{cmax} . They motivate this study using the example of angiosperm evolution and associated adjustment of physiological traits during the the Aptian age of the Lower Cretaceous. The study is interesting and worthwhile publishing, as it not only contributes to an improved understanding of the physiological adaptations and adjustments that accompanied the angiosperm evolution and radiation, as well as possible driving factors behind these physiological adjustments, but also offers insights on model sensitivity with regard to these parameters. The evolution of higher vein densities and associated increase in structural stomatal conductance concomitant with the angiosperm radiation must have been functionally beneficial and is therefore worthwhile to be studied in more detail in order to improve understanding of associated processes and effects.

The authors use the ORCHIDEE DGVM/land surface model and LMDz atmosphere general circulation model versions embedded in the IPSL-CM5A2 model, which implies that the underlying vegetation model is not suitable to directly simulate functional traits and trait diversity. The authors circumvent this constraint by mimicking the traits using parameters available in their model. This approach is valid, and part of the limitations as well as suggested improvements are discussed in the discussion section. However, it should be made more clear also with respect to the title of the study that it is not a truly trait-based modeling study.

With regard to stomatal regulation on daily basis (operational/dynamic stomatal regulation), I would like to have some clarification on the influence of water stress, because it did not become clear to me whether and how water constraint will down-regulate stomatal conductance.

The manuscript is structured clearly in most parts, the language is appropriate and understandable (although the English would benefit from additional grammar and style corrections). However, I have a variety of comments and suggestions on how the

manuscript could be improved further, which I am listing in the following.

Specific comments for the authors:

Title: I'm not sure whether the title is appropriate. Personally, I find it a bit misleading, because it made me expect a study using a trait-based DGVM that explicitly considers plant functional traits. Only after reading the manuscript it became clear that it is actually a three-parameter sensitivity study that indirectly emulates functional traits and is therefore limited compared to the full range of possibilities offered by trait-based adaptive DGVMs. I therefore suggest adjusting the title to make this more clear.

Introduction

l. 41 "showing a strong correlation with vein density": clarify in which direction: positive correlation (i.e., higher vein density correlated to larger and more dense stomata), or negative (e.g., more but smaller stomata associated with higher vein density).

l. 42 "veins allow the plants to efficiently transport water from the soil close to the site of transpiration": That's not only leaf veins, this is also dependent on xylem (type, diameter, reinforcement) in plant stems. The soil-plant-atmosphere continuum (SPA) also depends on the hydraulic capacity of the xylem and the associated suction pressure it can withstand before cavitation becomes substantial at high suction pressure (p50 concept). Xylem structure/anatomy also differs quite substantially between gymnosperms (pitted tracheids) and angiosperms (trachea/vessel elements). This is another trait that has implications for functionality with regard to water transport through the plant. It would be nice if you could at least write a little bit about that here, and whether and how this is accounted for in the ORCHIDEE model.

l. 43/44 "Dv is a reliable marker of hydraulic capacity": is Dv correlated with p50? I'd expect it to, at least to some degree.

l. 51 "bolster the current hydrological cycle": Find a more appropriate verb? Not sure what you mean to say exactly.

l. 54/55 At least mention the other traits associated with the SPA continuum that you are omitting, because it is the combination of all traits in the SPA continuum that mitigate the water flux between soil, plants and atmosphere.

I. 63 "Depending on the choices made": which choices?

I. 67/68 "Moreover, atmospheric $p\text{CO}_2$ is known to control the degree of stomatal opening and closing at very short-term": Are you talking about structural stomatal opening here, or about operational opening? Because operational opening would not be controlled by $p\text{CO}_2$ alone, but jointly with water availability in relation to atmospheric demand (vapor pressure deficit, VPD). This co-regulation by C-demand for assimilation vs. water demand by the atmosphere indeed happens on very short time scales, whereas structural stomatal changes occur on evolutionary time scales.

I. 75-77: Just a comment: This is an interesting question - why did the higher Dv evolve and become abundant? It must have been beneficial, otherwise it would not have spread and persisted. It's therefore worthwhile to investigate the associated effects and dedicate a study to that topic. In particular if this helps to better understand connections between physiology and function that may not be as well understood as required to adequately represent plant functional traits in vegetation models. It is important to translate observed plant traits, whether they are paleo-traits or contemporary, into functional meaning in order to understand and quantify their implications for vegetation reactions on environmental conditions.

What I am missing at the end of the introduction is a statement listing your research questions or research hypotheses. I suggest to add such an explicit statement of your main research questions or hypotheses here, because it makes it easier to evaluate your results in relation to the research goals of the study.

Methods

I. 87/88 Are the 4-meter soil depth a global parameter? Soil depth has a major influence on plant water availability as it defines the size of the bucket, especially in simple bucket model representations e.g., see Langan et al., 2017, *Journal of Biogeography*, doi:10.1111/jbi.13018). I suppose there is no possibility to infer soil parameters or soil depth from the Aptian time, so you have to make assumptions. Please also list this as a limitation in the discussion where you talk about other limitations and uncertainties associated to your study. Also not mentioned: what kind of other soil parameters does ORCHIDEE require (soil texture, wilting point, k_{sat} , etc), and how did you parameterize these parameters?

I. 92: "while carbon-related slow processes are computed on a daily basis": What carbon-related processes are these in detail that you define as "slow processes"? The temporal resolution for handling of C-related processes varies between DGVMs. Some DGVMs do carbon allocation and respiration on daily basis, others on even coarser time scales (monthly, annual).

I. 98-104: "leaf operational stomatal conductance to H₂O, g_s (mol m⁻²[leaf] s⁻¹), depends on the net carbon assimilation A...": Does the model also account for water limitation effects on stomatal regulation? When water demand required by the atmosphere, via water vapor deficit (VPD) cannot be met by the quantity of water that can be supplied via the SPA continuum, stomata should close in response to the water shortage. In more detail, this means that as long as the water demand required by the atmosphere can be met, the stomata regulation can be driven by the carbon side, i.e., the carbon demand of photosynthesis, as represented by C_i , under the given limiting conditions to photosynthesis (J_c , J_e , J_s). But if the water demand by the atmosphere cannot be served any more by the soil-plant continuum due to low water content/resistance that exceeds the transport capacity required to fulfill the atmospheric demand, this should also trigger stomatal closure, at least up to the point where stomatal conductance just about equals the maximum water loss possible under the water constraint, i.e., the quantity of water that can be provided through the SP-system. Under such conditions, photosynthesis, via water-limitation-induced stomatal closure or partial closure, should be constrained by stomatal conductance, rather than stomatal conductance being constrained by assimilation capacity. This water-stress-induced stomatal closure will not only down-regulate photosynthesis under water stress, but at the same time reduce transpirational cooling of leaves as latent heat flux decreases and sensible heat flux concomitantly increases, which leads to an increase in leaf temperature under water stress and impacts temperature-dependent V_{cmax} . What is required to fully account for this is a photosynthesis routine that simultaneously iteratively solves for stomatal conductance, assimilation, transpiration and leaf temperature under the constraints imposed by energy balance and system-internal resistances. In this context, also see the publications by Schymanski & Or (2017, Hydrology and Earth System Sciences, doi:10.5194/hess-21-685-2017) and Tuzet et al. (2003, Plant, Cell and Environment, doi:10.1046/j.1365-3040.2003.01035.x).

General note: Variable Symbols and abbreviations: it would be good to have a reference table for all used variable symbols and abbreviations, so that these are collected in one place to look them up as necessary.

I. 110, Eqn. 2: How about substrate limitation (often abbreviated as V_s , or J_s)?

I. 114: How about leaf nitrogen contents, or are these tied to leaf age, i.e., leaf age is a surrogate for N_{leaf} ? (see Sakschewski et al., 2015, GCB, doi.org/10.1111/gcb.12870). What makes V_{cmax} different among PFTs? Temperature-dependence relationship/optimum temperature?

I. 122/123 "This factor depends on both the soil moisture and the root profile given per PFT, trees having deeper roots than grasses.": Do you, in ORCHIDEE, account for plant-internal resistances to water transport (coupling of resistances associated with soil-root transition, root-internal transport resistances, stem-internal resistances, stomatal resistance, boundary layer resistances)?

I. 135: I like the idea of separating into structural vs. dynamical/operational resistance due to stomatal conductance. Here, I would explicitly state that the structural resistance

defines the upper boundary condition that constrains the dynamical resistance, i.e., stomatal regulation varies very quickly based on daily environmental conditions (C-demand by assimilation as a function of light availability and temperature, water-stress driven regulation of stomatal conductance), but the maximum aperture and associated conductance that can be assumed dynamically is defined by the structural constraint (if I understood that correctly).

I. 137, nitrogen stress: state here that you used ORCHIDEE, not ORCHIDEE-CN for this study, i.e., that you did not account for nitrogen-cycle-related aspects. Otherwise, in O-CN, would leaf nitrogen content influence V_{cmax} (see Sakschewski et al., 2015, <https://doi.org/10.1111/gcb.12870>)?

I. 151: "At the canopy level (Fig. 1), the canopy conductance g_c depends on both leaf level conductance g_s , and LAI.": How about coupling to boundary layer conductance? That should have an influence as well?

I. 154 "A low soil water content will induce a water stress limiting the V_{cmax} and V_{jmax} that will indirectly also reduce g_s .": Is that how water stress is accounted for in the model? I don't think the mechanistic effect of soil water stress on stomatal closure is via V_{cmax}/V_{jmax} – do you have a reference for that? As I said before, decreasing soil water contents should increase the resistance in the SPA system and limit the amount of water that can be transpired compared to the actual atmospheric demand, and the maximum aperture under water stress should be defined by the quantity that can be provided through the SPA-resistance, i.e., it should be maximum wide enough to allow no more transpiration than can be provided to be transpired.

I. 168: Why do you set VPD to a constant value? It ought to change based on the relative humidity in the boundary layer of the leaf and the coupling between leaf boundary layer and canopy boundary layer (moisture transport away from the leaf)? I suppose the atmosphere model simulates changes in relative humidity/VPD?

I. 176-179: This should be made clear earlier on – that this is not a direct functional trait-based modeling study, but mimics functional constraints indirectly by constraining maximum g_s with different caps depending on the structural conductance.

I. 181/182: "...we performed climate model simulations...": What does not really become clear to me here is whether you modeled the vegetation dynamics of the land surface, or whether you described the PFT-distribution rather than letting it develop. I suppose the former, based on your statements in discussion and conclusion section. Please explicitly mention here, and also briefly justify why you refrain from modeling vegetation dynamics.

I. 185 (paleobotanical data, reference Sewall et al., 2007), and Figure 3: During the

Aptian, there should be no C3 grasslands! Also, in the Sewall paper, I did not find anything about grass or grassland, or grassy biomes. C3 grass evolution likely did not really start before the end of the Upper Cretaceous, and their spread to dominance in open grassland biomes only happened during the Tertiary, to my knowledge. See, for example, the review paper by Caroline Stromberg (Evolution of Grasses and Grassland Ecosystems, 2011, Annu. Rev. Earth Planet. Sci., 2011 (39), 517-44), and chapter 5 in William Bond's recent book "Open Ecosystems – ecology and evolution beyond the forest edge (Oxford University Press)". In my opinion, having the C3 grass biome present and as widely spread at that time is a mistake, if the simulations are truly supposed to represent Aptian biomes. In addition, I find it a bit hard to attribute the different kinds of greens in the map to the corresponding fields in the color bar, although I am not color-blind (but: one and the same hue in the map may look subjectively darker or lighter depending on the color hue next to it). Could you use more colors (the online version will be color-based)? Color-blind-friendly palettes can be found, for example, here: <https://thenode.biologists.com/data-visualization-with-flying-colors/research/>

l. 187/188 "We set the solar radiation at 99% of the current value and the orbital parameters as today" => reference/justification for that?

l. 207 (ANGIO, Table 1): I'd call that the reference control experiment.

l. 210-213: relationship between $g_s/g_{s_max_anat}$: I'm not so sure about that assumption. I understand $g_{s_max_anat}$ to be the upper constraint on operational g_s , but why should the ratio between g_s and $g_{s_max_anat}$ be constant? It ought to vary on a daily time scale depending on the environmental factors that drive assimilation and transpiration, whereas $g_{s_max_anat}$ on short time scales remains a constant?

l. 213: "the experiments were run for 60 years": I suppose you conducted equilibrium simulation runs. What about spin-up duration prior to the 60-year simulation? It must likely take longer than 60 years for biomass and PFT distribution to fully develop and equilibrate?

One general methodological question: What's the native temporal resolution of your output variables – daily, monthly sums/means, annual sums/means)

Results

I suggest to give subtitles to the different parts in the results section, e.g., 3.1 Stomatal conductance, 3.2 LAI and vegetation cover, 3.3 Canopy conductance, 3.4 Transpiration, 3.5 Water use efficiency (WUE); to make it easier to find the respective sections. You have structured it accordingly already, so just add the section titles for easier orientation.

I. 216/217: "... is given by a unit of foliar surface where exposure to sunlight is maximal." i.e., top-of-canopy leaf layer?

I. 122: "... and the C3 grass PFTs...": Again: I'm pretty sure there should be no C3-grass PFT during that time of the Cretaceous. 'Weedy' angiosperms maybe (according to William Bond's book on Open Ecosystems), but no C3-grass dominated biomes. Weedy angiosperms would not be grasses, but herbaceous non-woody life history forms.

I. 230/231: Logically makes sense within the assumptions of the framework - higher photosynthetic efficiency allows earlier closure of stomata with respect to the carbon aspect of stomatal regulation, because need for CO₂ is satisfied earlier, that is, with less open stomata.

General question: Do stomata generally in all plants open less fully under high pCO₂, or only when water becomes limiting? I imagine there may be different strategy types concerning this - for example, do swamp plants that never experience water stress open their stomata only to the degree required to take up the amount of CO₂ required to support the maximum rate that can be processed in the Calvin cycle, or do they simply not care, because transpirational water loss is never a constraint?

I. 240 LAI unit question: Is per m² of ground in reference to the actual vegetation-covered ground of a grid-cell (i.e., averaged across all PFTs), averaged across the canopy cover of the the different PFTs, or the total grid cell area (i.e., potentially including bare-ground)? It would potentially be interesting to also see how much the bare ground area changes between the different factorial combinations, as bare ground proportion and vegetation density also indicate how well vegetation is performing.

I. 241 (and other occurrences) "peculiar". I would not use the term "peculiar", as it has a judgmental connotation. It may seem peculiar compared to present day, but was normal back then.

I. 244-246: That is to be expected at CO₂ concentrations exceeding 1000 ppm, i.e., concentrations that are likely beyond the discussed CO₂ saturation point of C3 photosynthesis.

Figures/maps: given how different the Cretaceous conditions are from present day, I would find it extremely useful to have access to additional supplementary maps that show the climatic boundary conditions, at least average annual mean temperature and annual precipitation. In particular because V_{cmax} (at least in our DGVM) is also temperature-dependent, i.e., a modulation of the reference V_{cmax25} with temperature, and a temperature optimum beyond which V_{cmax} declines again due to increased competitive binding of O₂ by the Rubisco, and ultimately starting degeneration of enzymes at yet

higher temperatures.

I. 264 ff: Maybe emphasize more strongly and explicitly that, unlike g_s , g_c is the combined result of changes in g_s AND changes in vegetation biomass and leaf area, i.e., both have an influence that can either be reinforcing or counterbalancing. Personally, I find it more interesting to look at g_s than g_c , because that's where the physiology kicks in, whereas the g_c aspect is more obscure due to the vegetation dynamics effect .

Fig. 4 and 6: Are these the global-scale annual averages for each PFT, or what exactly is the reference basis? I would expect strong spatio-temporal variations here on short time scales, depending on soil water content/water stress, temperature, soil conditions, etc. How about showing error bars/standard deviations in addition to the means, or are these too large to show on this type of figure?

In addition: It's a bit surprising to see that there are reductions for the NOANGIOp and NOANGIOhp scenarios for the temperature needleleaf evergreen vegetation, as these gymnosperms were not manipulated with respect to stomatal conductance and/or photosynthetic capacity. These effects therefore (given no mistakes were made) must be indirect. Is it because the global area covered by this PFT and its spatial distribution are different due to the change in angiosperm performance and distribution? I'd expect that g_c (and g_s) are also very variable spatially as well as temporally. In any case, this point needs to be discussed/explained.

I. 266: "... by surface unit of ground...": surface unit ground attributed to the PFT? Surface unit ground actually covered by crown area of the PFT?

I. 275/276: "Indeed, at the canopy scale, the closing of the stomata at high pCO_2 is compensated by the decrease in LAI at low pCO_2 ." I'm not sure I understand that sentence. Do you mean that higher g_c at low pCO_2 just makes up the LAI loss, so that the lower g_c at high pCO_2 x higher LAI is just about balanced against each other?

I. 284: GPP, Fig S2: GPP is in units "per m^2 ". Is this per m^2 of leaf area, per m^2 ground area covered by vegetation, per m^2 canopy area, per m^2 of grid cell area...?

I'd find it easier to see the differences between the scenarios that are solely due to the physiological manipulations if GPP were normed to unit leaf biomass, or unit leaf area. Could you provide such a figure in addition to Fig S2?

I. 286: "... and have only an indirect effect on GPP...": I'd say that's a rather direct effect, not indirect, as it directly affects assimilation due to C-limitation of assimilation?

l. 293: "... that depends on air humidity...": I find it physically more accurate to say it depends on the vapor pressure deficit.

l. 294/295: "... the capacity of plants to transpire, driven by the canopy conductance.": In detail, it's a combination of coupled conductance terms (or maybe not in ORCHIDEE?) - stomatal conductance, leaf boundary layer conductance, and canopy boundary layer conductance?

l. 301/202: "Parameterizing the vegetation without the modern angiosperm hydraulic and photosynthetic capacities systematically leads to lower transpiration rates (Fig. 7).": In absolute terms, that's no surprise, given that there is less leaf area available to transpire water. However, does this also hold in relative terms, i.e., when looking at the amount of water transpired per unit leaf area or per unit leaf biomass, per year?

l. 306/307: "Transpiration also significantly drops when photosynthetic capacity alone is reduced...": This is most likely due to the decrease in leaf biomass/LAI, right? Again, to allow focusing on the physiological reactions without the confounding effects resulting from differences in leaf biomass and leaf area, norming transpiration to either state variable would be helpful.

l. 315: Transpiration anomalies: Would be interesting to also have information on the latent heat flux deficit and latent heat flux deficit changes, i.e., the ratio between actual transpiration and potential evapotranspiration, as this is an indicator for water stress.

l. 319: "... while arid belt regions are less sensitive to any change in g_c .": I guess transpiration is already constrained by water shortage there, so the upper stomatal conductance limit is not the limiting factor anyway. If that is true, maybe explicitly mention that as an explanation?

l. 134/135: "... with a $1.7 \text{ gC kgH}_2\text{O}^{-1}$ (+30%) increase compared to ANGIO (Fig. 8a and c)." Show anomaly-to-control figs in supplementary material?

Discussion

l. 362/363: "Hence, a lower maximal stomatal conductance at high $p\text{CO}_2$ appears as an advantage compared to modern angiosperm because of a better optimization of carbon uptake over water loss.": Here, I'm struggling a bit conceptually. Yes, a lower maximal stomatal conductance at high $p\text{CO}_2$ is an advantage in terms of water loss, but does not

impact GPP, because C_i is not limiting even under reduced stomatal conductance. That much is clear. However, does it necessarily have to be the structural conductance that needs to be lower to achieve this effect? Would it not also be possible for modern angiosperm plants with high structural conductance to achieve the same effect, simply by keeping the stomata only as much open as is required to satisfy the maximum carbon demand required to just make C_i not limiting any more? This goes into the direction of optimality in "operational" stomatal regulation, in the sense of which environmental factor is limiting under given circumstances. Given water is not limiting, it should be in a plant's interest to open the stomata just wide enough to acquire enough carbon to satisfy the demand from the photosynthesis, i.e., to take up the amount of carbon that can instantaneously be processed in the Calvin cycle, so that C_i is not limiting. Under these circumstances, carbon drives stomatal regulation. If water becomes limiting, the plant may have to balance maximum water loss against carbon gain, by closing the stomata enough to, maximally, only allow the amount of water to be transpired that can be provided through the SPA-continuum. In this case, water availability should drive stomatal regulation, which implies that C_i can become limiting for photosynthesis due to the water constraint, if C_i would demand a stomatal opening exceeding the one allowed by water availability. Stomatal closure under water stress will also lead to a reduction in transpiration, i.e., latent heat flux. To fulfill the energy balance, this entails an increase in sensible heat flux associated with an increase in leaf temperature, which, via temperature dependence of V_{cmax} , affects assimilation and therefore C_i . To solve this, an approach is required that simultaneously solves for stomatal conductance, assimilation, leaf temperature and transpiration.

I. 367: "by decreasing modern V_{cmax} ": By what mechanism would such a reduction of modern V_{cmax} have been accomplished - maybe briefly discuss. Rubisco binding efficiency per unit Rubisco molecule should have been the same as today, unless there was a different version of Rubisco back then that was less efficient. So likely a reduction would have been associated with lower concentrations of Rubisco in plant cells?

I. 384/385 "They argue that modern angiosperm trees have 2 times higher stomatal conductance sensitivity response to driving factors than gymnosperm trees": How does V_{cmax} of modern gymnosperm trees compare to that of modern angiosperm trees? Is it relatively lower as well, and if, then by how much?

I. 394/395 "However, lowering only the hydraulic capacity while keeping the high V_{cmax} as in the modern vegetation induces a nitrogen cost.": This nitrogen cost would also exist under high hydraulic conductivity. It might only have a lower impact if the entire C-balance of the plant is improved due to the improved stomatal conductivity, i.e., under circumstances where stomatal conductivity is limiting to C_i .

I. 395 "Although our model does not represent the nitrogen cycle...": You should mention that already in the model description, in particular because there is an ORCHIDEE version that has a nitrogen cycle (ORCHIDEE-CN).

I. 404/405: Do not most of the modern DGVMs and land surface models do that anyway

for quite a long time now?

I. 408/409: "... leaf stomatal conductance is only 3-time lower than the reference": That is acutally one of the points that merits a bit more explanation, because it is somewhat unexpected/counterituitive. My guess would be that the stomatal conductance in the control scenario is not always and everywhere at its maximum, therefore the relative reduction compared to a value that was already constrained in the control scenario (e.g., due to light limitation on photosynthesis or water limitation effects on stomatal conductance) is less than the full possible range?

I. 411/412: "we suggest to explicitly represent changed in hydraulic and photosynthetic capacities.": I'd suggest that the gold standard to aim for should be a fully coupled SPA-water transport continuum based on coupled resistances that is linked to assimilation/assimilatory demands and leaf temperature regulation, constrained by energy balance requirements (sensible heat flux vs. latent heat flux).

I. 418/419 "... and water availability in the soil...": In addition also to VPD (potential gradient between near-saturated conditions in leaf-intercellular air space vs. leaf-exterior conditions).

I. 450 "compilation and spatialization of the Aptian paleobotanical records (Sewall et al., 2007)": Looking at Sewall et al, plus other literature resources, there should be no C3-grass biomes existing during the Aptian, because C3 grasses likely did not evolve in abundance before the Maastrichtian, and their rise to dominance in open biomes did not happen before the Tertiary.

I. 456/457 "by allowing PFTs to spatially settle in regions where the simulated climate is the most appropriate": It would be even better to go beyond PFT-based dynamic vegetation modeling, for example by directly using DGVMs as land surface scheme that are trait-based and therefore allow for direct inclusion of trait-based modelling approaches.

I. 358: studies on Paleozoic vegetation transitions: the Cretaceous period that you are interested in is part of the Mesozoic, not the Paleozoic.

I. 461/462 Aside from Vuichard et al., 2019, also cite Soenke Zaehle's older work on OC-N here? Or has that by now become obsolete for the development of the N-cycle branch of ORCHIDEE?

I. 462/463 "provided that good constraints can be obtained regarding the C:N ratio of

Cretaceous vegetation and soils" => that will very likely always be a big source of uncertainty. Also, I'm not sure when symbiotic N-fixation evolved and whether it would already have mattered during the Aptian, i.e., how abundant symbiotic N-fixers would have been if they already existed.

I. 473/474 Yes, this is also where I see the future. Stomatal conductance, the way I perceive it, is a two-way road that links C-gain against associated water loss. Depending on which factor is more limiting, either the one or the other will be driving stomatal regulation.

I. 478/479 "It emphasizes the need, in the future, to improve the parameterization of stomatal conductance in global mode by explicitly modelling both structural and dynamic conductance." => Do you have a more concrete suggestion on how this should be implemented, and an estimate how much different it would make simulation results?

Conclusions

I. 484 "with an ecophysiological model based on angiosperm fossil records." => "motivated by an ecophysiological model" is more appropriate. You are mimicking some of the constraints of the ecophysiological model, but do not fully implement it.

I. 503 "even at an expense of possible increasing water loss" => The water loss aspect should be treated/discussed in a more differentiated manner: where and when water is not limiting, it is a secondary problem. Where and when water IS limiting, the question is whether an increased structural conductance actually really results in an increased water loss. I have some doubts about that, because under the aspect of optimality, it is likely that plants, even with a higher structural conductance, would nonetheless close the stomata enough to limit water loss to the amount that can be provided through the SPA-continuum. In that case, one would not necessarily expect drastically increased water loss although it would be potentially possible. So in both cases, the problem of increased water loss should be secondary.

I. 511/512 "Furthermore allowing dynamic vegetation would be an important future refinement of this research to model feedbacks between vegetation and climate." => In addition, also moving beyond PFT-based approaches towards truly trait-based approaches, e.g., such as the ones pursued by Scheiter et al. with the aDGVM2 model, or the JEDI model developed by Pavlick and colleagues. It would allow a more direct accounting for changes in functional traits, as well as a dynamic evolutionary selection for those trait strategies that are competitively successful under given environmental conditions.

Data availability

How about code availability? In the interest of Reproducible Science, making source code required to reproduce the results available is about to become standard. Is the source code used for the simulations in this study available, or can it be made available (e.g., in an online repository such as Github)? If not, please state why it is not possible.

Suggested minor corrections and changes:

l. 8 generates => generate

l. 61 links => link

l. 171 lower => smaller

l. 187 orbitals => orbital

l. 101 suggested => suggesting

l. 205 modern-like => modern-type

l. 260 which plays at => which plays a role at

l. 280: "LAI changes described earlier act as a feedback between gs and gc": I'd rather say: "LAI changes described earlier modulate the relationship between changes in gs and gc."

l. 301 angiosperms => angiosperm

l. 315 come from => result from

l. 330 plants adaptation => plant adaptation

I. 334: NAANGIOh => NOANGIOh

I. 358 "... to account for the decrease of maximal stomatal conductance": ... to account for the lower maximum stomatal conductance..." (decrease has a temporal connotation, for a change from first high to then low).

I. 360 decreasing fcpl => lower fcpl

I. 363 modern angiosperm => modern angiosperms

I. 364 "... because of the positive feedbacks of the LAI on the canopy stomatal conductance," => "because a reduced LAI entails a reduction of canopy stomatal conduction,"

I. 387 "..., that remains enough to sustain the LAI...": "that remains sufficient to sustain LAI values close to those of the control scenario"

I. 399 consistent with previous study => consistent with a previous study

I. 402 while sustaining high productivity => that allowed nonetheless to sustain a high productivity

I. 403 as in the modern vegetation => as found in the modern vegetation

I. 403 preserve => maintain

I. 408 3-time => either "3-times" or "3-fold"

I. 425 basals angiosperms => early angiosperms

I. 425 was as low as the other plant types => was as low as that of other plant types

I. 427 At that time => for this time

I. 427 "... we confirm the hypothesis..." => "... our results support the hypothesis..."

I. 427 "... evolved towards leaves more and more densely irrigated together with..." => "... evolved towards leaves with increasing vein density combined with a..."

I. 428 increasingly stomatal conductance => increasing stomatal conductance

I. 429 Among others => Among other factors

I. 430 dominating the vegetation of the period to colonize => dominating the vegetation of the period that enabled them to colonize

I. 431 with that of Franks => with those of Franks

I. 432 "periods with high $p\text{CO}_2$ strengthen GPP, meanwhile a potential decrease of transpiration rate by the closing of the stomata" => "periods with high $p\text{CO}_2$ enhanced GPP while simultaneously allowing a reduction of transpirational water losses due to reduced stomatal conductance"

I. 438/439 invested increasingly energy => invested increasingly more energy

I. 440 in densely water transport networks => in dense water transport networks

I. 458 studies about Paleozoic vegetation transitions => studies on Paleozoic vegetation transitions

I. 490 which is not recorded in the fossil => which is in contradiction to the fossil record

I. 492 All the results taken together => All the results in combination

l. 495 "Therefore, the combining decrease of hydraulic and photosynthetic capacities..."
=> "Therefore, a combination of lower-than-modern hydraulic and photosynthetic capacities...". "Decrease" implies a temporal dynamic from high towards low

l. 498/499 This result is also consistent => Our results are also consistent

l. 500/501 "... was adapted to high $p\text{CO}_2$ by sustaining productivity and a high WUE." =>
"... was adapted to high $p\text{CO}_2$, where the combination of both physiological constraints nonetheless allowed high productivity and WUE."

l. 501 "it was not adapted to lower $p\text{CO}_2$ as GPP collapses" => "it would not have been able to exist under low $p\text{CO}_2$, where we simulated a collapse of GPP under such physiological parameter configuration."