Final manuscript corrections

We thank you for acceptance of our manuscript and we have made the changes to the final uploaded word document of the text (added the links to the Dryad repository and the Daycent documentation).

Thank you!

Tara Hudiburg, Philip Higuera, and Jeff Hicke

Relevant changes made in the manuscript per the reviews:

1. Climate scenario has been removed as a primary objective/hypothesis. The objectives of the study have been clarified and the modeling goals. We also discuss the modeling limitations given the lack of paleoclimate data.
2. Many portions of the text regarding methods, the site description, the model description, and the vegetation history has been revised and clarified (see specific comments).
3. The figures have been revised per the recommendations.
4. Many other changes regarding typos, citations, and wording have also been made per the recommendations.

Response to Editor comments

Editor comment 1 (rev 1 comment): I ask you to consider using existing AR4 or AR5 climate change scenarios to apply them to DayCent for your study region because these climate scenarios provide physically consistent climate variables for a 2-degree warming. Otherwise, the error propagation is too high and your results can be biased.

Editor Comment: Please make sure that this approach is thoroughly explained in the methods section. Also explain, why you cannot derive such type of information from your climate forcing data.

Author response: We agree that using climate forcing data that includes the other variables (like precipitation) would be a better way to test the impact of climate (rather than just warming). However, because our prescribed fire events are decoupled from climate in the model simulations, we chose not to pursue downscaled climate datasets with more physically constant variables as they would not influence the fire events (in the model). Finally, as requested by the editor, we have decided to go with option (2) advised by Rev 1 and eliminate the climate warming scenario from our hypotheses.

In terms of other abiotic influences (precipitation and radiation), we agree they are important, but again, we do not and cannot easily acquire paleoclimate data for this watershed, making these impacts beyond the capability of the current study. Per the request, we have clarified this in the manuscript and discussed the limitations of the climate forcing data.

3. Net ecosystem responses cannot be derived from simulating fire pattern alone. Please re-consider your response and revise your manuscript as demanded by reviewer 1.

Author response: We agree that net ecosystem response cannot be derived from simulating fire pattern alone. We utilize a comprehensive, mechanistic, biogeochemical model (DayCent) that includes the important processes that affect ecosystem response (vegetation, climate, disturbance, plant growth, decomposition, etc) because of this reason. Per option 2 suggested by Rev 1, we will "…explicitly present this study as a first-step modelling approach integrating only the fire regime information and therefore only testing it" and remove the third hypothesis related to climate. We will also discuss the limitations of the study regarding the climate forcing data.

4. Reviewer 1 has offered you two options for improving your manuscript. Please reconsider to take one of the options to allow this manuscript getting published.

Author Response: As suggested by the editor, we are choosing option 2 (remove climate scenario) as suggested by the reviewer and including text about the limitations of our climate forcing data. In the discussion, we note the impact that 2 °C of warming in the model has on plant growth and decomposition, relative to the changes from fire themselves. This sensitivity analysis provides some coarse context for interpreting the magnitude of change from fire activity, without implying that we have simulated past climate or coupled climate-fire-ecosystem dynamics.

Editor comment 2: Reviewer 2:

1. Provide the information demanded by the reviewer in the manuscript text, accordingly.

Cf. Reviewer 2: Materials and Methods: L165 What exactly is the size of the simulated area? Are fires spatially-explicit? Or just based on random selection of cells? Perhaps a few word on this.

Response: We have edited the text per Rev 2's requests, specifically where more information is necessary.

2. Explore all available options for validating also vegetation composition or productivity as demanded by reviewer 2: "This removes the necessity to do the paleo-informed, but nevertheless paleodata comparison is necessary as a validation step" and describe it in the manuscript.

Author response: We have addressed this issue in the text. Specifically, we have clarified that the vegetation composition has not changed and cited this information. There has not been any dominant vegetation changes at this site for the study record. Also, we compare/evaluate our productivity numbers with the only values available to us. We have also clarified this in the text.

Editor comment: In addition to these changes that need to be taken into account in the revision of the current manuscript, all other changes demanded by the reviewers need to be considered. You have announced that these changes were or will be conducted in the revised manuscript. These changes will be essential.

Author response: We have edited the text and made the changes as requested and outlined in our response.

Response to SC1

We thank the reviewer for thoughtful and helpful comments and have addressed many of the suggestions (see specific replies below).

- Page 2, line 48: we suggest changing the word “great” to “greater” since it is followed

by the word “than” and in comparison, certain adjectives such as great should get an “er” or “est” at the end.

Response: This sentence has been removed.

- Page 4, line 83: we would change “significance influence of fire” to significant influence since it makes more sense

Response: We have chosen to keep “of fire” as it more explicitly defines what we are referring to (rather than climate).

For a better understanding and conception, we suggest the following: - Page 2, line 40: we would find a definition of “C trajectories” helpful

Response: We have added the following clarification: “(i.e. future states or directions)” - Page 3, line 61: it is somewhat unclear what the authors mean by pool sizes, we suggest that they indicate which elements pool sizes they specifically mean (e.g. carbon or nitrogen or etc.,)

Response: Done.

- Page 3, line 71: it is not clear what is meant by Net Ecosystem Carbon Balance (NECB)

Response: Yes, this was unclear until the methods. Thank you for pointing this out. We have now added text describing NECB (the balance between net forest carbon uptake and forest losses through fire emissions).

- Page 4, line 86: the term “spin up” is confusing. We suggest that the authors try to explain and clarify this term in a more understandable wording perhaps by defining this term with a simple example before using it.

Response: We added the following sentence for clarification: "To initiate the model, C and N pools need to develop, as they start from ‘bare soil’ with no vegetation; as vegetation grows the modeled soil pools increase, and it takes hundreds to thousands of simulation years during this "spin-up" period for the C and N pools to equilibrate.

- Page 5, line 139-141: “Day Cent” Is well described but already mentioned in section 2.1, therefore we suggest the description should come earlier

Response: We switched the order of the sections so that the Model Description is now Methods section 2.1 and the study site is section 2.2.

- Page 6, line 151-152: is L:N and lignin to nitrogen the same? It is not mentioned in the text

Response: Yes, we changed the L:N to lignin to nitrogen for consistency.

- Page 7, line 182: from our point of view, the "key difference" between the two fire types should come at the beginning of the paragraph

Response: We moved "The key difference between the two fire types simulated is the associated soil erosion" to the beginning (second sentence; line 181 now) of the paragraph.

- Page 8, line 208: timeframe CE, is that defined as common era?

Response: Yes, we added "common era" in parentheses.

- Page 8, lines 211-219: we think the explanation of different scenarios can be expressed in a more precise and separated way. The description of additional scenarios make it difficult to understand and follow the subject since they're told altogether. Perhaps by separating the scenarios and explaining each of them on an independent paragraph, the concept can be easier to follow. The use of that many brackets makes it more confusing than helping anything.

Response: We agree the descriptions were confusing. The text has been separated in to distinct paragraphs with more explanation of each scenario.

- Page 9, line 248: isn't the data fitted? Not surprising that it is "broadly in agreement"

Response: Fire occurrence is "fitted", but not C losses. We include the comparison to indicate that DayCent is capable (some models are not) of replicating the expected C emissions from fire in this region.

- Page 13, line 360-365: very long and complicated sentence. We would suggest making more than one sentence out of it for a better understanding

Response: This text has been changed (and edited).

- Page 13, line 369: the word "woody pool" should be clarified

Response: Done.

- Page 14, line 383 & 388: are "ecosystem states" and "biogeochemical states" the same? Here we would need simplification or a better definition

Response: We are using them interchangeably, but decided to just use biogeochemical states.

Concerning the figures: - Implement results in Table 1

Response: We think providing the results in Table 1 would be repetitive, and thus unnecessary.

- Figure 1: For a better visual understanding, it would be nice to have at least two different colors for the different types of fire. Also, different symbols could be used. The spacing between the line is very big and could be better used. It would be sufficient to have only one legend as it is the same, and we can read the word "high severity fire" four times in a small figure. That could be simplified.

Response: We changed the fire severities to two different symbols (open vs closed) and now use only one legend as well as making the symbols larger.

- Figure 2: It is too confusing that the grey Equilibrium line and the yellow Equilibrium + 2 degrees have the same value on the y-axis but it’s not shown.

Response: We have removed the warming scenario from the figure.

- Figure 1, 2 and 4: In the text the time data is in CE. In the Figures time data Cal BP is used. We would suggest to only use one time specification.

Response: Generally, tree-ring records that extend back several centuries (e.g., the tree-ring inferred fire date at Chickaree Lake), are reported in years CE, while lake-sediment records, which extend back thousands of years, are reported in years BP (to avoid negative values, prior to 0 CE). We understand how this can be confusing, so we added years BP to the few places in the text where we refer to year CE.

Reviewer 1 comment

First of all, even though the authors refer to past published studies, they should present or document the reconstructed response of vegetation (changes or not) the site recorded at least with the same level of information as for the fire reconstruction they provide.

Response: The pollen record at this site indicates the dominance of subalpine forest taxa (lodgepole pine) for the duration of the record presented here, which is consistent with other regional records (and therefore we so not vary the vegetation over time). We have clarified this in the text. To support this statement, we provide the citation to the original paper with the pollen record, as well as other studies from the region: Caffrey and Doerner 2012, Dunnette et al. 2014, Higuera et al. 2014.

Secondly, and most importantly, I wonder why authors have used only the same fixed 30-year time series for climate data whatever the time frame simulated over the last 4500 years BP instead of using past climate simulations from GCM or ESM whose many have Holocene climate as well as Future climate runs…. whereas several studies have documented and discussed about the potential counter-effect of precipitation increase in compensating the effect of temperature increase on fire occurrences and spread….

Response: We agree that using paleo and/or future climate scenarios would be very interesting and useful. However, in this paper we are purposefully isolating the potential impacts of fire-regime variability. Our intent is not to replicate the exact dynamics that occurred at Chickaree Lake; rather, we are using DayCent as a tool to test alternative hypotheses and using the fire history of Chickaree Lake as an example of realistic variability in fire activity. In DayCent, we thus prescribe when fire events occur, which automatically decouples the fire events from climate from a modeling point of view. Even if we had a perfect paleoclimate data, few (if any) models would be capable of replicating the Chickaree Lake record, which would turn the paper into a model development project. Additionally, we also prescribe the erosion events associated with fires, again decoupling them from precipitation events.

This would have prevent authors from saying that fires and climate are disconnected which is absolutely not true, or at least need to be tested for each ecosystem studied. Moreover, instead of just increasing the 30-year time series temperature by 2°C, they could have used the full climate time series for the 21st century simulated by the same climate or earth models that provided the Holocene runs. They even could have tested different IPCC scenarios and their impact of the NECB. The use of climate model data would have provided precipitation time series as well, whose changes could also have impacted soil nutrient (and C) leaching. Indeed, it is easy to show that fire regime change outweighs climate change when such climate change may be unrealistic or only taken into account through temperature increase whereas several studies have documented and discussed about the potential counter-effect of precipitation increase in compensating the effect of temperature increase on fire occurrences and spread.

Response: We certainly do not believe that climate and fire are disconnected, and much of our own work explores fire-climate relationships in these and other ecosystems. To clarify this, we added a note in the study area description, briefly specifying the nature of fire-climate relationships in regional subalpine forests and citing a key reference. In DayCent, the only impact of using forced climate (with the forced fire and erosion events) would be the feedbacks to plant growth, which would increase or decrease the biomass available to burn given certain climate conditions. This is why we implemented the simple warming scenario: to see if/how our results would differ when biomass accumulation rates were higher (due to warmer temperatures). Our results indicate that the impacts of climate, as reflected by plant growth, is insignificant compared to the disturbance impacts in the model. However, we agree that this is not a good way to test the impact of climate on C cycling over time at this site and because this was not our intent, we have removed the warming scenario from study design in manuscript. We refer to the impacts of a 2 °C warming simply as a sensitivity analysis within the context of the DayCent model only, and not as a scenario representing coupled climate-fire-ecosystem dynamics.

Finally, because the charcoal record indicates when fire events occur, incorporating a paleoclimate record at the daily timestep and for a single location in the Rocky Mountains would likely add significant uncertainty, in both the precipitation regime and certainly if fire was "dynamic" and occurred in response to simulated climate.

Reviewer: It is even more important in the studied system as authors suggested and used two types of high severity fires: those with and those without erosion. Stand-replacing fires (95% mortality) are not really severe fire if post-fire regeneration is occurring in the next following years from naturally adapted species. Fire severity would rather refer to the difficulty of post-regeneration encountered in special cases. Stand-replacing fires are usually very intense and fuel consumption includes all the litter and humus layers, leaving the mineral soil exposed. So, if erosion in the burned watershed occurs (towards the lacustrine receptacle), it is performed during (heavy) rainfall events. Therefore, this is another argument to show that it would have been valuable to use past simulated precipitation over the last 4500 years BP, in order to test if rainfall (even as mean annual rainfall) changes could have occurred contemporaneously to erosive events just after some fires as compared to others.

Response: In western North America, subalpine forests like our study area are classified as "high-severity fire regimes," where "severity" refers to the immediate impacts of a fire on the ecosystem, often measured (directly or indirectly) by the amount of vegetation killed. In most cases, post-fire regeneration in subalpine forests does indeed start in the year immediately following fire, but we consider this an ecosystem response. While we appreciate the shortcomings of the concept of "fire severity," this is the standard terminology used, and we have added some references to support this use (i.e., Keeley 2009, Int. Journal of Wildland Fire). We simulated consumption of litter and humus layers in DayCent. In fact, the fires were parameterized to consume (combust) the forest biomass pools given known combustion coefficients for these types of forests (which includes 99% removal of the litter layer). With respect to climate forcing, again, we are forcing the erosion events to occur regardless of precipitation, based on the reconstructed fire history record. It would be ideal to test if the erosion events occurred with large precipitation events/years, but this is beyond the scope of this study.

Moreover, authors provide no information on the vegetation compartment modeled except the Net Ecosystem

Production for outputs, so we have no idea about which plant types are used for this site nor why 30cm deep was chosen as the targeted depth to analyze the site response. Finally, in the current version, except from NEP, we have not idea about the effect of vegetation change in terms of composition nor structure through time, we cannot see the direct as well as indirect effects of climate change on vegetation nor climate on fire as climate dataset was fixed and repeated along the 4500 years BP, even though fire ignition and fire spread conditions may have been more or less favorable.

Response: Our purpose in this study is not to predict the effects of climate (or fire) on vegetation change over time (or the effects of CO2 or nitrogen deposition, etc). The study site description includes a description of the known vegetation cover and based on the previously published pollen record from this site and others, we are confident that this general forest type did not change over the duration of our record (as noted above). DayCent (and most biogeochemical models) can only model soil C dynamics to a depth of 30 cm, primarily because this is the most active zone. The vegetation history has been more thoroughly described in the text, with additional references for support.

For all these reasons I see two options that require to modify the manuscript:

Option 1: to do the modelling experiment exercise once again but using climate data that represent the studied Holocene period for the first part and the 21st century for the second part. Even though climate data come from GCM and are not perfect, they will still be better than present-day ones applied to past and/or future periods, especially if climate is tested and its relative impact compared to that of fire regime variability. In parallel to temperature and precipitation datasets, authors should explain how they deal with air CO2 concentration as it should have been modified from 280 ppmv until 1750 to the historical recorded concentration until nowadays, and for the Future, at least a mean CO2 increase should be used if authors do not want to test several RCP scenarios. By keeping the CO2 at a fixed concentration could still be acceptable but once more, as they are tracking C pools, I think that the atmospheric C input should be taken into account.

Response: This is beyond the scope of this study and we are concerned that this activity would introduce large amounts of uncertainty (given modeling limitations) rather than actually clarifying our results. Again, our purpose here was not replicate the exact Holocene dynamics of this site (although we agree this is an important next step/project).

Option 2: keep the modelling experiment in the current version but authors need at least to remove the third objective as climate has not been properly taken into account as compared to the fire regime factor. In such case, they should explicitly present this study as a first-step modelling approach integrating only the fire regime information and therefore only testing it. All sentences related to climate effect should be modified in order to rather present or discuss limit of non-using proper climate data. This would better fit with the balanced way results must be discussed. In such a case, the first two objectives are still OK. Results and conclusions should be fairly presented without omitting that the climate data used may be a limit to the interpretations done.

Response: We agree the climate objective should not be a ‘main focus’ or main objective of the paper. We have removed the third climate objective.

Otherwise, I found pertinent the improvements suggested in the M.W.I. Schmidt’s comment posted for improvement definitions, more detailed explanations and improvement in figure quality so I encourage the authors to take them into account. They will facilitate the reading of the manuscript for people not fully familiar with model requirements and functioning such as the need of a spinup period, the use of several pools or compartments… If supplementary material is allowed I suggest to add such information there, even with a scheme presenting how the DayCent model works.

Response: We have addressed and utilized many of the comments from Schmidt. DayCent has excellent documentation online (powerpoints, step by step instructions, publication lists; http://www.nrel.colostate.edu/projects/daycent-downloads.html). If allowed we will include the link in the manuscript. We will also post our model input and output on the Dryad repository (not allowed until manuscript is published).

Response to Rev 2

Also, aside from discussing the biogeochemical elements, it could be interesting to also compare some of the ecological attributes like age distribution of forest stands between the paleoinformed and equilibrium approaches. Clearly the distribution of ages will be quite different, which could have implications if eventually model simulations become a tool for forest management guidelines aiming at sustainability of ecological services.

Response: We agree examining other ecological attributes would be interesting. The reviewer has hit on a frustrating problem in the ecosystem modeling world, especially as it pertains to providing useful tools for management. Unfortunately, DayCent (and most BGC models) do not model age distributions or forest structural changes, as there are no ‘trees’ explicitly modeled. To model individual trees, one needs to use forest landscape/succession models, which either lack the biogeochemistry or operate a spatial scales much too large for this project (like LPJ as suggested below). We also believe the soil model in released/validated versions of LPJ is insufficient for this project.

Specific comments

Introduction:

L87-93 Would this rather illustrate that many models that perform a spin-up period lack a validation of their simulated biochemical cycle?

Response: Spin-up is a necessary step given the need to reach steady state (and have an ecosystem with ‘states’ to model). We agree that it is/has been difficult to validate spin-up and spin-up as rather been used to reflect realistic ‘steady states’. With the advent of more paleo data, more spin up validation could be done.

Typically, the period after spin-up (what we refer to as equilibrium in this study) is validated against current ecosystem states, given information available. For DayCent, validation of the biogeochemical cycling has been performed in 100s of studies for 1000s of data points, originally published as the CENTURY model (Parton et al. 1983) with many publications in all types of terrestrial ecosystems since then.

Materials and Methods:

L165 What exactly is the size of the simulated area? Are fires spatially-explicit? Or just based on random selection of cells? Perhaps a few word on this.

Response: This was a ‘point’ simulation (size is not explicitly modeled) for a single study site. The simulation represents the watershed (c. 30 hectares) that would be affected in a high-severity fire with erosion. The fire is spatially-explicit to the single point, as there are no other points/grids. We have clarified that this is a point simulation in the text.

L176 So climate and radiation are constant. This may be problematic because in the eventuality that climate was different during the late-Holocene, as compared to the Anthropocene, likely the simulation will be misleading the productivity levels. So I guess this is another argument for doing the +2C and -2C simulation experiments (L217-224). Not using paleoclimatic simulation is an important weakness of this study and I would recommend that authors put more emphasis on the importance of this temperature sensitivity analysis. However, they should note that temperature is not the only driver of NPP; radiation and precipitation are also important.

Response: As pointed out by Rev. 1, climate impacts are not (and should not be) a main focus of the study. We agree that using paleo and/or future climate scenarios would be very interesting and useful. However, in this paper we are purposefully isolating the potential impacts of fire-regime variability. Our intent is not to replicate the exact dynamics that occurred at Chickaree Lake; rather, we are using DayCent as a tool to test alternative hypotheses and using the fire history of Chickaree Lake as an example of realistic variability in fire activity. In DayCent, we thus prescribe when fire events occur, which automatically decouples the fire events from climate from a modeling point of view. Even if we had a perfect paleoclimate data, few (if any) models would be capable of replicating the Chickaree Lake record, which would turn the paper into a model development project.

In terms of the temperature sensitivity, we show that net C balance is not sensitive to temperature relative to the impacts of disturbance, and this was really just a check on what we already know about climate vs. disturbance impacts (as pointed out by Rev. 3). In terms of other abiotic influences (precipitation and radiation), we agree they are important but again, we do not and cannot easily acquire paleoclimate data for this watershed, making these impacts beyond the capability of the current study. We include the temperature sensitivity results as a simple test on the model, although they are no longer a main focus.

L182-185 More details are needed in regard to the validation dataset. What kind of datasets are these observations? How were they derived? Why select these over others? What do you mean by ‘similar-aged’?

Response: There are very few observations (carbon, nitrogen pools, NPP, etc) for old (200+ yr) stands of lodgepole pine in the Rocky Mountains. The studies were chosen given that they had reported variables the most similar to our model output, were for the same species or taxa, and were in similar environmental/climate conditions. ‘Similar-aged’ means the same forest age. We do not consider these comparisons with reported observations a robust validation dataset; rather, this is the only means of validating some of the model output. We have clarified this in the manuscript.

Results and Discussion:

L241 What are the plus and minus signs for? Standard deviation or confidence intervals? What is the sample size? Area under analysis? Seems that crucial details are missing.

Response: The plus/minus signs are the standard deviation for the range of bulk density and soil organic matter percent reported for the dominant soil type that occurs in the Chickaree watershed. Soil carbon can be derived from STATSGO data (US federal database). This has also been clarified in the manuscript.

L274-278 This statement about disturbance free or intensified disturbance periods is partly false, because DGVMs now have the capacity to run fire dynamics using paleoclimate simulations that feed into a dynamic fire behaviour and growth model (e.g., LPJ-LMfire). This removes the necessity to do the paleo-informed, but nevertheless paleodata comparison is necessary as a validation step.

Response: Yes, there are models (and not just DGVMs) with prognostic fire, so yes there could be predictions of disturbance-free periods (and more intense ones). However, there are few models that actually duplicate known records of ignitions, burn area, and most importantly for this study, carbon combustion; we are unaware of any models with reasonable accuracy at the point scale. We chose DayCent because of its proven ability to predict above and belowground C dynamics at daily to millennial scales. We are also unaware of downscaled paleoclimate simulations that are ‘readily available’ at high spatial resolutions for this region.

L294-298 This is not really new and has been known for decades. The impact of fire versus vegetation is quite obvious considering that fire has the potential to exclude treed vegetation from landscapes despite generally improving growth conditions with warming and CO2

Response: Yes, we agree and have changed the wording to reflect that our results confirm what has been known about the impacts of individual fire events, for decades. The ‘new’ information has more to do with the impacts of the varying timing/sequence and severity of events over centuries to millennia. Certainly, any given fire will outweigh climate impacts in early post-fire recovery. Here, we show that the timing and severity of events over centennial and millennial scales strongly influences the state and trajectory of biogeochemical properties.

L343 “the lack of paleoclimate data” : this is an important weakness of this study. A few sentences about this is needed here to help readers unfamiliar with this issue to understand what is meant by ‘paleoclimate data’.

Response: We agree that not using paleoclimate data is an important limitation of our study, and our intention in this portion of the text is to clearly frame our results in this context. Although paleoclimate proxies exist for other regions in Colorado, for example in the form of lake-level reconstructions and oxygen isotope records, these records are far from the detailed climate information needed to drive DayCent. Thus, utilizing paleoclimate proxies to develop climate drivers for DayCent is a project in itself. For example, it involves developing methodologies to downscale paleoclimate proxies in space (to the elevation and location of Chickaree Lake), in time (to daily value), and to the specific metrics required by DayCent (e.g., from a relative moisture proxy to daily precipitation). We added text to further clarify this limitation and why this was not done in this study.

Figures: Figure 4 This figure is not obvious to read. Perhaps put on separate panels.

Response: Thank you for the comment. We have separated the panels.

Response to Rev. 3

General comments…Globally, the text is clearly written, the scientific context and knowledge gaps are clearly exposed as the problematic and the general hypothesis. Also, the questions addressed here are very pertinent. That said, I advise the authors to follow previous comments and advises from SC1, RC1 and RC2. Moreover, a more deeper review of fire ecology with respect to carbon cycling could: i) help to better understand the choice of DayCent for this study; ii) bring a more critical interpretation/discussion of the processes you mentioned (line 99-100) linked in DayCent model and improve the interpretation and discussion of the results.

Response: We thank you for the careful review and suggestions. Please see our specific comments below for our planned improvements.

I also noted several improvement possibilities (see also Technical corrections): 1/ Structure: Mixing results and discussion is sometimes confusing (especially for section 3.4). Because section 3.1 to 3.3 are not full discussions but rather descriptions and comparisons between your model estimates with values of other studies, it should not will be difficult to separate results and discussion. For example, discussion could contain a section on the limits, a section with the implications for projecting future ecosystem states and another for research development needs.

Response: We will consider revising the structure to separate the results and discussion based on the final revised manuscript. Because of what we address from the first 3 reviewer comments, the structure and text has changed enough that doing these structural improvements may no longer be straight forward.

2/Hypotheses: Based on Kelly et al. (2016), the general hypothesis assuming forest carbon budget modeling would be different between equilibrium runs and paleo-informed runs is explicit. Nevertheless, the alternative hypotheses that you mentioned (line 103) and results that were “expected” (line 301) are not explicitly described. You could add these hypotheses in the introduction.

Response: Thank you for pointing this out. We have changed the introduction to more explicitly state theses hypotheses.

3/ Model parameterization: According to SC1, DayCent is quite well described. Unfortunately, I was not able to access the model input and parameterization file. While is it clear that you informed the model with paleo-fire reconstruction from Dunette et al. (2014), it is less clear what you do with the vegetation data. You wrote that you “pair a paleoecological record of vegetation and wildfire activity” (line 98) and that DayCent requires input of vegetation cover (line 145), but no information is provided on vegetation in section 2.3. It would be important to get more details.

Response: The comments here is in agreement with Rev 2, and we realize details need to be expanded regarding the simulations. We will add the details (note that the ‘vegetation’ did not change at this site per the record). We plan to post the DayCent input files on Dryad, however, this is not allowed until publication.

Specific comments

10. Is the overall presentation well structured and clear? Yes, but could be improved (see General comments). 11. Is the language fluent and precise? Yes. 12. Are mathematical formulae, symbols, abbreviations, and units correctly defined and used? Yes, but see SC1 comments for [date] CE.

Response: We have clarified this.

13. Should any parts of the paper (text, formulae, figures, tables) be clarified, reduced, combined, or eliminated? Yes. Values for equilibrium scenario should appear in Figure 3 or equilibrium scenario should be removed in lines 301-305. As the Chickaree Lake watershed is the object of this study, some characteristics such as the watershed size and topography (slope characteristics) could be mentioned. Moreover, you defined 8 partial paleo-informed scenarios but only 4 are represented in Figure 1. To facilitate the reading, I suggest to represent all partial paleo-informed scenarios in Figure 1 or you can specify that you show only 4 on the 8 scenarios in the figure caption.

Response: We improved the figures and text as suggested.

14. Are the number and quality of references appropriate? Yes.

Technical corrections Line48: should read“greater than simulated under an equilibrium and climate warming scenarios”?

Response: This text has been removed from the abstract.

Line 71: NECB appears for the first time here but is defined at lines 162 163.

Response: This has been addressed.

Line 103: the “alternative hypotheses” are not clearly exposed and should appear here.

Response: As noted above, we have revised the hypotheses.

Line 112-114: should be in the Discussion or Conclusion section.

Response: This text has been removed (it was basically repeated in the discussion).

Line 117: same comment as SC1 Line 125: should read “Dunette et al. (2014)”

Line 125-127: the sample resolution of the core results from the chronology based on 14C dates. I suggest to reorder the sentence.

Line 129: should read “Dunette et al. (2014)”

Line 160: autotrophic respiration is accounting in NPP yet.

Response: We have revised based on the suggestions above.

Line163: how fire emissions are calculated in the model?

Response: We added text to clarify this. Basically, the fire is parameterized by pool (woody, litter, coarse wood, live or dead C) to combust a fraction of each pool based on the fire ‘severity’.

Line234: what is STATSGO?

Response: The definition and a general description of the database will be added (USDA soils database from the Natural Resource Conservation Service).

Line252: should read “Figure2” instead of “Figure1”.

Line275: should read “Kelly et al. (2016)”. Line275: should read “Together, this work and ours”.

Line 280: it is not clear what the equilibrium scenario is doing here.

Line 286: can you justify the threshold of 1 Mg C ha-1?

Response: Again, thank you for the careful reading! We addressed the corrections, clarified what equilibrium is doing and, yes, we can justify the threshold based on previous work and what we consider to be stable soil C.

Line 296: should read “stand-replacing”.

Line 303: “lower” compared with equilibrium or paleo-informed scenario?

Line 301: “As expected” refers to a hypothesis? I think you should present this hypothesis in the introduction.

Line 301-305: you mention the equilibrium scenario in your comparison and refer to the Figure 3, but values for the equilibrium scenario don’t appear in this figure.

Response: As noted above, we changed the introduction as suggested and the figure is comparing the final values to equilibrium (they are deltas).

Finally, I recognize the great potential of this paper and the important gap it helps to fill in the carbon cycling-related fire history knowledge. I am happy to see that such research is unfolding and I advise the authors to consider previous comments to improve their manuscript.

Response: Thank you!

Fire-regime variability impacts forest carbon dynamics for centuries to millennia

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Abstract

Wildfire is a dominant disturbance agent in forest ecosystems, shaping important biogeochemical processes including net carbon (C) balance. Long-term monitoring and chronosequence studies highlight a resilience of biogeochemical properties to large, stand-replacing, high-severity fire events. In contrast, the consequences of repeated fires or temporal variability in a fire regime (e.g., the characteristic timing or severity of fire) are largely unknown, yet theory suggests that such variability could strongly influence forest C trajectories (i.e. future states or directions) for millennia. Here we combine a 4500-year paleoecological record of fire activity with ecosystem modeling to investigate how fire-regime variability impacts soil C and net ecosystem carbon balance. We found that C trajectories in a paleo-informed scenario differed significantly from an equilibrium scenario (with a constant fire return interval), largely due to variability in the timing and severity of past fires. Paleo-informed scenarios contained multi-century periods of positive and negative net ecosystem C balance, with magnitudes significantly larger than observed under the equilibrium scenario. Further, this variability created legacies in soil C trajectories that lasted for millennia. Our results imply that fire-regime variability is a major driver of C trajectories in stand-replacing fire regimes. Predicting carbon balance in these systems, therefore, will depend strongly on the ability of ecosystem models to represent a realistic range of fire-regime variability over the past several centuries to millennia.

1. Introduction

Wildfire is a pervasive disturbance agent in forest ecosystems, strongly shaping ecosystem structure and function, including vegetation composition, nutrient cycling, and energy flow. While the immediate impacts of disturbance can be dramatic, the longevity of these impacts is less clear. In ecosystems where disturbance is historically prevalent, vegetation and biogeochemical properties typically return to pre-disturbance conditions over years to decades (Dunnette et al., 2014; McLauchlan et al., 2014), motivating the concept of “biogeochemical resilience” (Smithwick, 2011). Characterizing biogeochemical resilience emphasizes understanding pool sizes and changes to inputs or outputs of key elements (McLauchlan et al., 2014; Smithwick, 2011). In the context of wildfire, biogeochemical resilience is determined by pool sizes (e.g., carbon, nitrogen) prior to a fire event, elemental losses and transformations that occur during and shortly after a fire event (e.g., from volatilization and erosion), and post-fire changes in elemental pools, which in turn are determined by the rate and composition of post-fire revegetation (McLauchlan et al., 2014; Schlesinger et al., 2015; Smithwick, 2011).

Changes in the characteristic frequency or severity of fire (i.e., the fire regime) are therefore predicted to lead to compounding and potentially long-lasting changes or shifts in biogeochemical states. For example, increased disturbance frequency can deplete key growth-limiting nutrients (Yelenik et al., 2013), potentially influencing ecosystem trajectories for decades to centuries (McLauchlan et al., 2014). Net ecosystem carbon balance (NECB; the balance between net forest carbon uptake and forest losses through fire emissions; Chapin et al., 2006) is also highly sensitive to disturbance (Hudiburg et al., 2011), and while NECB trends towards 0 under a uniform disturbance regime, shifting disturbance regimes may alter NECB over centuries to millennia (Goetz et al., 2012; Kelly et al., 2016). While these ideas have a strong conceptual basis and empirical support on decadal timescales, we have lacked the data needed to test them over longer timescales – and to consider their implications for future projections – until only recently.

Coupling paleo observations (i.e. "paleo-informed") with ecosystem modeling provides an important tool for assessing the impacts of fire-regime variability on biogeochemical dynamics by combining the mechanistic representation of ecosystem processes with actual patterns of fire activity reconstructed from the past. For example, in Alaskan boreal forests paleo-informed ecosystem modeling highlights fire as the dominant control on C cycling over the past millennium, far outweighing the effects of climate variability (Kelly et al., 2016). Given the significance influence of fire, estimates of modern C states (“initial conditions” for modeling future C states) can be highly sensitive to assumptions about the past fire activity. Ecosystem models typically require a 'spin up' period to equilibrate C and N pools and can include a fixed disturbance interval (e.g., a constant fire return interval), resulting in ecosystem C and N trajectories that are in 'equilibrium' with climate, ecosystem properties, and the disturbance regime. To initiate the model, C and N pools need to develop, as they start from ‘bare soil’ with no vegetation; as vegetation grows the modeled soil pools increase, and it takes hundreds to thousands of simulation years during this "spin-up" period for the C and N pools to equilibrate. Following centuries of equilibrium, known disturbance events from the historical record are included, and the final results are used for initial conditions (baseline) for future scenarios. However, paleo-informed disturbance histories spanning many centuries can result in initial conditions that differ from equilibrium runs. In the boreal example, forests were a small net C source over the past several decades in paleo-informed simulations, whereas forests were a small net C sink when a constant fire return interval was assumed (Kelly et al., 2016). We would expect a similar sensitivity of C dynamics to fire in other stand-replacing fire regimes, although specific trajectories and impacts on modern states could vary widely, contingent on the specific history of fire activity.

Here, we pair a paleoecological record of vegetation and wildfire activity in a subalpine forest (Dunnette et al., 2014) with an ecosystem model to evaluate the sensitivity of forest ecosystem processes to fire-regime variability over a 4500-year period. Our paleoecological record reveals the timing and severity of past wildfire activity within a subalpine forest watershed that was consistently dominated by lodgepole pine (*Pinus contorta*). We use this record to drive fire disturbances in an ecosystem model and test alternative hypotheses that help reveal the potential patterns and mechanisms causing past ecosystem change, focusing on a slowly varying carbon pool (soil C) and net ecosystem carbon balance (NECB). The resulting trends provide theoretical insight into how observed fire-regime variability can affect carbon trajectories from decadal to millennial scales. Through a series of paleo-informed and control modeling scenarios, we address two key questions about the biogeochemical impacts and legacies of wildfire activity: (1) how does centennial-to-millennial-scale variability in fire activity impact biogeochemical processes that regulate soil C and NECB, and (2) for how long does the legacy wildfire activity impact current biogeochemical states? In addition to testing the general hypothesis that that forest carbon storage will differ between equilibrium and paleo-informed simulations, we also evaluate the impact of increasing or decreasing fire frequency, relative to that inferred from the paleo record.

2 Materials and Methods

2.1 Model description

DayCent is the globally recognized daily timestep version of the biogeochemical model CENTURY, widely used to simulate the effects of climate and disturbance on ecosystem processes including forests worldwide (Bai and Houlton, 2009; Hartman et al., 2007; Savage et al., 2013). DayCent is a logical choice for our purposes, because it includes soil C pools that have long turnover times, spanning months to 4000 years, and thus can represent long-term ecosystem change. As used here, DayCent is aspatial, representing our c. 30-ha study watershed as a single ‘point.’ Detailed model documentation and publication lists can be found on the following website: http://www.nrel.colostate.edu/projects/daycent-downloads.html.

Required inputs for the model include vegetation cover, daily precipitation and temperature, soil texture, and disturbance histories. DayCent calculates potential plant growth as a function of water, light, and soil temperature, and limits actual plant growth based on soil nutrient availability. The model includes three soil organic matter (SOM) pools (active, slow, and passive) with different decomposition rates, above and belowground litter pools, and a surface microbial pool associated with the decomposing surface litter. Plant material is split into structural and metabolic material as a function of the lignin to nitrogen ratio of the litter (more structural with higher lignin to nitrogen ratios). The active pool (microbial) has short turnover times (1-3 months) and the slow SOM pool (more resistant structural plant material) has turnover times ranging from 10 to 50 years depending on the climate. The passive pool includes physically and chemically stabilized SOM with turnover times ranging from 400 to 4000 years. For this study, DayCent was parameterized to model soil organic carbon dynamics to a depth of 30 cm. Model outputs include soil C and N stocks, live and dead biomass, above- and below-ground net primary productivity (NPP), heterotrophic respiration, fire emissions, and net ecosystem production (NEP, defined as the difference between NPP and heterotrophic respiration). We define net ecosystem carbon balance (NECB) as the difference between NEP and fire emissions.

Disturbances in DayCent are prescribed and can be parameterized to reflect “severity” through associated impacts to the ecosystem (e.g., biomass killed, nitrogen lost, soil eroded). The fire model in DayCent is parameterized to include the combusted and/or mortality fraction of each carbon pool (live and dead wood, foliage, coarse and fine roots, etc) that occurs with each fire event. Erosion is also scheduled as an event in DayCent and was prescribed to occur in the same month of the observed high-severity fire events. The erosion events are thus decoupled from precipitation in the model.

2.2 Study sites

We studied the biogeochemical consequences of fire-regime variability by informing the DayCent model with fire history data derived from sedimentary charcoal preserved in Chickaree Lake, Colorado (Dunnette et al., 2014). Chickaree Lake (40.334 °N, 105.841 °W, 2796 m above sea level) is a small, deep lake (c. 1.5 ha surface area; 7.9 m depth) in a lodgepole pine-dominated subalpine forest in Rocky Mountain National Park. The even-aged forest surrounding the lake regenerated after a high-severity (i.e., stand-replacing) fire in 1782 CE (common era) (Sibold et al., 2007). The fire regime in subalpine forests of Rocky Mountain National Park is characterized by infrequent, high-severity crown fires (c. 100-300 yr mean return intervals) associated with severe seasonal drought (Sibold et al. 2006). Mean monthly temperature is -8.5 °C in January and 14 °C in July, and average total annual precipitation is 483 mm (Western Regional Climate Center 1940-2013 observations, from Grand Lake, CO).

Detailed methods for the collection and analysis of the Chickaree Lake sediment record are found in Dunnette et al. (2014). Briefly, the 4500-year record has an average sample resolution of four years, and a chronology constrained by 13 ^{210}Pb dates spanning the upper 20 cm and 25 accelerator mass spectrometry ^{14}C dates for deeper sediments. Pollen analysis indicates that the site was continuously dominated by lodgepole pine for the duration of the record presented here, with successional changes following inferred fire events (Dunnette et al., 2014). The persistence of subalpine forest over the past 4500 years is also supported by near-by pollen records in Rocky

Mountain National Park (Caffrey and Doerner, 2012; Higuera et al., 2014). Dunnette et al. (2014) used macroscopic charcoal and magnetic susceptibility (a soil-erosion proxy) from Chickaree Lake to infer the timing and severity of wildfires, identifying “high-severity catchment fires” (those with associated erosion) and “lower severity/extralocal fires” (those without associated soil erosion). Thus, while all fire events were likely stand-replacing, the difference between these two fire types was the association with soil erosion. Here, we use the Chickaree Lake fire history record to inform the disturbance component of the DayCent ecosystem model by prescribing the timing and severity of past fire events within a simulated lodgepole pine-dominated subalpine forest.

2.3 Model parameterization

DayCent submodels associated with tree physiological parameters, site characteristics, soil parameters, and disturbance events were modified using available site-specific observations (Dunnette et al., 2014; Sibold et al., 2007), values from the literature (Kashian et al., 2013; Turner et al., 2004), and publically available climate and soils databases. Climate data required for DayCent include daily minimum and maximum temperature and precipitation which were obtained for a 30-yr period from DAYMET (Thornton, 2012). For all model runs, the 30-yr climate dataset was “recycled” for the duration of the run; thus, climate was functionally non-varying over the duration of the simulations (beyond the variability within the 30-yr dataset). Soil texture and classification were identified using the NRCS SSURGO database (NRCS, 2010). Model input and parameterization files are available for download as supporting information files.

We defined two types of stand-replacing fire to distinguish between the two types of fires identified in the paleo record. The key difference between the two fire types simulated is the associated soil erosion. High-severity catchment fires from the paleo record were simulated by 95% tree mortality and a soil erosion event with ~1 Mg ha^{-1} of soil loss from the watershed (Miller et al., 2011); we refer to these as high-severity fires with erosion. Lower-severity/extra local fires from the paleo record were simulated by 95% tree mortality with no associated soil-erosion event; we refer to these as high-severity fires without erosion. After parameterization, we evaluated modern modeled aboveground NPP, soil C, total ecosystem carbon, and disturbance C losses against observations of similar-aged lodgepole pine stands in the Central Rockies ecoregion (Hansen et al., 2015; Kashian et al., 2013; Turner et al., 2004).

2.4 Model experiments

We performed a series of modeling experiments to address our questions using the Chickaree Lake paleo-fire record, varied disturbance histories, and varied climate (Table 1). First, DayCent was 'spun up' and equilibrated to soil C and NPP levels characteristic of mature lodgepole pine stands in the region with a constant return interval of 145 years between high-severity fires with erosion, replicating the estimated fire rotation period (and mean fire-return interval) for the broader study area (Sibold et al., 2007). This spinup period lasted for 2000 years, and it represents what would be done for model use, in the absence of the long-term fire history information from the paleo record. All experimental simulations were extended from this spinup equilibrium simulation starting 4500 years before present (BP, where "present" is 1950 CE) and running through 2010 CE, for a total of 4561 simulation years. We defined our model simulation that would normally be used in the absence of paleo-informed disturbance histories ("equilibrium scenario") as a continuation of the equilibrated spinup with the same climate and fire regime, with only the last known fire event (1782 CE) explicitly simulated.

In addition to this equilibrium scenario, we implemented three additional scenarios that together helped illustrate the duration, magnitude, and relative importance of fire-induced changes to forest biogeochemistry. First, to test the impacts of variability in fire timing and severity on important biogeochemical states, we compared the equilibrium scenario to a "paleo-informed scenario," which had a mean fire return interval of 120 years for all fires, and 334 years for the high-severity fires with erosion. Climate was identical in each simulation (i.e., 30-yr recycled modern climate), as we are not testing the influence of climate on the timing and severity of fire, but rather the influence of the known timing and severity of fires (from the charcoal record) versus a constant fire return interval interval.

Second, to identify the duration of a legacy effect from fire-regime variability, we constructed eight "partially paleo-informed scenarios," which included increasingly longer periods of information from the paleo-fire record, spanning the past 500 to 4000 yr, in 500-yr increments that ended in 2010 CE ("Paleo_{500}", "Paleo_{1000}", …, "Paleo_{4000}"; Figure 1a). For example, the

Paleo_{500} scenario includes the most recent 500 yr of fire history while the Paleo_{4000} scenario includes the most recent 4000 yr of fire history.

Thirdly, to identify how a systematic shift in fire frequency would impact carbon balance, we created two additional scenarios with shortened and lengthened fire return intervals. Beginning with the observed paleo-fire record, we modified each interval between fires to be (a) shortened by 25% (“Increased fire frequency”) or (b) lengthened (“Decreased fire frequency”) by 25% (Figure 1b). The corresponding mean fire return intervals of these two additional runs were 90 yr for the “Increased fire frequency” and 155 yr for the “Decreased fire frequency” scenarios.

Because fire events in DayCent are decoupled from climate, the climate data did not impact the timing or severity of fires in the simulations. We evaluated the results from each scenario in terms of modern end points of soil C, soil N, and NECB as well as total cumulative changes in NECB over the entire record. We define cumulative NECB as a running total, such that the sum at any given year represents the integrated impacts of past disturbance events. For example, when return intervals between disturbance events are shorter than C recovery times, cumulative NECB will remain negative. Finally, we considered uncertainty in our estimates based on the uncertainty in the reconstructed fire history record, our assumptions about soil erosion, and our use of recycled modern climate. While there is also uncertainty associated with modeled estimates of soil C, NECB, and other C fluxes presented, we are not attempting to provide estimates that are any more precise than measured modern states (e.g. STATSGO derived soil C). Rather, we compare the variability in biogeochemical states arising from fire-regime variability to the uncertainties in the model that are revealed when evaluated against modern observations from the literature.

3 Results and Discussion

3.1 Model parameterization and evaluation

We compared our model results with reported values from ecological studies in the region that examined some aspect of the carbon balance in the similar-aged subalpine forests in order to evaluate our model estimates. We found few reported observations (e.g., for C, N pools, NPP) for old (>200 yr) lodgepole pine stands in the Rocky Mountains in the literature. Therefore, we also compare our results with results for the same genus (*Pinus*) and with the soil C content reported by the United States National Resource Conservation Service (NRCS) as part of the national soil survey. Our modeled estimates of modern soil C (to 30 cm) of 54 and 62 Mg C ha^{-1}, for the equilibrium and paleo-informed scenario, respectively (Figure 2), compare well with the NRCS-derived estimates (STATSGO2, NRCS, 2010) of 66 ± 16 Mg C ha^{-1} for the Chickaree Lake region, and with measurements of current soil C (to 30 cm) ranging from 51 to 73 Mg C ha^{-1} in similarly aged (> 200 yr) Rocky Mountain *Pinus* stands (Bradford et al., 2008). Modeled estimates of aboveground NPP were also in agreement with observations averaging 156 and 172 g C m^{-2} for the equilibrium and paleo-informed simulations, respectively, compared to estimates from the Northern or Central Rockies ranging from 100 to 200 g C m^{-2} (Hansen et al., 2015). Finally, fire emissions from our modeled estimates range from 20 to 30% loss of aboveground C, broadly in agreement with other studies (Campbell et al., 2007; Smithwick et al., 2009).

3.2 Fire-regime variability impacts soil C and NECB

When DayCent was driven with the paleo-informed fire history, soil C accumulation was 8 Mg ha^{-1} more at the end of the simulation than in the equilibrium scenario (Figure 2). Total NEP summed over the 4561-year period was also higher in the paleo-informed scenario (1276 Mg C ha^{-1}) compared with the equilibrium scenario (1171 Mg C ha^{-1}), directly reflecting NPP rates that were higher than heterotrophic respiration (Figure 3, black bar). In the paleo-informed scenario, cumulative emissions due to combustion losses (i.e., “fire emissions”) were lower than NEP over the entire record, resulting in a cumulative NECB of 27 Mg C ha^{-1} more than the equilibrium scenario (Figure 3; black bars).

The paleo-informed scenario showed substantial variability in soil C (Figure 2) and NECB (Figure 4) trajectories, and higher total accumulations relative to the equilibrium scenario. In fact, the range of variability in soil C over the paleo-informed simulation, from c. 45 to 65 Mg C ha^{-1}, nearly spanned the range of observations of current soil C (to 30 cm) in similarly aged (> 200 yr) Rocky Mountain *Pinus* stands (Bradford et al., 2008). For the first ~2000 years of the paleo-informed scenario, long-term mean soil C was similar to baseline levels of soil C in the equilibrium scenario (Figure 2), averaging around 54 Mg C ha^{-1}, though with substantial variability on centennial time scales. Following this period, the soil C trajectory increased distinctly in the paleo-informed scenario during a 500-year period with only one high-severity fire without erosion (c. 2500 cal yr BP). Despite a return to a mean fire return interval closer to the equilibrium scenario, soil C persisted at this elevated level for the following 2000 years (c. 2000 cal yr BP to present), resulting in 8 Mg C ha^{-1} (15%) more than the equilibrium scenario at the end of the simulation (2010 CE). A similar trend was observed for NECB (Figure 4), where the paleo-informed scenario maintained a lower NECB in the first half of the record compared the second half. In the latter half of the record, NECB was more consistently positive, ultimately storing more ecosystem C than the equilibrium scenario. The dynamism in NECB over time is consistent with the findings of Kelly et al. (2016). Together, this work and ours highlights the value of examining the ecosystem impacts of past fire-regime variability, which may include disturbance-free or intensified disturbance periods that are not currently represented in or predicted by ecosystem models.

3.3 Impacts of fire-regime variability last for millennia

We compared the partially paleo-informed scenarios to the equilibrium scenario to determine the length of time necessary to arrive at the same inferences about soil C and NECB as in the full paleo-informed scenario. The CE 2010 endpoints for each partially informed scenario were compared to the CE 2010 endpoint for the equilibrium scenario. We found that disturbance-regime legacies lasted for millennia. The number of years needed to simulate the CE 2010 values was between 2000 and 2500 years (Figure 5). Specifically, total NECB and soil C (endpoints that serve as initial conditions for future modeled states) were nearly the same when using 2500 to 4500 years of the paleo-fire record, but differed by more than 1 Mg C ha^{-1} when using only 500 to 2000 years of the paleo-fire record. We used the 1 Mg C ha^{-1} as a significant threshold for changes in ecosystem C flux (total or soils) both because changes less than this indicate the ecosystem is stable and it is a standard amount of annual C flux into or out of an ecosystem that is considered significant for carbon sequestration (mitigation) activities (Anderson-Teixeira et al., 2009).

Differences between the paleo-informed and equilibrium scenario can be interpreted in the context of other model parameters that are known to affect biogeochemical processes, including plant productivity and decomposition rates. Chief among these is growing season temperature, which strongly affects NPP and plant and microbial respiration in DayCent. In a simple sensitivity analysis where we repeated the equilibrium scenario with a uniform 2 °C warming during the growing season, we found that variability in the paleo-informed scenario was an order of magnitude greater than in the scenario with warming. Specifically, warming resulted in a small net decrease in soil C of 0.3 Mg C ha^{-1}, and a reduction in NECB by 0.2 Mg C ha^{-1} relative to equilibrium scenario. Our results imply that C dynamics in lodgepole pine forests are far more sensitive to variability in the timing and severity of fire activity than to modeled changes to plant growth and decomposition introduced by climate warming alone. This inference is also consistent with findings from strand-replacing fire regimes in Alaskan boreal forests, where C dynamics over the past 1200 years were more strongly shaped by fire activity than by climate variability (Kelly et al., 2016).

3.4 Implications for projecting future biogeochemical states

To evaluate the effects of changing fire regimes on our results, we varied the paleo-informed disturbance regimes by increasing and decreasing the frequency of events by 25%. As expected, increased fire frequency (i.e., shorter return intervals) resulted in a cumulative loss of ecosystem C compared to equilibrium and paleo-informed scenarios, with NECB 13 Mg C ha^{-1} lower compared to equilibrium over the entire simulation period (Figure 3), and with periods of net carbon loss lasting nearly 800 years (Figure 4; red line). The losses reflect large increases in fire emissions, without concurrent proportional increases in NEP (Figure 3). In contrast, with decreased fire frequency (i.e., longer return intervals), NECB increases by 67 Mg C ha^{-1} compared to equilibrium, and by 40 Mg C ha^{-1} compared to the original paleo-informed scenario. Again, this is primarily due to an unbalanced increase in NEP compared to fire emissions (Figure 3).

While the differences in NECB (27 Mg C more) and soil C (8 Mg C more) between the paleo-informed and equilibrium scenarios are ultimately small for this single watershed, the impact of fire-regime variability will depend on the synchrony of events at the regional and sub-continental scales (Kelly et al., 2016). This is especially important when considering the trajectory of NECB compared to equilibrium simulations during the periods of the paleo record when fire frequency or severity were higher than in the past few centuries. Cumulative NECB was negative, serving as a net source of C to the atmosphere, for periods of up to 500 years in the paleo-informed scenario and up to 1000 years under scenarios with increased fire frequencies.

Given the strong correspondence between observed and simulated modern C stocks, we have high confidence that DayCent accurately simulated the key processes shaping biogeochemical properties in our study area. Important sources of uncertainty in our estimates of past carbon dynamics stem from uncertainty in the timing and severity of past fires. The fire history reconstruction has an estimated temporal precision of several decades (±10-20 years) (Dunnette et al., 2014), but because C dynamics unfold over centuries to millennia, this level of uncertainty has negligible effects on our inferences. Another important source of uncertainty is the potential for false positives or false negatives in the fire history reconstruction: failing to detect a fire that occurred in the past, or identifying a fire that did not affect the Chickaree Lake watershed. While the Chickaree Lake record clearly identified the most recent high-severity fire in the watershed (Dunnette et al., 2014), we cannot quantify accuracy over the past four millennia. However, the range of variability in individual fire return intervals reconstructed at Chickaree Lake (20-330 year) is consistent with the range of intervals reconstructed from other lake-sediment records in Colorado subalpine forests (Calder et al., 2015; 75-885, 45-750, 30-645, 30-1035 yr, Higuera et al., 2014), suggesting that the C dynamics highlighted here are not unique to this single fire history reconstruction.

In addition to fire timing, simulated C dynamics were also a function of variability in fire severity, which in this study reflects the degree of soil erosion associated with stand-replacing fire events. Watershed soil C losses were partially driven by the erosion events accompanying the "high severity catchment fires" reconstructed in the paleo record. Because we have prescribed both fire and erosion, we cannot predict the range of soil C loss that may occur due to changes in precipitation regimes or if any erosion occurs with the lower severity events; however, these results provide an estimate of expected changes in soil C for at least the higher severity events. With expected changes to future precipitation regimes, including intensification of rain events that could lead to increased erosion following fire (Larsen and MacDonald, 2007;

Miller et al., 2011), ecosystem model development should include prognostic erosion to account for variability in this ecosystem process, especially at regional scales.

Finally, the most important limitation of our study is the fact that our modeling framework does not integrate realistic paleoclimate variability, nor does it represent the important coupling among climate, vegetation, and fire activity. Although paleoclimate proxies exist for nearby regions in Colorado, for example in the form of lake-level reconstructions and oxygen isotope records (Anderson 2011, 2012; Shuman et al. 2010), these records are far from the detailed climate information needed to drive DayCent. Thus, utilizing paleoclimate proxies to develop climate drivers for DayCent is an important next step, but beyond the scope of this study. For example, it will involve developing methodologies to downscale paleoclimate proxies in space (to the elevation and location of Chickaree Lake), in time (to daily value), and to the specific metrics required by DayCent (e.g., from a relative moisture proxy to daily precipitation). While our simulated past carbon dynamics are limited by the lack of available paleoclimate data to drive DayCent, our temperature sensitivity analysis suggests that C dynamics are much more sensitive to the timing and severity of fire events than to even relatively large changes in climate (e.g., 2 °C warming). Further, because we have decoupled climate from fire by using prescribed fire events, the lack of a paleoclimate does not affect our conclusions about the impacts of fire-regime variability on C balance. While we used the paleo-informed modeling scenarios to test general hypotheses about the impacts of fire-regime variability on biogeochemical dynamics, future efforts to simulate the coupled climate-fire-ecosystem dynamics of the past clearly require independent paleoclimate drivers.

4 Summary and Conclusions

Our simulations highlight fire-regime variability as a dominant driver of C dynamics in lodgepole pine forests, with periods of unusually high or low fire activity creating legacies lasting for centuries to millennia. Anticipating the impacts of future climate or disturbance-regime change on forest carbon balance, therefore, should be done in the context of past variability, with the duration dependent on the frequency and variability of relevant disturbance processes. In the case of stand-replacing wildfires this requires information spanning at least several centuries, and at Chickaree Lake this required several millennia, well beyond the length of both observational and tree-ring records. Many studies have reported ecosystem impacts or recovery times from individual fire events and then extrapolated to infer scenarios that would lead to C gain or loss (Dunnette et al., 2014; Kashian et al., 2013; Mack et al., 2011; Smithwick et al., 2009). In contrast, our paleo-informed scenario highlights the importance of variability in fire timing and severity over multiple fire events for carbon cycling dynamics, independent of complete shifts in a fire regime.

Our findings also have implications for ecosystem and Earth system model development, which are increasingly including prognostic fire components (Lasslop et al., 2014), primarily driven by climate and fuels. Some models are also representing post-fire C and N dynamics beyond simple combustion of live and dead biomass or only the dead-wood pools (fuels). Development of these modules depends on observations of fire and climate interactions, fuel availability, and post-fire C and N dynamics. We suggest that this requires accurately accounting for the (often high) variability inherent in stand-replacing fire regimes, independent from or in response to climate variability. Our results indicate that even utilizing tree-ring record that span several centuries may not be sufficient to capture this variability. Further development of prognostic (predictive) fire processes in ecosystem models would benefit from the use of paleo-fire records to evaluate fire occurrence and severity, and if combined with paleoclimate data, model algorithms could be further improved to accurately reflect past variability.

The importance of fire-regime variability in determining ecosystem C dynamics implies that equilibrium scenarios are a poor assumption for conceptualizing and simulating fire regimes in ecosystem and Earth system models. Particularly at spatial scales larger than an individual site, such a simplification may result in C-balance projections that are grossly inaccurate. We demonstrate how variability in the timing and severity of disturbances can potentially have long-lasting and compounding impacts on biogeochemical states, such that modern (or future) states can reflect dynamics that have unfolded over centuries to millennia. For our modeling scenarios in lodgepole-pine dominated forests, the effects lasted approximately 2500 years. The duration of these legacies will depend on the ecosystem, and the degree of variability in disturbance frequency and severity, relative to an equilibrium scenario. Ultimately, the implications of fire-regime variability on biogeochemical states will depend strongly on the synchrony of fire activity across spatial scales larger than a single watershed. If fire activity is synchronized at landscape to regional scales, as in past (Calder et al., 2015; Marlon et al., 2012; Morgan et al.,

2008) and as anticipated for the future (Westerling et al., 2011) in Rocky Mountain forests, we would expect to see similar centennial- to millennial-scale dynamics in biogeochemical states revealed here, which would have important implications for carbon cycling, including potential feedbacks to CO_2-induced warming.

5 Data Availability

The following datasets are available at Dryad.org (http://dx.doi.org/10.5061/dryad.74b2c): ~~The following datasets are available at Dryad.org <url TBD>:~~ the fire history record generated from the charcoal record, the relevant model output, and model input files and climate input file.

Author Contributions. T.W. Hudiburg and P.E. Higuera designed the study, analyzed the data, and prepared the manuscript with contributions from J.A. Hicke.

Competing interests. The authors declare that they have no conflict of interest.

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References

Anderson, L.: Holocene record of precipitation seasonality from lake calcite 18O in the central Rocky Mountains, United States. Geology, 39, 211– 214, 2011.

Anderson, L.: Rocky Mountain hydroclimate: Holocene variability and the role of insolation, ENSO, and the North American Monsoon. Global and Planetary Change, 92–93, 198–208, 2012.

Bai, E., and Houlton, B. Z.: Coupled isotopic and process-based modeling of gaseous nitrogen losses from tropical rain forests, Global Biogeochemical Cycles, 23, 2009.

Anderson-Teixeira K.J., Davis S.C., Masters M.D., and Delucia E.H.: Changes in soil organic carbon under biofuel crops. Global Change Biology Bioenergy, 1, 75 –96, 2009.

Bradford, J. B., Birdsey, R. A., Joyce, L. A., and Ryan, M. G.: Tree age, disturbance history, and carbon stocks and fluxes in subalpine Rocky Mountain forests, Global Change Biology, 14, 2882-2897, 10.1111/j.1365-2486.2008.01686.x, 2008.

Caffrey, M. A., and J. P. Doerner.: A 7000-Year Record of Environmental Change, Bear Lake, Rocky Mountain National Park, USA. Physical Geography, 33, 438-456, 2012.

Calder, W. J., Parker, D., Stopka, C. J., Jiménez-Moreno, G., and Shuman, B. N.: Medieval warming initiated exceptionally large wildfire outbreaks in the Rocky Mountains, Proceedings of the National Academy of Sciences, 112, 13261-13266, 2015.

Campbell, J., Donato, D., Azuma, D., and Law, B.: Pyrogenic carbon emission from a large wildfire in Oregon, United States, Journal of Geophysical Research: Biogeosciences, 112, G04014, 10.1029/2007JG000451, 2007.

Chapin, F., Woodwell, G., Randerson, J., Rastetter, E., Lovett, G., Baldocchi, D., Clark, D., Harmon, M., Schimel, D., Valentini, R., Wirth, C., Aber, J., Cole, J., Goulden, M., Harden, J., Heimann, M., Howarth, R., Matson, P., McGuire, A., Melillo, J., Mooney, H., Neff, J., Houghton, R., Pace, M., Ryan, M., Running, S., Sala, O., Schlesinger, W., and Schulze, E. D.: Reconciling carbon-cycle concepts, terminology, and methods, Ecosystems, 9, 1041-1050, 2006.

Dunnette, P. V., Higuera, P. E., McLauchlan, K. K., Derr, K. M., Briles, C. E., and Keefe, M. H.: Biogeochemical impacts of wildfires over four millennia in a Rocky Mountain subalpine watershed, New Phytologist, 203, 900-912, 2014.

Goetz, S. J., Bond-Lamberty, B., Law, B. E., Hicke, J. A., Huang, C., Houghton, R. A., McNulty, S., O'Halloran, T., Harmon, M., Meddens, A. J. H., Pfeifer, E. M., Mildrexler, D., and Kasischke, E. S.: Observations and assessment of forest carbon dynamics following disturbance in North America, Journal of Geophysical Research-Biogeosciences, 117, 10.1029/2011jg001733, 2012.

Hansen, E. M., Amacher, M. C., Van Miegroet, H., Long, J. N., and Ryan, M. G.: Carbon Dynamics in Central US Rockies Lodgepole Pine Type after Mountain Pine Beetle Outbreaks, Forest Science, 61, 665-679, 2015.

Hartman, M. D., Baron, J. S., and Ojima, D. S.: Application of a coupled ecosystem-chemical equilibrium model, DayCent-Chem, to stream and soil chemistry in a Rocky Mountain watershed, ecological modelling, 200, 493-510, 2007.

Higuera, P. E., Briles, C. E., and Whitlock, C.: Fire-regime complacency and sensitivity to centennial-through millennial-scale climate change in Rocky Mountain subalpine forests, Colorado, USA, Journal of Ecology, 102, 1429-1441, 2014.

Hudiburg, T. W., Law, B. E., Wirth, C., and Luyssaert, S.: Regional carbon dioxide implications of forest bioenergy production, Nature Climate Change, 1, 419-423, 10.1038/nclimate1264, 2011.

Kashian, D. M., Romme, W. H., Tinker, D. B., Turner, M. G., and Ryan, M. G.: Postfire changes in forest carbon storage over a 300-year chronosequence of Pinus contorta-dominated forests, Ecological Monographs, 83, 49-66, 10.1890/11-1454.1, 2013.

Kelly, R., Genet, H., McGuire, A. D., and Hu, F. S.: Palaeodata-informed modelling of large carbon losses from recent burning of boreal forests, Nature Climate Change, 6, 79-82, 2016.

Larsen, I. J., and MacDonald, L. H.: Predicting postfire sediment yields at the hillslope scale: Testing RUSLE and Disturbed WEPP, Water Resources Research, 43, n/a-n/a, 10.1029/2006WR005560, 2007.

Lasslop, G., Thonicke, K., and Kloster, S.: SPITFIRE within the MPI Earth system model: Model development and evaluation, Journal of Advances in Modeling Earth Systems, 6, 740-755, 10.1002/2013MS000284, 2014.

Mack, M. C., Bret-Harte, M. S., Hollingsworth, T. N., Jandt, R. R., Schuur, E. A. G., Shaver, G. R., and Verbyla, D. L.: Carbon loss from an unprecedented Arctic tundra wildfire, Nature, 475, 489-492, 2011.

Marlon, J. R., Bartlein, P. J., Gavin, D. G., Long, C. J., Anderson, R. S., Briles, C. E., Brown, K. J., Colombaroli, D., Hallett, D. J., and Power, M. J.: Long-term perspective on wildfires in the western USA, Proceedings of the National Academy of Sciences, 109, E535-E543, 2012.

McLauchlan, K. K., Higuera, P. E., Gavin, D. G., Perakis, S. S., Mack, M. C., Alexander, H., Battles, J., Biondi, F., Buma, B., and Colombaroli, D.: Reconstructing disturbances and their biogeochemical consequences over multiple timescales, BioScience, bit017, 2014.

Miller, M. E., MacDonald, L. H., Robichaud, P. R., and Elliot, W. J.: Predicting post-fire hillslope erosion in forest lands of the western United States, International Journal of Wildland Fire, 20, 982-999, 2011.

Morgan, P., Heyerdahl, E. K., and Gibson, C. E.: Multi-season climate synchronized forest fires throughout the 20th century, northern Rockies, USA, Ecology, 89, 717-728, 2008.

NRCS: Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Available online at http://soildatamart.nrcs.usda.gov. Soil Survey Geographic (SSURGO) Database for Eastern US, 2010.

Savage, K. E., Parton, W. J., Davidson, E. A., Trumbore, S. E., and Frey, S. D.: Long-term changes in forest carbon under temperature and nitrogen amendments in a temperate northern hardwood forest, Global change biology, 19, 2389-2400, 2013.

Schlesinger, W. H., Dietze, M. C., Jackson, R. B., Phillips, R. P., Rhoades, C. C., Rustad, L. E., and Vose, J. M.: Forest biogeochemistry in response to drought, Global Change Biology, 2015.

Shuman, B., Pribyl, P., Minckley, T.A. and Shinker, .J.: Rapid hydrologic shifts and prolonged droughts in Rocky Mountain headwaters during the Holocene. Geophysical Research Letters, 37, L06701, 2010.

Sibold, J. S., Veblen, T. T., Chipko, K., Lawson, L., Mathis, E., and Scott, J.: Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park, Ecological Applications, 17, 1638-1655, 2007.

Sibold, J. S., T. T. Veblen, and M. E. Gonzalez.: Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. Journal of Biogeography, 33, 631-647, 2006.

Smithwick, E. A. H., Ryan, M. G., Kashian, D. M., Romme, W. H., Tinker, D. B., and Turner, M. G.: Modeling the effects of fire and climate change on carbon and nitrogen storage in lodgepole pine (Pinus contorta) stands, Global Change Biology, 15, 535-548, 10.1111/j.1365-2486.2008.01659.x, 2009.

Smithwick, E. A. H.: Pyrogeography and biogeochemical resilience, in: The Landscape Ecology of Fire, Springer, 143-163, 2011.

Thornton, P., MM Thornton, BW Mayer, N Wilhelmi, Y Wei, RB Cook . : Daymet: Daily surface weather on a 1 km grid for North America,1980 - 2008. In: Daymet: Daily surface weather on a 1 km grid for North America,1980 - 2008., Acquired online (http://daymet.ornl.gov/) on 20/09/2012 from Oak Ridge National Laboratory Distributed Active Archive Center, O. R., Tennessee, U.S.A. doi:10.3334/ORNLDAAC/Daymet_V2. (Ed.), Daymet: Daily surface weather on a 1 km grid for North America,1980 - 2008., 2012.

Turner, M. G., Tinker, D. B., Romme, W. H., Kashian, D. M., and Litton, C. M.: Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA), Ecosystems, 7, 751-775, 2004.

Westerling, A. L., Turner, M. G., Smithwick, E. A. H., Romme, W. H., and Ryan, M. G.: Continued warming could transform Greater Yellowstone fire regimes by mid-21st century, Proceedings of the National Academy of Sciences, 108, 13165-13170, 2011.

Yelenik, S., Perakis, S., and Hibbs, D.: Regional constraints to biological nitrogen fixation in post-fire forest communities, Ecology, 94, 739-750, 2013.

Tables

Table 1. Model simulation scenarios, including climate, fire regime, duration, and summary description.

Scenario	Purpose	Climate*	Fire Regime	Duration (yr)	Description
Spinup	Spin up C, N pools to equilibrium conditions	Ambient	Fixed 145-yr return interval; high severity with erosion	2000	DayCent initialization run for NPP and C to reach equilibrium conditions.
Equilibrium	Run with fixed fire interval	Ambient	Fixed 145-yr return interval; high severity with erosion	4561	Equilibrium run extended from the spinup run for the length of the paleo-fire record.
Paleo-Informed	Run with observed paleo-fire intervals and severity	Ambient	Paleo-record; high severity with and without erosion	4561	A 4561-year simulation with fires matching the timing and severity from the paleo-fire record.
Increased fire frequency	Run with paleo-fire intervals decreased by 25%	Ambient	Modified Paleo-record; 90-yr MFRI with high severity with and without erosion	4561	A 4561-year simulation with the timing between fires in the paleo-informed scenario decreased by 25%.
Decreased fire frequency	Run with paleo-fire intervals increased by 25%	Ambient	Modified Paleo-record ;155-yr MFRI with high severity with and without erosion	4561	A 4561-year simulation with the timing between fires in the paleo-informed scenario increased by 25%.
$Paleo_{500}$… $Paleo_{4000}$	Test influence of length of paleo record on modern states	Ambient	Paleo-record; high severity with and without erosion	500 - 4000	Branches from the equilibrium scenario at varying points in time, in 500-yr increments**. All scenarios ends in CE 2010.

* 30-year recycled historical record (DayMet)

** For example, the 500 year simulation starts in the year 1510 (CE) and runs until the end of 2009

Figures

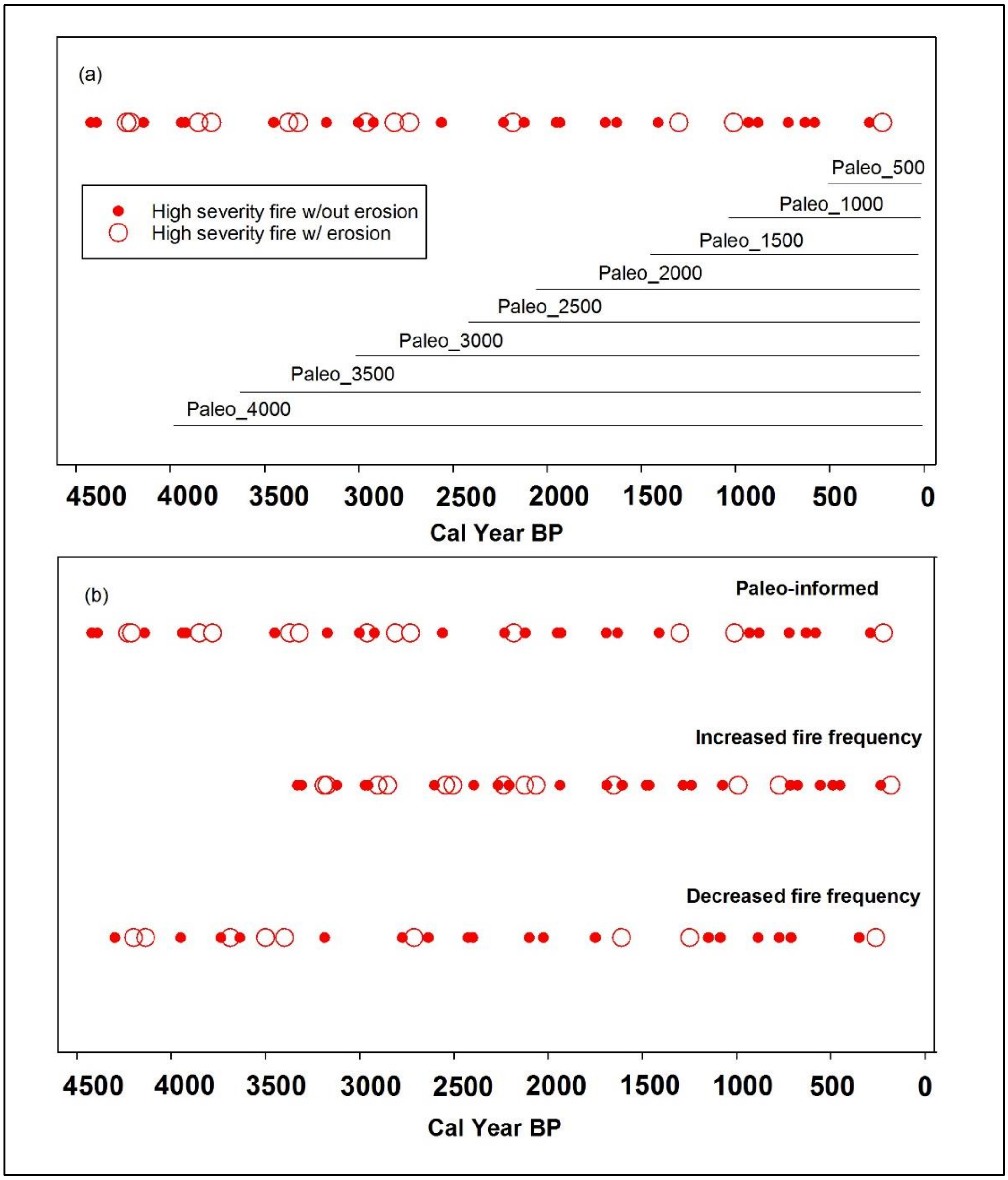

Figure 1. Paleo-informed fire history scenarios used to drive the DayCent model. (a) Fire history record form Chickaree Lake (red circles), with horizontal lines illustrating the duration of the record used in the incremental "partial paleo-informed" scenarios (Paleo_500…4000). (b) The same full Chickaree Lake fire history record used in the paleo-informed scenario (top), with the two additional scenarios representing a 25% increase and 25% decrease in fire frequency (bottom two scenarios).

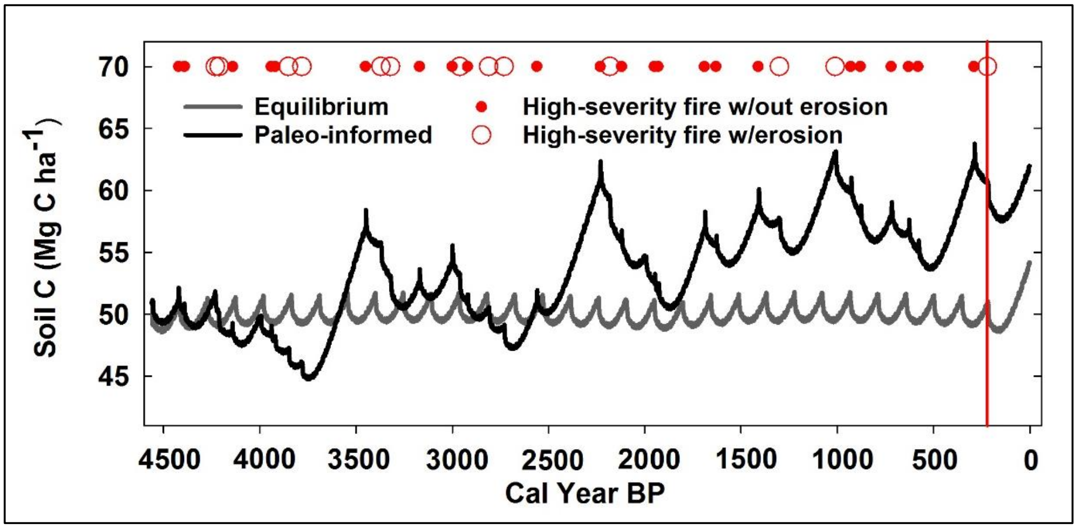

Figure 2. Model simulations of equilibrium (grey) and paleo-informed (black) total soil carbon (C) in Mg C ha^{-1}. Each simulation branches from a 2000-year equilibrium spinup starting at the same soil C baseline and runs for 4561 years (4500 BP to CE 2010). The large open circles represent the years of the high-severity fires with erosion, and the small closed circles are high-severity fires without erosion used to drive the paleo-informed model run. A constant 145-year fire return interval was used for the equilibrium run. The vertical red line indicates the most recent stand-replacing fire (1782 CE), reconstructed from the tree-ring record (Sibold et al., 2007).

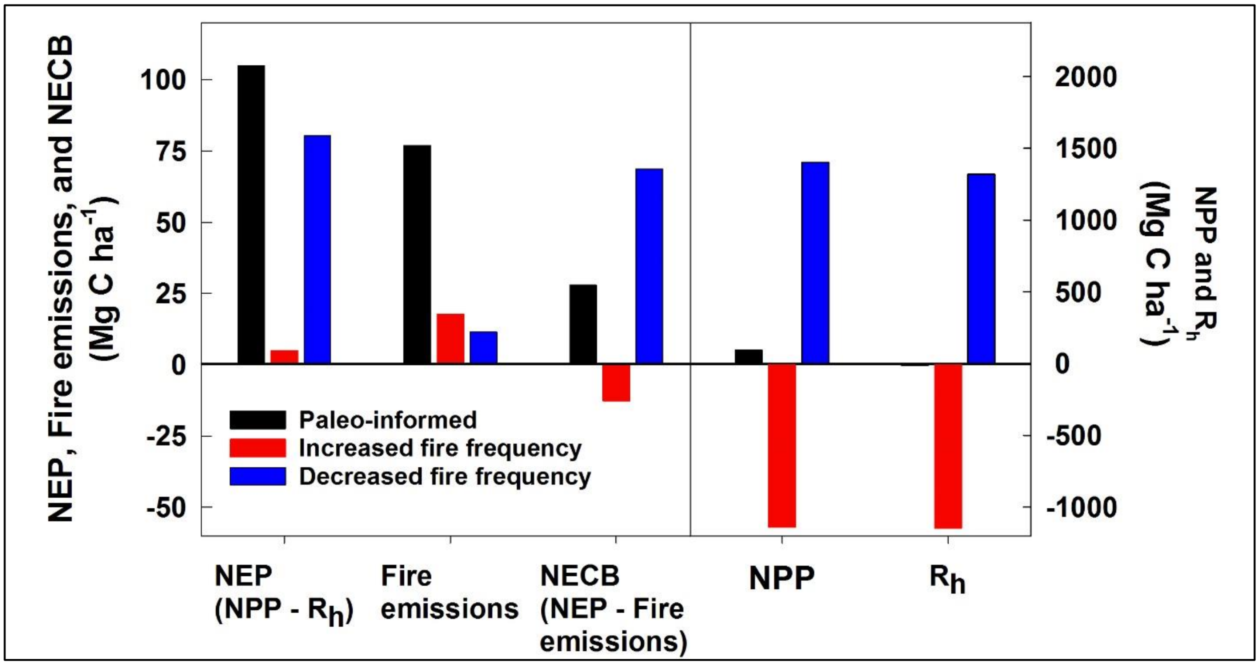

Figure 3. Accumulated anomalies in fluxes relative to equilibrium scenario, in Mg C ha^{-1}, summed over the entire 4561-year simulation period. NEP, fire emissions, and NECB (left y-axis) and NPP and Rh (right y-axis) for the paleo-informed (black), increased fire frequency (red; 155 year mean FRI), and decreased fire frequency (blue; 90 year mean FRI) scenarios. Negative (positive) numbers indicate a decrease (increase) in total carbon flux compared to the equilibrium scenario.

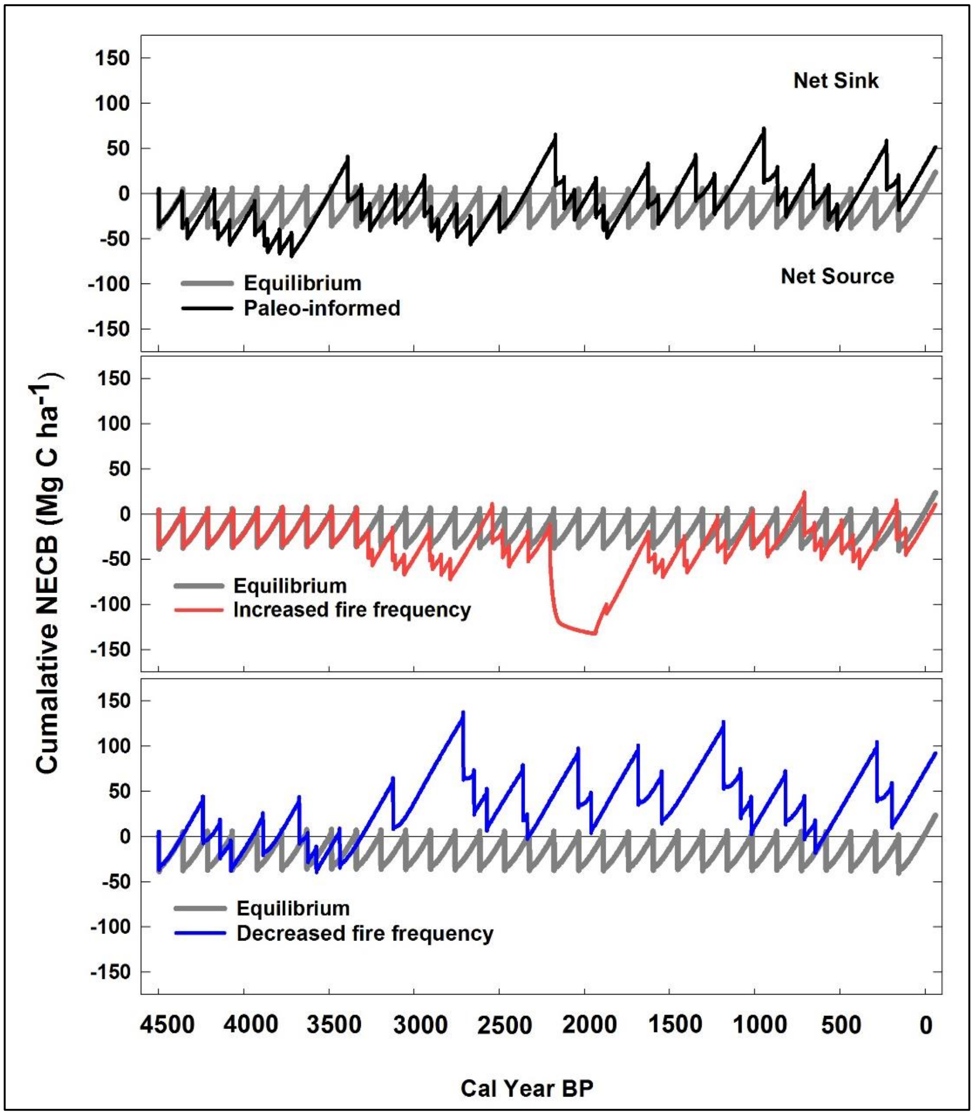

Figure 4. Trends in cumulative net ecosystem carbon balance (NECB) over time for the paleo-informed, increased fire frequency, and decreased fire frequency scenarios compared to equilbrium over the last 4561 years. Positive numbers indicate a cumulative net sink while negative numbers indicate a cumulative net source.

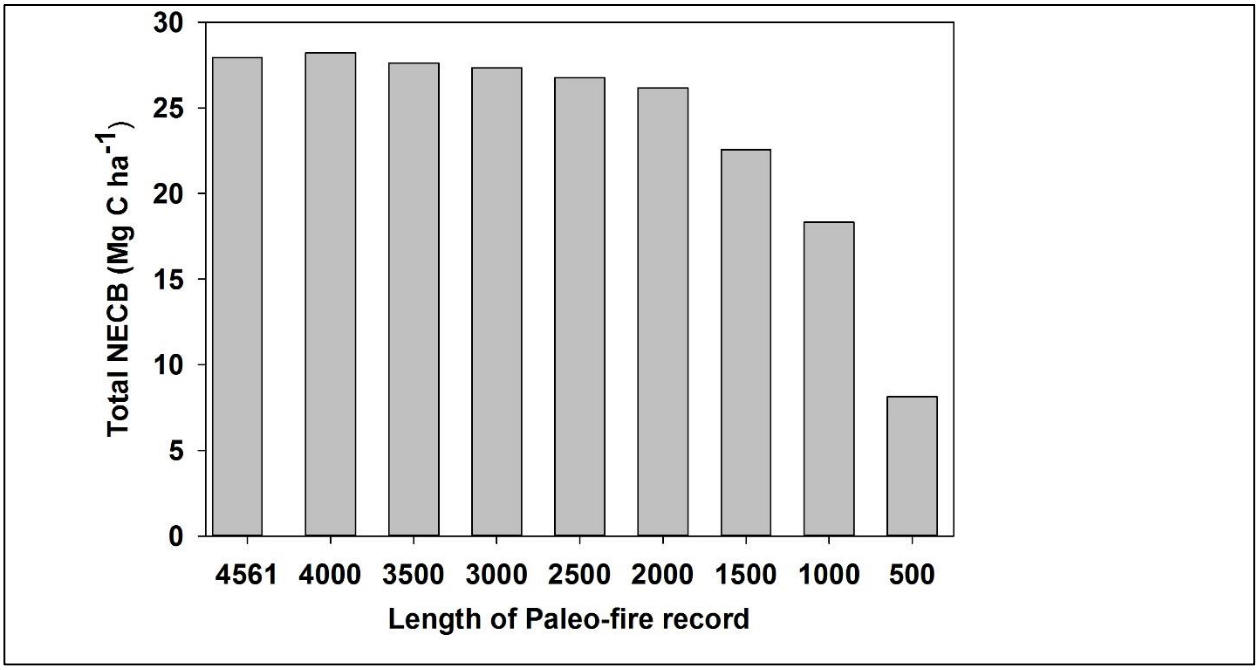

Figure 5. Total NECB (NPP - Rh - fire emissions) for the 4561-year simulated period and for each of the partially paleo-informed scenarios (Paleo_500, Paleo_1000, etc. in Figure 1). Each partially paleo-informed scenario branches from the equilibrium scenario in the year indicated on the x-axis. For example, the 500-year record only includes fires that occurred in the most recent 500 years of the paleo-fire record (1511-2010 CE).