Dear Dr. Lopez and reviewers,

Thank you for the positive feedback provided by you and the reviewers on the previous version of the manuscript. On behalf of my co-authors, it is my pleasure to send you a revised version. We have taken most of the comments into consideration, detailing the scale and time frame we were focusing on (i.e. shorter than the year). We also have restructured the text shortening the first two frames, and incorporating the third one into the text, with some elements to the model improvements that could be expected, although it appeared too far from the scope to detail this point very much. The figures were also more detailed.

I hope you will find it improved enough to be recommended by PCI Forest and Wood Science.

Best regards

Guillaume Charrier and co-auhors

Post scriptum: please find below point-by-point responses to reviewers' comments.

Reviews

Reviewed by Jordi Martínez Vilalta, 2020-05-23 21:03

In this paper, Charrier et al. discuss the interaction between drought and frost impacts on tree ecophysiology, focusing on the relative timing of these two stress factors in relation to each other and to key phenological processes, and stressing their impact on the tree water and carbon economy. I concur with the authors that the study of the interactions between drought and frost in a temporal context is clearly underrepresented in the literature, and yet it is critical to understand plant responses to climatic constrains in the wild. The topic is thus timely and important. I have to say, however, that I had a hard time reading the text and found it difficult to follow several of the arguments and to understand the general flow of ideas. The paper as currently written is a combination of a review and an opinion piece, but in my view it lacks a clear message that would be effective at moving the field forward. The authors do not provide a common framework that unifies drought and frost impacts on a temporal context, nor give clear indication of what they think should be done in order to improve our understanding of this important interaction. Some of the figures seem a bit disconnected from the text and Figure 1 in particular does not convey a clear message (or I fail to grasp it; see specific suggestions below).

In my opinion the paper needs to be restructured to provide a clearer and more coherent contribution. In many instances the authors mix different temporal, spatial and organizational scales without properly acknowledging the different factors at play. To give just an example, in the paragraph starting in L325 the authors start discussing freeze/thaw-induced embolism and frost cracks, end up by discussing stand-level effects on competition for water (L331-332) and start the next paragraph referring to changes in the density and porosity of the pit membrane (L333-…). I find it essential to clarify the scale of the mechanisms being discussed from the beginning of the paper (perhaps narrowing the focus to within-year seasonal patterns) and then organize the text in a logical way so that the reader knows what to expect in each section. It seems to me that it would be much more effective to consider several scenarios regarding the order and seasonal timing of drought and frost and discuss the key knowns and unknowns in each case. Somehow the paper now fails to provide a clear agenda to advance the study of drought – frost interactions.

The text also needs a careful revision by the authors to improve English usage and the clarity of several sentences. I provide specific suggestions below, but they are not exhaustive.

Thank you for these comments, we have made profound changes to the text structure, focusing on the within year pattern. The type of *scenarii* were included into two distinct sections: drought following frost (L249) and frost following drought (L213).

More detailed or technical comments:

Title: you mean '...rethinking the timing of risk'?

That seems more topical indeed.

L17: 'areas'

This typo has been corrected (L24).

L25, 26, 30, …: I think that something like 'stress factors' would be more appropriate than 'constraints' here and elsewhere in the ms.

This is right; we have replaced the term constraint by stress factor where appropriate.

L34-35: I do not understand this sentence.

The sentence has been modified, to clarify its meaning. It now reads: "This vulnerability can also be modulated by a shift in the annual phenological cycle induced by a previous constraint." (L41-42)

L48: I would tone down a bit the text, for example 'abiotic factors are typically more relevant…'
We totally agree with respect to the relevance of biotic factors and the objective was not to discard them. Despite we did not think the previous version was too exaggerated (we were citing both factors as the main drivers), we have down-tuned a bit the beginning of the abstract and of the introduction as suggested by both reviewers

L53-55: that seems to be very a temperate-centered view, which is fine, but the biome or ecosystem type you are referring to should be clear from the beginning.

This aspect has been clarified upper in the introduction (L57-58): "Within the boreal, alpine, temperate and Mediterranean areas, plants are likely to be exposed to both drought and frost stress, although it may not happen every year."

L79: 'composition' better than 'biodiversity'?

This has been changed accordingly.

L85: and ecologists?

And ecologists as well.

L91: I would limit the use of Latin phrases, as they tend to make the text unnecessarily obscure.

'In fine' has been replaced by 'ultimately'

L101: delete 'can'.

Typo corrected

L101-104: this is not exact. See, for instance: Miao et al. 2009 (American Naturalist 173: 113-118), Anderegg et al. 2013 (Tree Physiology 33: 701–712), Batllori et al. 2017 (Ecosphere 8: e01906), Hossain et al. 2018 (Tree Physiology 39: 6–18).

Thank you for the information we were not fully aware about these relevant studies. They are now mentioned in the text.

L114: 'chaotic behavior' has a very specific mathematical definition, so I suggest using a more general term here (e.g., 'complex behavior').

This is right, it has been replaced accordingly.

L121-122: simplify text (e.g., 'to promote an integrative perspective…').

This has been simplified accordingly.

L123: replace 'damages' by 'stress factors'?

This has been changed accordingly

L126: 'How do…'

This has been changed accordingly

Frames #1 and #2: it seems to me that these boxes should be synthesized substantially and simply provide a short summary of our current understanding of drought and frost stress, if possible in a single paragraph for each stress factor. In the case of drought the framework seems to be almost entirely based on McDowell et al. (2008), which was obviously an extremely influential paper but that in my opinion no longer reflects the consensus view on drought-induced mortality. When a water balance approach and consideration of tissue dehydration is advocated for, a reference to Martínez-Vilalta et al. 2019 (New Phytologist 223: 22-32) would seem appropriate.

Both frames were considerably reduced and refer to more topical reviews, to allow the main text to focus only onto the interactions.

In Frame #2 (2nd paragraph) you seem to imply that water in plant tissues freezes as temperatures go below 0 ºC, which is not the case (substantially lower temperatures are required in many cases).

You are right, this was a misunderstanding. This part was removed, though.

Frame #3: similarly, I think the arguments here could be greatly synthesized (e.g., the text in L148-153 could be deleted). In addition, I would consider moving the key ideas developed in this box to the main text of the ms. instead of presenting them in a box.

As suggested, the 3rd frame has been reduced and integrated as a final part of the main text.

L202: what does 'structural vs annual' mean?

This was meant 'perennial vs annual'. This part was removed, though.

L207-208: the theory underlying the relationship between water content and water potential in plant tissues have been developed extensively for at least 50 years; why refer to an equation developed for soils?

You are right, this part was also removed.

L250: 'approximation' instead of 'approach'?

This has been modified accordingly

L251: 'make'.

This has been modified accordingly

L253-255: but this seems to contradict the previous sentence.

We have clarified this point as follow: "This hypothesis fed into the so-called 'boxer theory', suggesting the successive stresses would cause trees to decline (Wargo, 1996; Breda & Peiffer, 2014). However, due to the difficulty of conducting such long-term studies, few studies have been able to characterize the ecophysiological processes affected."

L256: you mean 'concepts' instead of 'hypotheses'? In any case, it is important to clarify the terminology you introduce. For instance, what is the difference between 'memory' as you define it and 'acclimation', a much more widely used concept in plant ecophysiology?

We used the term concepts in the present version; however, memory is slightly different from acclimation. We made this point clearer.

L279-280: you mention that on passing, but this is quite critical, right? (Autumns tend to be very wet in many if not most temperate systems).

This is completely true and probably did not happen much often in the past but, there is chances that it may more regularly happen in the future, with longer drought periods such as predicted by CC *scenarii*. This point has been made explicit.

L290, 297: it is totally unclear to me what this 'drought stress intensity' is exactly.

As the interspecific variability in the response to drought stress is wide, we used the term intensity to offer a relative assessment of drought stress.

L304: please explain all abbreviations ('FT').

The FT abbreviation was removed and explained in plain text.

L316: but this section deals with the opposite effect, right? Please clarify the text.

This was a transition sentence, it has been clarified

L329: why 'should result'?

As, stem flow would be reduced, under similar VPD, leaf water potential would reach lower values affecting stomatal conductance. Partially open stomata allow sufficient CO2 diffusion while limiting the amount of transpired water, increasing the WUE. It has been changed as: "Lower hydraulic conductivity would also limit plant transpiration, which should result in lower leaf water potential and stomatal conductance. As partially open stomata allow

sufficient CO_2 diffusion while limiting the amount of transpired water, it is likely that water use efficiency would be increased."

L333-348: this whole paragraph is confusing to me.

It has been completely changed and split into different part of the ms

L387-388: 'diurnal dynamics' of what?

We were describing diurnal dynamics of temperature. The sentence has been modified accordingly.

L395. 'Keenan'.

Typo corrected

L398: delete 'thus'?

'Thus' has been removed

L411: 'events'.

Typo corrected

L412-415: but reduced leaf area should be advantageous under drought, right?

This is a typically complex effect where temporality is crucial: reduced leaf area would limit water consumption, potentially delaying water stress later in the season (considering a single species).

L436: 'interaction' instead of 'crossing effects'?

This has been modified accordingly.

L449: delete 'as mentioned' and refer to '(Frame 3)'.

This has been modified accordingly.

Figure 1: there are several aspects of this figure I don't fully understand. For instance, why is 'frost hardiness' between 'summer' and 'winter'? why is starch associated to 'summer' and solutes to 'winter'? What does a positive effect of 'Budburst' on water stress mean? Are you referring to the timing of budburst? Please be more clear and specific. In addition, using solid and dashed lines for positive and negative relationships would make the diagram clearer, I think.

As suggested, we modified the figure and the explanation in the caption:

*"***Figure 1.** Involved processes affected by water (mainly during summer period) and frost stress (mainly during winter period). Positive (solid) and negative (dashed) effects of stresses are expected on three functional components, namely carbon status, phenological processes and hydraulic safety.

Positive relations between timing events (phenological stages such as leaf fall and budburst) and other processes indicate that earlier event induce higher level, and vis-versa). All represented processes are interrelate either directly and indirectly. Both winter and summer stresses affect the same processes either synergistically or antagonistically. Main effects are reported, although non-linear and thresholds could make the response more complex. The numbers refer to studies that document these effects (1. Morin *et al.*, 2007; 2. O'Brien *et al.*, 2014; 3. Améglio *et al.*, 2004; 4. McDowell *et al.*, 2008; 5. Bréda *et al.*, 2006; 6. Tyree *et al.*, 1993; 7. Schuster *et al.*, 2014; 8. Xie *et al.*, 2015; 9. Rinne *et al.*, 1997; 10. Chaves *et al.*, 2002; 11. Charrier *et al.*, 2011; 12. Ghesquière *et al.*, 2014; 13. Hanninen, 1991; 14. Sperry *et al.*, 1998; 15. Charra-Vaskou *et al.*, 2016; 16. Charrier *et al.*, 2014). »

Figure 3: a more explicative caption and a clearer connection with the main text is required here, I believe.

The figure was explained in the caption and cited in the relevant text parts.

"**Figure 3.** Alternative pathways that would explain why contrasted frost vulnerabilities are observed after previous drought exposure. Osmolarity of intracellular sap, controlled notably by the ratio between soluble carbohydrates and water content, could be considered as the main driver. On the right path, intense and/or late drought is expected to concentrate cell sap, increasing the probability of extra cellular ice nucleation. The low chemical potential of ice would pull water, further increasing cell osmolarity. On the left path, long and/or early drought prevents timely increase in solutes, through reduction in carbon reserves. Intracellular freezing through is expected to happen more often and at higher freezing temperature, inducing cellular damages."

Figure 4: a 'Late drought' in February?

The stress factor can have a lagged effect on further phenological processes such as late summer drought onto winter dormancy release. This point has been clarified in the legend.

Reviewed by Sean Gleason, 2020-06-05 00:59

General comments

The authors offer a theory and framework for developing process-based models with the aim to provide better prediction of species distribution limits in the face of climate change. This is certainly an important topic and I found their approach intuitive and well-thought-out. The figures were also helpful in explaining their ideas and I enjoyed reading the manuscript. Although it could be argued that much of what is presented is not especially novel in itself (e.g., modeling interactions, drought tolerance vs frost tolerance, etc), I don't think this detracts from the manuscript. For example, the fact that there has yet been no successful attempt to model these kinds of interactions (hydraulics, carbon, phenology) to predict the outcome of climate change, does indeed suggest that the manuscript and topic are timely.

One suggestion I have would be to explain a little better how the empirical relationships they so well-describe could be used (or are being used) to build models representing underlying processes and their interactions. For example, the end of the introduction states, "This framework would be crucial to understand local mortality dynamics and ultimately to improve actual species distribution models". I agree strongly with this. And although they

discuss the theory and conceptual steps needed to develop such a model (and identify important obstacles) (Frame 3), it's not clear to me exactly how this would happen… and I think the authors' thoughts on this would be very helpful to others. Do the authors see this a being a grass-roots effort to build a model from scratch, which has all the ingredients (e.g., processes, functions, sub-models, etc) needed to examine these interactions, or do they see this more like a patchwork effort that would take models or parts of them (the actual code) and integrate these together into one massive model such that all interactions can be assessed? Would this be a land-surface model or an ESM then? If so, should we start with something like CLM5 and modify it such that it has all the bits and pieces needed to assess these important interactions (this seems contrary to Frame #3)? Or do we start somewhere else entirely? I guess I'm looking for a paragraph that lays out the way (or ways) forward. Are there models and labs out there that could start working together on this issue (maybe they already are?). Would this require additional funding, or additional leadership? Where could these resources potentially come from? I'm not looking for much – just a paragraph or two about how all this could potentially happen (or is already happening). On the other hand, maybe this is beyond the scope of what the authors want to accomplish with this manuscript.

Thank you for this feedback, the main aim of this paper was to bring attention on the potential role of interaction between stress factors on tree functioning. We have tried to clarify the potential use for model developers, including ourselves. However, we feel that detailing too much the model types would fall beyond the scope of the paper and would make the text more complex. Some examples of process-based models that we are familiar with, have been mentioned (L120-121).

On lines 447 – 449 the authors suggest it is a "prerequisite" that we first improve our understanding of these interactions (presumably via field experiments/observations). Do they really mean this, i.e, that model development should wait until we can improve our understanding of the biology. It seems to me that a properly parameterized model with even a few of the discussed process would help inform our understanding the biology itself, or at least re-direct our experimental efforts.

Actually, we are convinced that all aspects (experiments, observations and models) should constantly interact. It should be noted that fitting functions to one peculiar phenomenon as a black box could bring some completely unrealistic behavior (see Chuine et al., 2016, with respect to endodormancy release or Hänninen et al 2019). Designing a proper bifactorial experiment is indeed very time consuming but should be used as a safeguard to validate parameterized models. We have down tuned a bit the sentence:

L 429-431 "This would improve existing mechanistic models simulating these interacting processes in order to predict accurately the effect of cumulative stress on tree physiology and survival."

Chuine, I., Bonhomme, M., Legave, J. M., García de Cortázar-Atauri, I., Charrier, G., Lacointe, A., & Améglio, T. (2016). Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Global Change Biology*, *22*(10), 3444-3460.

Hänninen, H., Kramer, K., Tanino, K., Zhang, R., Wu, J., & Fu, Y. H. (2019). Experiments are necessary in process-based tree phenology modelling. *Trends in Plant Science, 24*(3), 199-209.

Specific comments

16: Really? Do we know this? For example, considering the second sentence ("heat waves and drought") have the competitive interactions between species been experimentally eliminated from the effects of heat and drought in these studies? ...seems like this should still be a very open area of research (environment vs competition). That said, I agree with the authors that models examining the interactions discussed here should not (at least initially) consider competition.

We totally agree with respect to the relevance of biotic factors and the objective was not to discard them. See the response to R1

34: I might suggest, "...exposure to a constraint".

This has been modified accordingly.

42: Rather than "the tree", I might suggest something more general (e.g., "plants", "species", etc).

We have changed to 'plants'.

45-47: The authors should be allowed their interpretation of the literature. However, for me, it's a very bold statement to suggest that abiotic factors are ***in fact*** *the main drivers of distribution limits and evolution. I'm not saying that I think they are definitely wrong (in fact, I'm incline to at least partially agree), but I don't think the evidence is very strong for their claim. For example, the cited Klanderud et al paper suggests that there is a shift in the relative importance of abioitc and biotic drivers across the temperature gradient, and also emphasized interaction between biotic and abiotic factors. I would also question the efficacy of correlative analysis to address this question altogether. Just to make my point, I can very easily find two papers (the number cited by the authors) in support of the opposite claim, i.e., that competitive exclusion is the main factor defining distribution boundaries (e.g., doi.org/10.1111/jbi.12907). Perhaps it would be more fair to point out that this is still an open question, and an important one. I'm also not sure it's really necessary to eliminate competition as a important factor at the edges of distributions. I think the authors' aims with this work and their analyses are just as valid and important.*

We totally agree with respect to the relevance of biotic factors and the objective was not to discard them. See the response to R1

Box 1: "...depends to a large extent…"

Box 1: It's not clear what is meant by "hydric insulation".

Frame 2: Delete extra ")" after "...Koerner 2015)."

Boxes 1 and 2 have been deeply shortened.

Frame 3(ii): By "based on experimental data" do the authors mean that this initial model should be wholly empirical, or should it be mechanistic but validated using experimental data? Or, is this a recipe for building models more generally (process-based and empirical)? I'm just trying to understand the gory details of how the linkages between responses and inputs (or independent variables) work.

The recipe is essentially designed for process based models where drivers are identified. Empirical models could easily make a shortcut in the process, for instance predicting frost hardiness from temperature changes.

205: "McDowell"

The typo has been corrected

207: I would think that the main difficulty would not be water-release relationships so much (i.e., psi ~ soilwatercontent), but rather, the unsaturated soil water conductance (i.e., solution of the Richards equation), and thus, water flux within the soil and between the soil and root (xylem).

This is an interesting remark as soil texture and structure as well as the root system architecture would affect the relation between soil water content and predawn plant water potential through the mentioned processes. However, this part has been restructured and removed.

310: I might suggest a very short definition of what is meant by "fatigue", at least the explanation provided in the cited reference. Maybe something like, "...fatigue, i.e., physical or chemical deformation of the pit ultrastructure."

The change has been made accordingly

327: It is not clear what is meant by "punctuations of the vessels [conduits]". Do the authors mean that the frost crack is bringing air in closer proximity to conduits under tension, and therefore, facilitating air entry? If so, I don't think this would result in the spread of gas from "conduit to conduit" (i.e., air-seeding through the bordered pit connections).

This is right, this part was confusing. It now reads as: "Winter drought- and freeze/thaw-induced embolism increase the volume of gas within the xylem conduits, therefore facilitating the spreading of air through conduits (Lens *et al.*, 2011)." L263-265

368-369: Damn… I never considered this.

Figure 3. I might suggest replacing the Christian symbol here with something secular to represent cell death… skull and bones, perhaps? A picture of a McDonalds restaurant? Or perhaps just the words "death", to be clear?

The cross has been replaced by a dead tree (modified from hazard symbols).

I would like to thank the authors and editor for giving me the opportunity to review this interesting review. I sincerely hope that at least a few of my comments will be helpful towards revising their manuscript.

Kind regards,

Sean M. Gleason

Thank you for these comments