

**Point-by-point Response**

\* Reviewer comments in italics, author responses in regular text.

**Reviewer #1 (G. Retallack)**

- 1) *This is an excellent paper comparing seasonality changes in paleoclimate through the Paleocene-Eocene thermal maximum, and finding that the greenhouse spike did not have an equable climate compared with before and afterward, as some have predicted. This is an important qualification for understanding climatic change in a higher CO<sub>2</sub> world, in emphasizing seasonality of temperatures rather than averages. This paper is excellent and publishable with minor revision. I am familiar with most of the methods deployed and consider them skillfully applied to the problem. The authors have a high level of technical competence and understanding of limitations of each method.*

We would like to thank Dr. Retallack for his time in reviewing our manuscript, and for the positive evaluation of our work and its importance within the context of research into greenhouse periods.

- 2) *My main reservation is that I do not agree that the difference (ca 4°C) in temperature seasonality of the greenhouse spike compared with the times before and afterward is significant, given standard errors on the various proxies. I consider the temperature seasonality before, during, and afterward statistically indistinguishable. This is not quite the same as the interpretation given, but does make their point that greenhouse spike temperatures were far from equable.*

We too were concerned about the significance of the trend across the peak EECO due to the larger error inherent in these measurements, however we believe we have addressed this concern via the combination of 1) averaging larger numbers of replicates (e.g., Fernandez et al., 2017), and 2) applying common statistical tests (e.g., uncertainty of difference). By binning our temperature data into “peak” and “non-peak” periods we allow for larger datasets in calculating a mean value, which leads to lower error in the estimation of those means (Fernandez et al., 2017). Thus, our mean estimates for the two periods has a lower error than any individual estimate from the record. Additionally, we applied an uncertainty of difference test to these two populations, and find that the difference between the two populations is greater than the uncertainty, suggesting that the two populations are statistically distinguishable and not a result of high uncertainty (as describe in Section 4.2). We do also agree with Retallack that regardless of whether the peak EECO has a higher MART than the non-peak period, both periods suggest that greenhouse conditions do not lead to “equability” of seasonality, which is our primary conclusion.

- 3) *A minor quibble, is that my understanding of nearest living neighbor and other paleobotanical estimates of paleoclimates rely on an adequate number of species in the assemblage (usually at least 30 species). The number of taxa in each assemblage should be reported, perhaps most conveniently in the figure.*

We agree with Retallack that the number of taxa is an important consideration for examining the climatic tolerances of assemblages, and will add this information to Figure 3 before final publication of the manuscript. The number (and type) of taxa for each assemblage was previously reported in the supplemental information (Table C1), but should also have been included in the manuscript itself.

Reviewer #2 (N. Barbolini)

- 1) *This manuscript is a significant contribution to the field, combining multiple temperature proxies in an interdisciplinary fashion to reconstruct climatic ranges over the EECO. Bringing the focus onto detecting seasonality in the fossil record provides a more nuanced representation of past climates. Palaeobotanical temperature reconstructions are performed using the latest, statistically rigorous methodology, and an important synthesis on state-of-the-art is included. The presentation and quality of the work are excellent. The figures are well illustrated and comprehensive.*

We would like to thank Dr. Barbolini for her time in reviewing our manuscript, and for the positive evaluation of our work and its importance within the context of paleoclimate reconstructions.

- 2) *It is a pity that no CMMT (floral) data are available for the peak EECO. In order to represent this more realistically, I suggest modifying the straight line joining the two CMMT data points, separated by more than 2 Mya, in Figure 4. It could be represented either by a dotted line explained in the figure caption as an aliased signal, or omitted completely.*

We agree that it is unfortunate that there are no known preserved floral assemblages in this region during the peak EECO. As suggested, we will modify Figure 4 before final publication to include a dashed line between the youngest two assemblages, and will update the figure caption to explain the possibility of an aliased signal during this extended period.

- 3) *Other relevant points have already been raised by the other reviewer and resolved by the authors. The manuscript is publishable subject to this and the following technical corrections:*

*Line 89: "The GRB sequence is comprised of a series of terrestrial clastic...": Correct to either "sequence is composed of" or "sequence comprises".*

We have updated the manuscript text to read "sequence is composed of" as per the reviewer.

*Supplemental Table C.1: a) The heading "Floral group" should change to "Taxa"; b) when taxa are only identifiable to genus level, "sp." should be reformatted without italics (e.g. *Sabalites* sp.); c) taxa could be ordered alphabetically for easier future comparisons of floral lists.*

We agree with points A and B of the suggested changes to this supplemental table, and will update Table C.1 before final publication. With regard to point C, we list taxa in Table C.1 in this order to maintain the format of the originally published floral lists from these sites (Wilf, 2000), as we believe this will minimize confusion in future comparisons which may include both works. This original format lists taxa in order of abundance at each locality, an observation that we will add to the descriptive text of the table before final publication.

### Reviewer #3 (Anonymous)

*The manuscript 'Temperature seasonality in the North American continental interior during the early Eocene climatic optimum' by Hyland et al. presents new clumped isotope, soil geochemistry and paleofloral data from a section spanning the EECO from the Green River Basin. The authors use these proxies to reconstruct both mean annual, winter, and summer temperatures, and therefore to reconstruct Eocene seasonality in this region, and how seasonality changed over the EECO. Perhaps the most interesting finding is that seasonality during the peak EECO was similar to today, calling into question the hypothesis that past greenhouse intervals such as this were characterised by an 'equable' climate (warm/hot, but low seasonality). The data are interesting, and the subject of Eocene climate is certainly of relevance to a wide number of researchers across several disciplines. Therefore, the manuscript would certainly be suitable for Climate of the Past.*

We would like to thank the reviewer for their time in reviewing our manuscript, and for the positive evaluation of our work and its relevance for multiple disciplines.

### *Substantive Comments*

*Overall the authors do an excellent job of considering the uncertainties in the proxies utilised here, and as such I recommend that there should be clarification in the discussion of what is being reconstructed. My main issue is that there are no data on cold month mean temperature (CMMT) for the EECO, such that seasonality, i.e. the difference between WMMT and CMMT, is assumed to be twice the difference between mean annual temperature (MAT) and WMMT. The authors are honest about this (Tab. 1), and I agree that it is encouraging that MAT falls approximately midway between CMMT and WMMT in the pre-peak-EECO interval, but there is no a priori reason to assume that CMMT did not increase disproportionately during the EECO, and as such EECO seasonality is not really constrained here. I recommend rewording the abstract, discussion and conclusions accordingly.*

We fully understand and discuss the fact that we do not have CMMT estimates for this whole period (as shown in Figure 4 and Table 1); however, we disagree that this means "EECO seasonality is not really constrained here". We argue that the applied method of calculating MART as twice the difference between WMMT and MAT is robust for multiple reasons: 1) this calculation is common practice for estimating seasonality, and has been shown to be robust in comparisons to both paleobotanical and model-derived estimates (Snell et al., 2013; Suarez et al., 2017; Kelson et al., 2018); 2) as described in this work (Section 4.2), for periods where CMMT results do exist, the two methods (WMMT-CMMT and  $2 \times [WMMT - MAT]$ ) produce statistically indistinguishable results; and 3) calculations from modern environments worldwide using ERA-Interim climate reanalysis outputs consistently show that for all vegetated land surfaces, the difference between MART calculations derived from these two methods is  $< 1^\circ\text{C}$  (Burgener et al., in review). As a result, we believe that seasonality is indeed constrained by our chosen method for both the peak and non-peak EECO in this work, and therefore do not rewrite the Abstract/Discussion/Conclusions (except to improve clarity on this point).

*I found the discussion of seasonality under future climate scenarios to be a distraction from the rest of the manuscript. My suggestion would be to deal with this topic separately given that the Eocene data do*

*not necessarily inform us of the accuracy of the CMIP5 model ensemble into the future. A more interesting comparison, if the data are available, would be to compare these seasonality reconstructions to the EoMIP model ensemble rather than RegCM3 alone (which would also allow some uncertainty to be placed on the model seasonality).*

We believe that the comparison to seasonality under future climate scenarios is a key implication for this work, and that the inclusion of this comparison is important for piquing interest in the continued study of seasonality as part of understanding other climate regimes. We agree that it should not distract from the Eocene work, which is why we have limited discussion of that comparison to its own section at the end of the manuscript (Section 4.3). We do not intend for the Eocene data to inform about the accuracy of CMIP5 models (indeed we do not think that appropriate), merely to show that both sources suggest similar patterns of increased seasonality under greenhouse conditions. While we agree that comparing our Eocene data or reported CMIP5 results to an Eocene ensemble such as EoMIP would be ideal, the output for such a comparison does not currently exist. The reason we chose to use the RegCM3 regional model is that it provides high spatial resolution over this region (50 x 50 km), allowing us to make an accurate comparison of GRB proxy data with a model of the GRB itself. While the models of the EoMIP ensemble perform well on a global scale, their grid cell size is far too large (3.75 x 2.5°) to capture the characteristics of this continental region, and thus would be inappropriate for this work. Future work examining seasonality on a broader scale using data from multiple localities could certainly benefit from comparisons to the EoMIP ensemble, however we believe this is beyond the scope of our current study.

#### *Minor Comments*

*Section 2.1.1. For people like me, who are not familiar with the details of the use of soil geochemistry as a paleoclimate indicator, it would be useful to include a few sentences on how robust this proxy is to diagenetic alteration (e.g. through interaction with groundwater).*

As suggested by the reviewer, we have added text to Section 2.1.1 describing the robustness of soil geochemical proxies, which have been widely tested in a large number of environments and on timescales spanning the Cenozoic and beyond (Sheldon and Tabor, 2009 and references therein).

*Line 167. Please specify what you mean by ‘are corrected’ in this sentence. Do you mean that following the PBL correction the  $\delta 47\text{-}\Delta 47$  slope is also used to make a correction? If so, what is the gradient?*

Yes, we mean that we follow the common practice of using the slope of heated and water equilibrated CO<sub>2</sub> to normalize values (Huntington et al., 2009) and place them into the ARF (Dennis et al., 2011). The slopes of these lines are reported in the supplement (Tables B.1 and B.2), and we have added a reference to this in the text.

*Lines 177-180. Please clarify these sentences. The Kelson equation would certainly result in significantly different temperatures compared to at least some other calibrations [e.g. Zaarur et al., 2012], depending on what is meant by ‘moderate’. And why preliminary?*

We have updated the text to clarify the term “moderate” (20–40°C). We use the term “preliminary” because few data have been published using this calibration and direct comparison of estimates using multiple calibrations is uncommon. However, we are confident that this calibration is the most appropriate for our data and addresses many previous issues with discrepant calibrations (e.g., Zaarur et al., 2013; see Kelson et al., 2017).

*Section 2.2. The introduction and description of the model results is extremely brief which is ok given that these data are previously published (although a few more details would be helpful), but what I did miss was an explanation of why this model was chosen for comparison. Why not one (or the ensemble) of EoMIP simulations?*

We did not describe the models in detail because, as noted, each has been previously published. We have added text explaining where further information on each model may be located. Additionally, we have added text explaining why this Eocene model was chosen over the EoMIP ensemble (because the regional model provides better resolution over the GRB domain).

*Line 317. It would be useful to elaborate on what is meant by ‘isotopic data’. Is it that the clumped isotope results look reasonable, or do you mean calculated  $\delta^{18}\text{O}_w$  look reasonable? If the latter, state what these are in the text in this paragraph (perhaps around lines 323-326).*

We have modified the text to clarify that we were referring to clumped isotope data here. Additionally, we include a reference to Table B.1 in the subsequent sentence, which contains the data discussed in the  $\delta^{18}\text{O}_w$  comparison as well.

*Lines 363-366. This sounds encouraging except that a  $\pm 3^\circ\text{C}$  uncertainty in both WMMT and CMMT results in a seasonality uncertainty of  $6^\circ\text{C}$ , given that presumably there may be systematic biases across the reconstructed interval?*

We believe that the true error on these estimates is likely much smaller than the reported uncertainty of  $\pm 3^\circ\text{C}$ ; as explained in the text, we arrive at this uncertainty by doubling the calculated uncertainty (95% CI) for these measurements in order to account for any unforeseen systematic biases in the method or assemblages themselves. Regardless, if we assume that this maximum error is possible, this results in an MART uncertainty of up to  $6^\circ\text{C}$ , which still predicts higher ( $>20^\circ\text{C}$ ) MART during the early Eocene than previous work, as discussed at the end of Section 4.2.

*Section 4.2. Somewhere near the beginning of this section please state how EECO and pre-EECO seasonality were calculated. Are the seasonality estimates derived by comparing the mean of (e.g.) all CMMT data to the mean of all WMMT data for that interval? Judging by eye, there seems to be no difference between EECO and pre-peak-EECO MAT and WMMT if all the data are averaged.*

We agree that Section 4.2 lacked a description of how these values were calculated, and have added text to explain that the MART estimates for peak and non-peak intervals are derived by averaging all

WMMT and MAT (and CMMT) data for each interval (e.g., Table 1). As discussed in Section 4.2, these do produce different estimates that appear to be statistically distinct.

*Lines 397-398. It was not clear to me the first time I read this whether the numbers in brackets refer to the modern or Eocene seasonal range, especially on line 397, reword for clarity.*

Rearranged for clarity, as per reviewer.

*Lines 396-401. As you state earlier, both MAT and WMMT may be cool-biased though, so the agreements and uncertainties discussed here only apply if this is not the case. Consider reemphasising this.*

Cool-biasing in the paleobotanical records is often minimal (possibly 2–4°C; Kowalski and Dilcher, 2003), and any effect would likely impact both WMMT and MAT records, resulting in either no or a slight positive change in overall MART. Thus, it is unlikely to impact how well these proxy records and models agree, and any difference would make low MART values even less likely, further strengthening our argument that seasonality was not reduced during the early Eocene. The text of Section 4.2 has been updated to emphasize this, as per the reviewer.

*Lines 433-435. This sentence is worded too strongly. There are no reconstructions of CMMT during the EECO, but moreover the WMMT proxy in the EECO is different to the WMMT proxy in the pre-peak-EECO interval. This latter issue is especially problematic given that the clumped and paleobotanical evidence are not in agreement in the interval for which both are available. I fully sympathise with the authors in that continental climates are difficult to reconstruct, and as I said before, the recognition and discussion of uncertainties in this manuscript is excellent overall. However, I recommend stating these issues more clearly at this point in the text including a more thorough discussion of whether the peak and pre-peak EECO seasonalities are really distinguishable from each other.*

While we agree that it would be ideal to have both types of proxy data throughout this interval, the WMMT proxy is not entirely different for these periods, as clumped isotope data exists for both the peak and non-peak parts of the EECO (Figure 4). We fully discuss the relative uncertainties in both types of WMMT estimates (Section 4.1), and while it is possible that the observed trend of expanded MART during the peak EECO may be related to a lack of CMMT data for the interval, the consistency of both types of MART reconstruction (WMMT-CMMT and  $2 \times [\text{WMMT} - \text{MAT}]$ ) outside of the peak period suggests this trend is real (see response above). We have added text explaining this in greater detail (Section 4.3). Assuming these reconstructed MARTs are robust, statistical tests show that the peak and non-peak periods really are distinct (see comments above; Section 4.2).

*Figure 4. Either remove the left half of the peak EECO bar at the bottom of the figure or shade it white so that it is clear that this has not been reconstructed. Please clarify whether the tick marks represent the*

*midpoint between CMMT and WMMT or whether they are placed at the location of the mean MAT estimates.*

We have not removed the peak EECO bar as suggested because we argue that while this work does not directly reconstruct CMMT for that period, it is appropriate to reconstruct MART as twice the difference between MAT and WMMT (see response above). Thus, the full range should be represented on the figure as shown. As described in the figure caption, the vertical tick marks on MART represent the estimated MAT value, which coincidentally is very near to the statistical “midpoint”.

*Supplement. Please given ages with all reconstructions and not just heights, or at the very least state at which heights the peak EECO occurred.*

Not all samples have been assigned absolute ages; however, the supplement has been updated as per reviewer to indicate where in the stratigraphy “peak EECO” has previously been interpreted (Hyland and Sheldon, 2013; Hyland et al., 2017).

*Line 122 ‘elements’.*

Corrected as per reviewer.

**List of Relevant Changes**

Manuscript:

**Manuscript** text has been updated as described in the author's responses (see above) and detailed in the "marked-up" version of the manuscript (see below).

Figures:

**Figure 3** has been updated to include the number of species used in the calculation of temperatures for each floral assemblage (as per Reviewer #1).

**Figure 4** (and corresponding caption) has been updated to include a dashed line between the youngest two floral assemblages in order to indicate the possibility of an aliased signal due to the duration of this data gap (as per Reviewer #2).

Supplement:

**Table A.1** has been updated to include references to the original stratigraphy and the relationship between "peak" and "non-peak" EECO intervals (as per Reviewer #3).

**Table B.1** has been updated to include references to the original stratigraphy and the relationship between "peak" and "non-peak" EECO intervals (as per Reviewer #3).

**Table C.1** has been updated for terminology and reformatted for clarity (as per Reviewer #2).



# 1 Temperature seasonality in the North American continental 2 interior during the early Eocene climatic optimum

3 Ethan G. Hyland<sup>1,2\*</sup>, Katharine W. Huntington<sup>1</sup>, Nathan D. Sheldon<sup>3</sup>, Tammo Reichgelt<sup>4</sup>

4 <sup>1</sup> Department of Earth & Space Sciences, University of Washington, Seattle, WA 98195

5 <sup>2</sup> Department of Marine, Earth & Atmospheric Sciences, North Carolina State University, Raleigh, NC 27695

6 <sup>3</sup> Department of Earth & Environmental Sciences, University of Michigan, Ann Arbor, MI 48104

7 <sup>4</sup> Lamont Doherty Earth Observatory, Columbia University, Palisades, NY 10964

8 Correspondence to: Dr. Ethan G. Hyland (ehyland@ncsu.edu)

9

10 **Abstract.** Paleogene greenhouse climate equability has long been a paradox in paleoclimate  
11 research. However, recent developments in proxy and modeling methods have suggested that  
12 strong seasonality may be a feature of at least some greenhouse periods. Here we present the first  
13 multi-proxy record of seasonal temperatures during the Paleogene from paleofloras, paleosol  
14 geochemistry, and carbonate clumped isotope thermometry in the Green River Basin (Wyoming,  
15 USA). These combined temperature records allow for the reconstruction of past seasonality in  
16 the continental interior, which shows that temperatures were warmer in all seasons during the  
17 peak early Eocene climatic optimum and that the mean annual range of temperature was high,  
18 similar to the modern value (~~~25~~26°C). Proxy data and downscaled Eocene regional climate  
19 model results ~~actually~~ suggest ~~stronger~~amplified seasonality during greenhouse events, ~~and the~~  
20 ~~increased~~, Increased seasonality ~~indicated during~~reconstructed for the early Eocene is similar in  
21 scope to the higher seasonal range predicted by downscaled climate model ensembles for future  
22 high-CO<sub>2</sub> emissions scenarios. Overall, these data and model comparisons have  
23 ~~important~~substantial implications for understanding greenhouse climates in general, and may be

~~crucial~~important for predicting future seasonal climate regimes and their impacts in continental regions.

## 1. Introduction

The Paleogene was the last major greenhouse period in Earth's history and is characterized by extreme warming events and resultant biological shifts (e.g., Greenwood and Wing, 1995; Wilf, 2000; Zachos et al., 2001, 2008; McInerney and Wing, 2011), with prolonged warmth during the early Eocene climatic optimum (EECO) peaking from roughly 52 – 50 Ma (e.g. Zachos et al., 2008; Hyland et al., 2017). The early Eocene in general is thought to represent a warm and “equable” global climate state with high mean annual temperatures (MAT; e.g., Wilf, 2000; Zachos et al., 2008), low mean annual range of temperatures (MART; e.g., Wolfe, 1978, 1995; Greenwood and Wing, 1995), and low pole-to-equator temperature gradients (LTG; e.g., Spicer and Parrish, 1990; Greenwood and Wing, 1995; Evans et al., 2018). While high MAT during the Eocene now seems well established, the feasibility of “equable” conditions defined by low MART and low LTG is still in question as a result of increasingly complex global climate models which are unable to reproduce such conditions (e.g., Barron, 1987; Sloan and Barron, 1990; Sloan, 1994; Huber and Caballero, 2011; Lunt et al., 2012).

Recent proxy work on Paleogene warm intervals and hyperthermals such as the Paleocene-Eocene thermal maximum (PETM) has suggested that continental interiors may maintain higher or near-modern MART during these periods, implying that the “low seasonality” aspect of climate equability may not be reasonable under all greenhouse conditions (e.g., Snell et al., 2013; Eldrett et al., 2014). Despite this suggestion, it remains unclear whether proxy estimates from other basins, regions, and greenhouse periods can be reconciled with the range of feasible conditions provided by climate model studies. Quantitative ~~predictions~~reconstructions of

48 seasonality (MART) based on precise proxy estimates of mean annual temperature (MAT),  
49 warm month mean temperature (WMMT), and cold month mean temperature (CMMT) could  
50 help to resolve some of these model-proxy discrepancies by providing a robust and well-  
51 constrained set of seasonal observations for comparison to available climate model outputs;  
52 ~~which is.~~ Robust proxy reconstructions of seasonality are crucial for understanding this aspect of  
53 past greenhouse equability (Lunt et al., 2012; Snell et al., 2013; Peppe, 2013).

54 Seasonality estimates have previously been made using a variety of proxy  
55 paleothermometers in isolation, and can now be made with higher confidence using recently  
56 developed methods that target each of these individual temperature parameters: MAT can be  
57 estimated using a paleosol geochemistry-based thermometer, WMMT can be estimated using the  
58 carbonate clumped isotope ( $\Delta_{47}$ ) thermometer, and CMMT can be estimated using a nearest  
59 living relative (NLR) floral coexistence thermometer. The bulk major-element geochemistry of  
60 modern soils has been used to quantify the effects of weathering processes via a wide range of  
61 geochemical indices (see Sheldon and Tabor, 2009). The relationship between modern climate  
62 parameters like temperature and indices such as salinization (Sheldon et al., 2002), the paleosol  
63 weathering index (Gallagher and Sheldon, 2013), and the paleosol-paleoclimate model  
64 (Stinchcomb et al., 2016) has ~~lead~~ed to the development of climofunctions for MAT ~~which that~~  
65 have been used to estimate paleo-MAT during the Cenozoic (e.g., ~~Hyland and Sheldon, 2013;~~  
66 ~~Gallagher and Sheldon, 2013~~Retallack, 2007; Takeuchi et al., 2007; Bader et al., 2015;  
67 Stinchcomb et al., 2016). The clumped isotope ( $\Delta_{47}$ ) thermometer is based on the temperature-  
68 dependent relative enrichment of multiply substituted isotopologues of  $\text{CaCO}_3$  ( $^{13}\text{C}^{18}\text{O}^{16}\text{O}_2$ )  
69 within the solid carbonate phase, which is independent of the isotopic composition of the water  
70 in which the carbonate precipitated (e.g., Ghosh et al., 2006; Eiler, 2007). For pedogenic

carbonates in temperate regions, this growth temperature is linked to mean warm season soil temperatures (e.g., Quade et al., 2013; Hough et al., 2014), and has been used to estimate paleo-WMMT during the Cenozoic (e.g., Snell et al., 2013; Garzione et al., 2014). The nearest living relative (NLR) coexistence method has been developed based on the sensitive and highly conserved collective modern cold temperature tolerances of related floras to calculate cold month temperatures (e.g., Wolfe, 1995; Mosbrugger and Utescher, 1997). Those relationships have been refined and used to estimate quantitative paleo-CMMT during the Cenozoic (e.g., Greenwood et al., 2005; Thompson et al., 2012; Eldrett et al., 2014; Utescher et al., 2014; Greenwood et al., 2017).

Here we employ a multi-proxy approach using paleosol geochemistry, clumped isotope, and floral NLR coexistence thermometry methods from the same localities in order to address seasonality in the past, specifically applying it to the issue of early Eocene greenhouse equability in the North American continental interior. We estimate MAT, WMMT, and CMMT throughout the EECO including both defined peak (~51 Ma) and non-peak conditions (e.g., Hyland et al., 2017), and compare the resultant proxy estimates of temperature seasonality (MART) to the modern climate state of the region, as well as to downscaled climate model predictions of temperature seasonality during the Eocene and for future emissions scenarios.

## 2. Methods

The targeted early Eocene locality is the Green River Basin (GRB) in southwestern Wyoming (USA; Figure 1). The GRB sequence is ~~comprised~~composed of a series of terrestrial clastic rocks deposited during the early Eocene and EECO as a result of Laramide synorogenic fluvial and lacustrine sedimentation along the margin of endorheic paleo-lake Gosiute (e.g.,

94 Clyde et al., 2001; Smith et al., 2008, 2010, 2015). Contemporaneous multi-proxy records of  
95 peak and non-peak conditions during the EECO are from the interfingering Wasatch Formation,  
96 primarily fluvial sandstones and paleosols of the Ramsey Ranch and Cathedral Bluffs Members,  
97 and Green River Formation, primarily lacustrine shales and carbonates of the Wilkins Peak  
98 Member (Figure 1). The paleosols and pedogenic carbonates were sampled from the Honeycomb  
99 Buttes near South Pass, Wyoming (42.24°N, 108.53°W; Hyland and Sheldon, 2013), while the  
100 floral assemblages were sampled from the Latham coal (41.68°N, 107.88°W), Sourdough coal  
101 (41.91°N, 108.00°W), Niland Tongue (41.06°N, 108.77°W), and Little Mountain quarry  
102 (41.28°N, 109.30°W) outside Rock Springs, Wyoming (Figure 1; Wilf, 1998; 2000).

103

## 104 **2.1 Temperature proxies**

105

### 106 **2.1.1 Paleosol geochemistry**

107 The bulk major-element geochemistry of modern soils (specifically B horizons) has been  
108 used extensively to develop a number of composition-climate relationships, including those  
109 predicted by the paleosol-paleoclimate model (PPM<sub>1.0</sub>), which relates a broad suite of major  
110 element compositions to mean annual temperature (among other factors) at the site of soil  
111 formation (Stinchcomb et al., 2016). Stinchcomb et al. (2016) developed this nonlinear spline  
112 model using the largest available geochemical dataset from 685 modern soils across North  
113 America in order to derive proxy relationships between 11 major and minor oxides and MAT.  
114 This new proxy is calibrated over a wider range of climatic conditions, soil types, and parent  
115 materials than other available proxies (c.f., Sheldon et al., 2002; Gallagher and Sheldon, 2013),  
116 and has been validated via independent comparisons in both modern climosequences

(Stinchcomb et al., 2016) and Miocene paleosols (Driese et al., 2016). Following associated procedures, our bulk paleosol samples from selected upper Bt horizons of defined Alfisols (described in detail by Hyland and Sheldon, 2013) were prepared for major-element geochemistry by cleaning and grinding to a homogenous powder. Samples were analyzed using lithium borate fusion preparation and X-ray fluorescence (XRF) measurements at ALS Chemex Laboratory (Vancouver, BC), where analytical uncertainty for analyses was maintained at less than 0.1% for all elements, and replicate analyses had a mean standard deviation of 0.8% (Table A.1). Resultant major and minor ~~elements~~element data were not corrected for loss-on-ignition (e.g., Stinchcomb et al., 2016), and were input into the open-access PPM<sub>1.0</sub> model, which produces “low”, “best” and “high” MAT estimates; we present the “high” estimates as MAT here (~~Table A.1~~–see Section 4.1 for explanation; Table A.1). Broadly, soil geochemical proxies are consistent with other paleoclimate proxies (e.g., paleobotanical; Sheldon and Tabor, 2009 and references therein), and are more robust to diagenetic alteration under a wide variety of burial conditions (Hyland and Sheldon, 2016).

### 2.1.2 Clumped isotope geochemistry

The clumped isotope ( $\Delta_{47}$ ) thermometer is based on the theoretical temperature dependence of the overabundance of multiply substituted carbonate ion isotopologues (primarily  $^{13}\text{C}^{18}\text{O}^{16}\text{O}_2^{-2}$ ) within the solid carbonate phase, which is independent of the isotopic composition of the waters from which the carbonate precipitated (e.g., Schauble et al., 2006; Ghosh et al., 2006; Eiler, 2007). The enrichment of “clumped” isotopologues relative to the abundance expected for a random distribution of isotopes among isotopologues ( $\Delta_{47}$ ) varies with the growth temperature of the sampled carbonate (e.g., Ghosh et al., 2006; Dennis et al., 2011; Zaarur et al.,

140 2013; Kluge et al., 2015; Kelson et al., 2017). Clumped isotope thermometry of soil carbonates is  
141 a useful paleoenvironmental proxy in continental settings (e.g., Eiler, 2011; Quade et al., 2013),  
142 and studies of recent pedogenic carbonates indicate that their clumped isotope values record  
143 environmental temperature conditions during mineral growth. The timing of pedogenic carbonate  
144 growth is controlled by a combination of soil moisture, CO<sub>2</sub>, temperature, and other factors over  
145 10<sup>2</sup>–10<sup>4</sup> years (e.g., Cerling, 1984; Cerling and Quade, 1993; Breecker et al., 2009; Zamanian et  
146 al., 2016), and clumped isotope analyses show corresponding variability in recorded  
147 temperatures (e.g., Peters et al., 2013; Hough et al., 2014; Burgener et al., 2016; Ringham et al.,  
148 2016; Gallagher and Sheldon, 2016). However, for pedogenic carbonates forming in forest soils  
149 from mid-latitude regions, this growth temperature has been shown to be linked to mean warm  
150 season soil temperatures in most settings (e.g., Breecker et al., 2009; Passey et al., 2010; Quade  
151 et al., 2013; Garzzone et al., 2014; Hough et al., 2014; Ringham et al., 2016), and has been used  
152 to estimate paleo-WMMT during the Cenozoic (e.g., Suarez et al., 2011; Snell et al., 2013;  
153 Quade et al., 2013; Garzzone et al., 2014).

154 Pedogenic carbonate nodules from selected Bk horizons (paleosol depths ~20–240 cm)  
155 were thin-sectioned and analyzed under transmitted light and cathodoluminescence to identify  
156 primary micritic carbonate (Figure 2), which was microdrilled/homogenized for clumped isotope  
157 (Δ<sub>47</sub>) analysis. Extremely shallow (<50 cm) or deep (>200 cm) carbonates were analyzed  
158 specifically to examine temperature depth profiles in paleosols (Figure 2), while pedogenic  
159 carbonates from commonly sampled depths (50–200 cm; e.g., Cerling, 1984; Koch, 1998;  
160 Zamanian et al., 2016) were used for calculating and interpreting paleotemperature records.  
161 Powdered samples and carbonate standards were analyzed in replicate at the University of  
162 Washington's IsoLab, following methods of Burgener et al. (2016) and Kelson et al. (2017),

163 which are modified after Huntington et al. (2009) and Passey et al. (2010). Briefly, CO<sub>2</sub> is  
164 produced from 6–8 mg of pure carbonate reacted in a common phosphoric acid bath (~105%  
165 H<sub>3</sub>PO<sub>4</sub>) at 90°C. Evolved CO<sub>2</sub> is then cleaned via passage through a series of automated  
166 cryogenic traps and a cooled (-20°C) Poropak Q column using helium carrier gas through a  
167 nickel and stainless steel vacuum line, and the purified CO<sub>2</sub> is transferred to Pyrex break seals.  
168 Each sample is then analyzed on a Thermo MAT253 mass spectrometer equipped with an  
169 automated 10-port tube cracker inlet system and configured to measure m/z 44–49, using data  
170 acquisition methods and scripts presented by Schauer et al. (2016).

171 All analyses include an automatically-measured pressure baseline (PBL; He et al., 2012),  
172 are corrected using heated gas (1000°C; Huntington et al., 2009) and CO<sub>2</sub>-water equilibration  
173 (4°C, 60°C) lines during the corresponding analysis period, [\(Table B.1\)](#), and are reported in the  
174 absolute reference frame (ARF; Dennis et al., 2011). Following recent work (Daëron et al., 2016;  
175 Schauer et al., 2016), mass spectrometer data are corrected using the <sup>17</sup>O correction values  
176 recommended by Brand et al. (2010). Carbonate standards for these analyses include  
177 international standards NBS-19 and ETH-2, as well as internal standards C64 and COR, which  
178 are all reported relative to VPDB (δ<sup>13</sup>C, δ<sup>18</sup>O) and ARF (Δ<sub>47</sub>) in *Table B.1*. All samples were  
179 analyzed in replicate (3–5) to minimize standard analytical error, and data were reduced  
180 following Schauer et al. (2016). Carbonate growth temperatures (T[Δ<sub>47</sub>]) were calculated using  
181 the most current and extensive inorganic calcite calibration (Kelson et al., 2017), which was  
182 produced using the updated <sup>17</sup>O correction values of Brand et al. (2010) and is consistent with  
183 our analytical methods. Based on preliminary comparisons, the Kelson et al. (2017) calibration  
184 produces results not significantly different from data calculated using previous calibrations at



moderate Earth-surface temperatures (~~~20–40°C~~; Daëron et al., 2016; C. John and M. Daëron, pers. comm., 2016; *Table B.1*).

### 2.1.3 Floral coexistence analysis

Floral physiognomy and floral coexistence techniques are often applied in concert to arrive at terrestrial paleoclimate estimates (e.g. Spicer et al., 2014; Reichgelt et al., 2015; West et al., 2015). While floral leaf physiognomy has been used to develop character-climate relationships for parameters like CMMT and MART (e.g., Wolfe, 1995; Wolfe et al., 1998; Wing, 1998), other work has raised questions about the reliability of modern calibrations and possible covariability of seasonal temperatures recorded by floral methods (Jordan, 1997; Peppe et al., 2010). Similar questions have been raised regarding the nearest living relative (NLR) coexistence method (Grimm and Denk, 2012; Grimm and Potts, 2016). However, recent developments have addressed these issues including: 1) improvements or revisions to NLR assignments for paleofloral assemblages (e.g., Manchester et al., 2014; SIMNHP, 2015), 2) new global datasets of modern floral distributions (e.g., TROPICOS, 2015; USDA, 2015, GBIF, 2016), 3) high-resolution linked climatic datasets (e.g., Hijmans et al., 2005), and 4) the application of more rigorous statistical analyses (e.g., Eldrett et al., 2014; Utescher et al., 2014; Harbert and Nixon, 2015). As a result of this work, bioclimatic analysis has emerged as a refined version of this approach, employing the climatic range of modern living relatives of plants found together in a fossil assemblage and statistically constraining the most likely climatic co-occurrence envelope (e.g., Greenwood et al., 2005; Thompson et al., 2012; Eldrett et al., 2014; Greenwood et al., 2017).

207 Fossil assemblages were selected from the literature (e.g., Wilf, 1998, 2000) based on  
208 temporal fit, floristic diversity, and reliable taxonomy. Fossil taxa were each attributed to a  
209 modern taxon based on nearest living relative (e.g., MacGinitie, 1969; Hickey, 1977; Manchester  
210 and Dilcher, 1982; Wolfe and Wehr, 1987; Wing, 1998; Wilf, 1998, 2000; Manchester et al.,  
211 2014; SIMNHP, 2015), with unattributed or disputed placements assigned conservatively at  
212 higher taxonomic levels (*Table C.1*). Climatic envelopes of modern groups in North America  
213 and Asia were retained for the ancient taxa based on environmental niche conservation (e.g.,  
214 Wang et al., 2010; Fang et al., 2011). Modern taxa distributions (GBIF, 2016) were linked to  
215 high-resolution gridded climatic maps (Hijmans et al., 2005) to extract MAT, WMMT and  
216 CMMT using the Dismo Package in the R Statistical Program (R Core Team, 2013). Prior to  
217 calculating climatic ranges, plant distribution coordinate files were scrutinized for: 1) plants with  
218 dubious taxonomic assignments, as not all identifications were rigorous and not all collected  
219 specimens were taxonomically assigned by experts (only species-level identifications are  
220 included); 2) plants occurring outside of their natural ranges, as many plants occur outside their  
221 adapted environment due to agricultural or aesthetic translocation; and 3) redundant occurrences,  
222 as many duplicate coordinates or researcher entries exist for the same taxon and their inclusion  
223 may skew results toward given localities.

224 Quantitative paleotemperatures were estimated using a modified bioclimatic analysis  
225 approach (e.g., Greenwood et al., 2005; Thompson et al., 2012; Eldrett et al., 2014; Greenwood  
226 et al., 2017). ~~defining overlap~~. Overlap ranges of climatic tolerances for coexisting species from  
227 each assemblage were defined by calculating probability density functions of those climatic  
228 envelopes (Figure 3 and *Table C.2*) consistent with recent work (e.g., Thompson et al., 2012;  
229 Harbert and Nixon, 2015; Grimm and Potts, 2016; Greenwood et al., 2017). In order to avoid

inclusion of apparent coexistence intervals in which no modern occurrence is recorded, we calculate the collective probability density of taxa co-occurrence for each combination of MAT (x), WMMT (y), and CMMT (z):

$$f(x|t) = \frac{1}{\sqrt{2\sigma^2\pi}} e^{-\frac{(x-\mu)^2}{2\sigma^2}} \quad (1)$$

$$f(y|t) = \frac{1}{\sqrt{2\sigma^2\pi}} e^{-\frac{(y-\mu)^2}{2\sigma^2}} \quad (2)$$

$$f(z|t) = \frac{1}{\sqrt{2\sigma^2\pi}} e^{-\frac{(z-\mu)^2}{2\sigma^2}} \quad (3)$$

$$f(x, y, z, t) = \ln \left[ \left( f(x) \times f(y) \times f(z) \right)_{t_1} \times \dots \times \left( f(x) \times f(y) \times f(z) \right)_{t_n} \right] \quad (4)$$

Calculations are repeated such that the likelihood ( $f$ ) is calculated for each climatic combination, for each taxon ( $t$ ), dependent on the number of taxa ( $n$ ), using the mean and standard deviation of each taxon (*Table C.2*). Climate input parameters were individual occurrence data points (~32,000) derived from GBIF (2016), excluding combinations unlikely to represent the climatic envelope of the taxa in the assemblage by calculating a maximum likelihood probability density function that defines a precise estimate of temperature parameters with a low standard deviation for each selected assemblage (Figure 3).

## 2.2 Modern climate data and model downscaling

The modern temperature dataset was derived from 1981–2010 averaged climate normals from National Oceanic and Atmospheric Administration (NOAA) weather observation stations within the Green River Basin ( $n = 18$ ; NCDC, 2010), defined as the area 40.5–43°N by 107–110.5°W (Figure 1). Future model temperature projection results used a 10-model ensemble from the Coupled Model Intercomparison Project Phase 5 (CMIP5) under standard low (RCP4.5)

and high (RCP8.5) emissions scenarios (IPCC, 2014); specifics of each model/configuration are available from the World Climate Research Programme (2011). Results were averaged monthly for the final 10 years of the model run (2090–2099) and calculated over the same study area using standard bias-correction and spatial downscaling (BCSD) methods developed by PCDMI (2014). Eocene model temperature results used data from a modified three-dimensional regional climate model (RegCM3; Sewall and Sloan, 2006; Pal et al., 2007) with established Eocene boundary conditions including low (560 ppm; LoCO) and high (2240 ppm; HiCO) atmospheric  $p\text{CO}_2$  scenarios (Sewall and Sloan, 2006; Thrasher ~~et al., 2009; 2010~~ and Sloan, 2009; 2010); specifics of the model configurations can be found in Thrasher and Sloan (2009). Those results were averaged for the final 20 years of the model run at equilibrium and calculated over the same study area (40.5–43°N by 107–110.5°W) by integrating data across grid cells monthly for each model year within the above defined Green River Basin (e.g., Snell et al., 2013). This particular set of Eocene model configurations was chosen because it allows for the highest available resolution over the basin domain using the best available set of boundary conditions (c.f., EoMIP; Lunt et al., 2012). All modern climate normals and model downscaling results are reported in *Table D.1*.

### 3. Results

PPM<sub>1.0</sub> statistical model results for MAT from these paleosol samples range from 13.5 to 17.6°C ( $\mu = 15.2^\circ\text{C}$ ;  $\sigma = 1.3^\circ\text{C}$ ). Uncertainty for these estimates is reported as the root mean squared error of the model fit regression ( $\pm 2.5^\circ\text{C}$ ). Petrographic observation of carbonate nodules from all depths and selected soils identified dominantly micritic textures with minor components of sub-angular quartz grains and occasional sparry ( $>20\mu\text{m}$ ) calcite veins and cements; however,

we were able to identify and micro-sample unaltered fine-grained ( $<5\mu\text{m}$ ) calcite material in each of the examined samples ( $n = 14$ ; Figure 2). Clumped isotope  $\Delta_{47}$  values for these samples range from 0.582 to 0.631‰ ( $\mu = 0.607\text{‰}$ ;  $\sigma = 0.014\text{‰}$ ), which corresponds to an estimated WMMT range of 18 to 34°C ( $\mu = 25\text{°C}$ ;  $\sigma = 4\text{°C}$ ). Uncertainty for these estimates is reported as propagated error from analytical and equilibrated  $\text{CO}_2$  reference frame uncertainty (negligible); replicate standard error ( $\mu = 0.008\text{‰}$ ) or standard error from long-term standards, whichever is larger; and calibration standard error (e.g., Kelson et al., 2017); which have a combined error averaging  $\pm 3\text{°C}$ . Clumped isotope-based temperature depth profiles in the sampled paleosols show no clear trend with depth, and estimates are mostly within error for a given paleosol (Figure 2). Nearest living relative bioclimatic analysis minimum cold tolerances for these samples range from  $-28$  to  $24\text{°C}$  ( $\mu = 6\text{°C}$ ;  $\sigma = 7\text{°C}$ ), and maximum warm tolerances range from  $10$  to  $43\text{°C}$  ( $\mu = 28\text{°C}$ ;  $\sigma = 5\text{°C}$ ). Probability density functions define bioclimatic envelopes (Figure 3) corresponding to an estimated CMMT range of  $4.2$  to  $7.6\text{°C}$  ( $\mu = 5.9\text{°C}$ ;  $\sigma = 1.2\text{°C}$ ), an MAT range of  $15.2$  to  $18.2\text{°C}$  ( $\mu = 16.5\text{°C}$ ;  $\sigma = 1.1\text{°C}$ ), and a WMMT range of  $27.9$  to  $28.7\text{°C}$  ( $\mu = 28.3\text{°C}$ ;  $\sigma = 0.3\text{°C}$ ) for the collective floral assemblages. Uncertainty for these estimates is reported as  $2\sigma$  for individual assemblage PDF distributions, which average  $\pm 2\text{°C}$ . Proxy estimates from all three methods show a trend of increasing temperatures from non-peak conditions into the peak EECO ( $\sim 51$  Ma), after which temperatures decreased back to lower values (Figure 4).

Modern climate normals averaged monthly for the GRB range from  $-8.4$  to  $18.1\text{°C}$ , with an MAT of  $4.4\text{°C}$  (Table D.1). Downscaled Eocene climate model results averaged monthly for the GRB range from  $4$  to  $24\text{°C}$  (LoCO) and  $6$  to  $30\text{°C}$  (HiCO), with MATs of  $13\text{°C}$  and  $16\text{°C}$ , respectively (Table D.1). Downscaled future climate model results averaged monthly for the

GRB range from -5.0 to 20.4°C (RCP4.5) and -2.9 to 24.7°C (RCP8.5), with MATs of 7.1°C and 10.6°C, respectively (*Table D.1*). Monthly temperature trends maintain roughly the same shape for modern observational data, future model estimates, and Eocene model estimates; ~~however,~~ However, the Eocene modeled cases show substantially higher winter temperatures, and in both modern and Eocene modeled cases the higher emission/ $p\text{CO}_2$  scenario shows an enhanced summer signal relative to the lower emission/ $p\text{CO}_2$  scenario from the same time period (Figure 5).

## 4. Discussion

### 4.1 Temperature estimates

~~Based~~ Temperature estimates from the PPM<sub>1.0</sub> spline model are based on specifically selected uppermost B horizons of paleosols with comparable parent materials. These horizons were selected based on previous work describing and sampling paleosols from the Cathedral Bluffs Member in the GRB (Figure 1; Hyland and Sheldon, 2013), and based on the characteristics of soils sampled for the paleosol paleoclimate model dataset (Stinchcomb et al., 2016), ~~we were able to specifically select uppermost B horizons of paleosols with comparable parent materials~~ 2016, in order to generate the most robust input data for the PPM<sub>1.0</sub> spline model. While the PPM<sub>1.0</sub> model produces multiple possible estimates of paleo-MAT, the estimate shown to be most reliable via concurrent comparisons with other paleotemperature methods (paleobotanical and paleosol proxies) is the “high MAT” value we present here (Michel et al., 2014; Stinchcomb et al., 2016; Driese et al., 2016). We further justify our use of the “high” estimate because the PPM<sub>1.0</sub> training dataset heavily samples soils from temperate regions

(specifically the conterminous USA) which tend to have lower MAT ( $\leq 10^{\circ}\text{C}$ ) and therefore could place excess weight on low values in the model predictive space. This sampling bias likely produces the demonstrated pattern of “best” MAT predictions generally exhibiting positive residuals (Stinchcomb et al., 2016), which means that the PPM<sub>1.0</sub> model would be more likely to skew temperature estimates from paleosol and other modern samples toward lower-than-observed MAT values. The presented mean annual temperatures appear to coincide with a statistical mean between CMMT and WMMT estimates (Figure 4), and also agree within uncertainty with independent MAT estimates from other types of paleosol geochemistry (salinization index,  $\delta^{18}\text{O}$ ; Hyland and Sheldon, 2013) and broadly with updated physiognometric (Table C.3; Wilf, 2000) and coexistence analysis paleobotanical estimates from the GRB (Figure 4).

Formatted: Not Highlight

Based on the assessment of physical and isotopic data, our sampled pedogenic carbonate nodules appear to be primary records of Earth surface temperatures at the time of their formation. All sampled nodules preserve micritic carbonate, and transmitted light and cathodoluminescence images show limited recrystallization or void-filling spar and no evidence of pervasive remineralization (Figure 2). ~~Isotopic~~Clumped isotopic data also suggest primary and uncontaminated carbonate material;  $\Delta_{48}$  values remain low ( $\ll 1\text{‰}$ ; Table B.1), indicating a lack of hydrocarbon or sulfide contamination (e.g., Guo and Eiler, 2007; Huntington et al. 2009), ~~and temperature~~. Temperature and  $\delta^{18}\text{O}$  measurements remain well within the range of reasonable terrestrial values, particularly for continental interior basins with seasonal climates (Table B.1; e.g., Quade et al., 2013; Hough et al., 2014). Carbonates forming in temperate regions often exhibit summer/warm-month temperatures due to warm, dry conditions and low soil  $\text{CO}_2$  concentrations during those months (e.g., Breecker et al., 2009; Quade et al., 2013). Such

343 conditions are predicted for the GRB during the early Eocene based on regional climate models  
344 (Thrasher and Sloan, 2009; 2010), and are evident in paleosol features (Clyde et al., 2001;  
345 Hyland and Sheldon, 2013) as well as evaporative  $\delta^{18}\text{O}$  of source waters from nearby paleo-lakes  
346 Gosiute and Uinta (*Table B.1*; e.g., Sarg et al., 2013); [Frantz et al., 2014](#)). Further warm biasing  
347 of soil temperature with respect to air temperature can be imparted by radiant ground heating, but  
348 such effects are likely negligible in shaded forest soils (e.g., Quade et al., 2013; Ringham et al.,  
349 2016). Clumped isotope data from two soil depth profiles collected in the GRB agree within  
350 uncertainty below ~50 cm (Figure 2), suggesting that surface heating and depth attenuation of  
351 surface temperature variability does not significantly affect the samples used for our MART  
352 reconstructions (paleosol depths ~~~60~~50–200 cm; e.g., Ringham et al., 2016).

353         These results imply that the temperatures measured from our pedogenic carbonates  
354 broadly reflect warm month mean soil temperatures (WMMT) as observed in other records (e.g.,  
355 Peters et al., 2013; Hough et al., 2014; Burgener et al., 2016); ~~with the possible exception of the~~  
356 [Possible exceptions are](#) two samples at the base of the Honeycomb Buttes section (HB-109 and  
357 HB-18; *Table B.1*) which appear to ~~be closer to MAT~~ [correspond to MAT estimates from the](#)  
358 [same paleosols \(PPM<sub>1.0</sub>; Figure 4\)](#). These lowest temperature estimates from the base of the  
359 section may be artificially “cool” as a function of seasonal precipitation regimes spreading  
360 carbonate formation across other parts of the year, particularly in soils with deeper Bk horizons  
361 like these (e.g., Gallagher and Sheldon, 2016). Because of the likely bias toward MAT in these  
362 two samples, we exclude them from calculations of WMMT or MART as indicated in Figure 4;  
363 additionally, this effect means that all of our clumped isotope-based estimates of WMMT may be  
364 artificially low, suggesting that our calculated MART values could represent a minimum value.  
365 However, our resultant clumped isotope-based temperature estimates are mostly in agreement



366 with both regional climate model predictions of summer month air temperatures (e.g., Thrasher  
367 and Sloan, 2009; Snell et al., 2013) and paleobotanical coexistence estimates of warm month  
368 mean temperatures (Figure 4).

369 Paleobotanical coexistence methods have been shown to reconstruct paleo-temperatures  
370 robustly, particularly for warm and cold months in well-sampled and taxonomically rich  
371 localities such as these (e.g., Thompson et al., 2012; Grimm and Potts, 2016). However,  
372 uncertainties may be larger than accounted for by the described statistical methods applied to  
373 these assemblages because: 1) many fossil classifications within the GRB assemblages are not  
374 directly comparable to or identifiable as extant species, and coexistence analyses at a generic or  
375 familial level may introduce bias by broadening the temperature tolerance ranges of most groups  
376 (e.g., Wang et al., 2010); and 2) evolutionary or climatic preferences of Paleogene fossil taxa  
377 may not be fully conserved in extant groups, introducing potential sources of error (e.g., Fang et  
378 al., 2011). If we double estimated error to account for these unquantifiable uncertainties, the  
379 collective coexistence probability density functions from these assemblages still produce  
380 CMMT, MAT, and WMMT estimates defined by narrow “maximum likelihood” bioclimatic  
381 envelopes ( $< \pm 3^{\circ}\text{C}$ ; Figure 3; *Table C.2*), which suggest that the environmental characteristics of  
382 these fossil assemblages are well constrained despite some higher-level NLR assignments.  
383 Additionally, sampling bias from well-sampled temperate regions (e.g., North America) in the  
384 modern GBIF database may place undue weight on the cool end of plant ranges (e.g.,  
385 Greenwood et al., 2017), constraining paleotemperature estimates to lower values or smaller  
386 ranges than is appropriate; ~~this~~. This suggests that, similar to clumped isotope-based estimates,  
387 our plant-based MART values could also represent a minimum value. Despite this,  
388 paleobotanical coexistence CMMT estimates agree with regional climate model predictions of

winter month temperatures in the GRB (e.g., Thrasher and Sloan, 2009; 2010), MAT estimates agree broadly with multiple paleosol-based proxy estimates (Figure 4; Hyland and Sheldon, 2013) and with updated paleobotanical physiognomy estimates (Figure 4; *Table C.3*; Wilf, 2000), and WMMT estimates agree with regional climate model estimates (e.g., Thrasher and Sloan, 2009; Snell et al., 2013) and broadly with clumped isotope-based estimates (Figure 4). Taken together these proxy results paint a consistent picture of Earth-surface temperatures during the early Eocene, despite uncertainties inherent in each individual method.

## 4.2 Temperature seasonality

Because each of these proxies appears to represent different seasonal temperatures robustly, we combine these estimates to produce a new multiply constrained investigation of paleo-MART. By calculating the differences between CMMT from paleobotanical coexistence analysis, MAT from paleosol geochemistry or paleobotanical analyses, and WMMT from  $\Delta_{47}$  composition or paleobotanical coexistence analysis, we can directly estimate MART in the past and compare differences in seasonal temperatures independent of calculation method (c.f., Snell et al., 2013). In other words, our approach can define MART as: 1) the difference between WMMT and CMMT; or 2) twice the difference between MAT and either WMMT or CMMT, assuming that MAT falls half way between those estimates by definition (Table 1). Because our approach can calculate MART using both methods and an average of multiple proxies, this allows for a wide range of independent checks on our estimates, providing the most robust available paleo-MART (Table 1). Each method provides consistent answers ~~which~~that are statistically indistinguishable for a given time period (Student's *t*-test *p*-values = 0.4–0.9), lending confidence to calculations which show that MART ranged from ~~19.5–25.5~~21–26°C

412 during the early Eocene (Table 1). ~~MART was generally slightly lower than modern (~19.5–~~  
413 ~~22.5°C) across this interval, but appears to have increased to near modern ranges during the peak~~  
414 ~~EECO (~25.5°C; Figure 4; Table 1).~~

Formatted: Highlight

415 By averaging all data from each population (CMMT, MAT, WMMT) for the peak and  
416 non-peak intervals separately, calculated MARTs suggest that seasonality was generally slightly  
417 lower than modern across parts of the early Eocene (~21–23°C, non-peak), but appears to have  
418 increased to near-modern ranges during the peak EECO (~26°C; Figure 4; Table 1). The  
419 calculated uncertainty of the difference between these populations (S.E.D) is ~4°C, which makes  
420 the non-peak and peak intervals statistically distinct though nearly overlapping. Overall, this  
421 suggests that not only is seasonality not reduced during greenhouse periods (e.g., Snell et al.,  
422 2013), it may actually be expanded (Figure 5).

423 Estimates from the lower end of our reconstructed MART range are still higher than  
424 MART estimates from individual paleobotanical proxies (15–18°C; e.g., Greenwood and Wing,  
425 1995; Wolfe et al., 1998), but compare favorably to estimates from regional climate models with  
426 assumed lacustrine or paludal land cover (20–22°C; Thrasher and Sloan, 2010). However,  
427 estimates from the higher end of ~~our~~the reconstructed MART range compare more favorably to  
428 modeled MART values with assumed woodland or forested land cover (24–26°C; Thrasher and  
429 Sloan, 2010; Snell et al., 2013). The transient nature of paleo-lake Gosiute and the variable  
430 evolution of environments within the GRB throughout the early Eocene is well documented in  
431 stratigraphic archives, indicating that the basin may have been alternately dominated by the  
432 paleo-lake or by forested floodplains during this period (Smith et al., 2008; 2014). In this  
433 context, our results suggest that both lower (though still in excess of any previous paleobotanical  
434 estimates) and higher MART states may in fact be reasonable for this region at different points

during the early Eocene as the GRB evolved. Moreover, proxy and modeling work does not appear to be contradictory, instead having captured different portions of the range of possible MART values indicated for the peak vs. non-peak EECO in this part of the continental interior (Figures 4 and 5). Regardless, these results suggest that MART values lower than ~20°C (e.g., Greenwood and Wing, 1995; Wolfe et al., 1998) may be unreasonable during any part of the EECO, even in the context of variable climate and environmental conditions. This is particularly true because MART estimates using these proxy methods are more likely to underestimate than overestimate seasonality (see Section 4.1).

#### 4.3 Seasonality implications

~~These results~~Our new proxy data and model comparisons have important implications for continental climates, as they suggest two potential characteristics of seasonality in interior regions during warming events: 1) proxies tend to indicate continental temperatures on the high end of modeled ranges in all seasons, and 2) both proxies and regional models indicate that summer temperatures may increase disproportionately, actually broadening MART, at high atmospheric  $p\text{CO}_2$ . While proxy and model estimates of paleotemperature generally agree through the early Eocene in the GRB, proxy estimates consistently fall in the top half of all modeled values (Figure 5). Although these model and proxy results are not statistically distinct, they may suggest that realistic environmental responses could have a skewed distribution within the range of model-predicted climate outcomes, an observation which has been made previously for other regions and time periods (e.g., Roe and Baker, 2007; Diffenbaugh and Field, 2013).

Winter temperatures were generally high during the Eocene (Figures 4 and 5; e.g., Greenwood and Wing, 1995), ~~however~~but during the peak EECO summer temperatures appear

to have increased disproportionately, broadening the range of MART (Figures 4 and 5). While this apparent trend may be related to the lack of direct CMMT estimates during the peak EECO, the consistency of MART estimates using both reconstruction methods (see Section 4.2) suggests the observation is robust. Regional Eocene climate model output for the GRB predicts lower MART (~20°C) under low  $p\text{CO}_2$  conditions (LoCO scenario), and higher MART (~24°C) under high  $p\text{CO}_2$  conditions (HiCO scenario; Figure 5; *Table D.1*). Therefore, a theoretical transition from lower ( $\leq 500$  ppm) to higher ( $\geq 1000$  ppm) atmospheric  $p\text{CO}_2$  during the peak EECO (e.g., Hyland and Sheldon, 2013; Jagiecki et al., 2015) could effectively broaden MART and result in extreme summer temperatures during that period, which would be consistent with both regional model and proxy predictions in the GRB (Figure 5). Regional model-proxy agreement on the plausibility of variable moderate to high MART (20–26°C) in continental interiors fits with global simulations employing a reasonable set of radiative forcings and climate sensitivities, which project similar seasonality ranges during this and other greenhouse events (Huber and Caballero, 2011; Lunt et al., 2012). These temperature seasonality estimates also corroborate recent work on other regions and warm periods (e.g., Snell et al., 2013; Eldrett et al., 2014), and further support the interpretation that continental interiors were less “equable” than previously thought under greenhouse conditions (Snell et al., 2013; Peppe, 2013).

Increased seasonality and the disproportionate response of summer temperatures during greenhouse climates also has significant implications for predicting future change in continental interiors. Current projections for the next century using downscaled global climate model ensembles (PCDMI, 2014; *Table D.1*) indicate generally increased temperatures and changing seasonality in North America, and GRB temperatures are projected to increase particularly during winter months (Figure 5). However for high emissions scenarios that may be closer in

character to greenhouse conditions like the peak EECO or the PETM (RCP8.5; e.g., IPCC, 2007; Lunt et al., 2012), summer temperatures in the GRB increase more strongly, broadening MART (Figure 5; *Table D.1*). This trend in MART from peak EECO proxy data and high-emission/ $p\text{CO}_2$  model simulations in both the future and Eocene suggests a potential atmospheric  $p\text{CO}_2$  threshold for enhanced seasonality, and provides support for models and observations indicating that continental interiors may experience more extreme seasonality in the future under heightened greenhouse conditions (e.g., IPCC, 2007; Diffenbaugh and Field, 2013; Diffenbaugh et al., 2017). The mechanism for producing this increased seasonality remains unclear and requires further study in terms of both proxy applications and model development, although changes in land cover may play a crucial role at least in regional variability (Thrasher and Sloan, 2010; Diffenbaugh and Field, 2013).

## 5. Conclusions

Estimates of winter (paleofloral NLR coexistence), mean (paleosol geochemistry), and summer (clumped isotope) temperatures from the early Eocene in the Green River Basin of Wyoming (USA) provide new multi-proxy constraints on seasonality (mean annual range of temperature) in terrestrial settings during greenhouse periods. These records show that MART was variable but near (or above) modern values during the early Eocene climatic optimum, confirming both that seasonality in continental interiors may not remain constant, and that EECO conditions likely do not conform to at least the seasonality aspect of greenhouse “equability”. Comparisons between proxy data and regional/downscaled climate models further imply that temperature seasonality may respond differently at low vs. high atmospheric  $p\text{CO}_2$ . Overall, this suggests that our understanding of past greenhouse climates in continental interiors may be

504 incomplete when it comes to “equability”, and proposes the potential for extreme seasonality in  
505 these regions during past warming events and in the future, which likely has important  
506 implications for natural ecosystems and human infrastructure.

507

**Formatted:** Indent: First line: 0.5", Don't add space between paragraphs of the same style, Line spacing: Double

**Formatted:** Font: Not Bold

508 **Data Availability.** Summarized paleosol, isotope, floral, and modeling data are available in the  
509 Supplement, and detailed sample or locality data are available from the authors on request.

510

511 **Author Contributions.** EGH, NDS, and KWH designed the study; EGH and NDS collected the  
512 samples and conducted fieldwork; EGH conducted laboratory analyses; EGH, KWH, and TR  
513 conducted data analyses and reduction; all authors contributed to the writing of the manuscript.

514

515 **Competing Interests.** The authors declare that they have no conflicts of interest.

516

517 **Acknowledgments.** The authors thank D. Peppe, K. Snell, and XXX for manuscript comments;  
518 A. Schauer, L. Burgener, and P. Wilf for assistance with proxy data; PCDMI, WCRP, L. Sloan,  
519 and J. Sewall for archived modeling datasets; NSF grants EAR-1252064 and 1156134 (KWH),  
520 GSA's Farouk El-Baz grant (EGH), and the Quaternary Research Center and Future of Ice  
521 Initiative at the University of Washington for funding and support.

522



523 **References.**

- 524 Bader, N.E., Nicolaysen, K.P., Maldonado, R.L., Murray, K.E., and Mudd, A.C.: Extensive  
525 middle Miocene weathering interpreted from a well-preserved paleosol, Cricket Flat, Oregon,  
526 USA, *Geoderma*, 239, 195–205, 2015.
- 527 Barron, E.: Eocene equator-to-pole surface ocean temperatures: A significant climate problem?,  
528 *Paleoceanography*, 2, 729–739, 1987
- 529 Brand, W.A., Assonov, S.S., and Coplen, T.B.: Correction for the  $^{17}\text{O}$  interference in  $\delta^{13}\text{C}$   
530 measurements when analyzing  $\text{CO}_2$  with stable isotope mass spectrometry, *Pure Appl. Chem.*,  
531 82, 1719–1733, 2010.
- 532 Breecker, D.O., Sharp, Z.D., and McFadden, L.D.: Seasonal bias in the formation and stable  
533 isotopic composition of pedogenic carbonate in modern soils from central New Mexico, USA,  
534 *Geol. Soc. Am. Bull.*, 121, 630–640, 2009.
- 535 Burgener, L., Huntington, K., Hoke, G., Schauer, A., Ringham, M., Latorre, C., and Diaz, F.:  
536 Variations in soil carbonate formation and seasonal bias over >4km of relief in the western  
537 Andes (30°S) revealed by clumped isotope thermometry, *Earth Planet. Sc. Lett.*, 441, 188–199,  
538 2016.
- 539 Cerling, T.E.: The stable isotopic composition of modern soil carbonate and its relationship to  
540 climate, *Earth Planet. Sci. Lett.*, 71, 229–240, 1984.
- 541 Cerling, T.E., and Quade, J.: Stable carbon and oxygen isotopes in soil carbonates, *Geophys.*  
542 *Mono.*, 78, 217–231, 1993.
- 543 Clyde, W.C., Sheldon, N.D., Koch, P.L., Gunnell, G.F., and Bartels, W.S.: Linking the  
544 Wasatchian/Bridgerian boundary to the Cenozoic Global Climate Optimum: new  
545 magnetostratigraphic and isotopic results from South Pass, Wyoming, *Palaeogeogr. Palaeocl.*,  
546 167, 175–199, 2001.
- 547 Daëron, M., Blamart, D., Peral, M., and Affek, H.: Absolute isotopic abundance ratios and the  
548 accuracy of  $\Delta_{47}$  measurements, *Chem. Geol.*, 442, 83–96, 2016.
- 549 Dennis, K.J., Affek, H.P., Passey, B.H., Schrag, D.P., and Eiler, J.M.: Defining and absolute  
550 reference frame for clumped isotope studies of  $\text{CO}_2$ , *Geochim. Cosmochim. Ac.*, 75, 7117–7131,  
551 2011.
- 552 Diffenbaugh, N.S., and Field, C.B.: Changes in ecologically critical terrestrial climate  
553 conditions, *Science*, 341, 486–492, 2013.
- 554 Diffenbaugh, N.S., Singh, D., Mankin, J.S., Horton, D.E., Swain, D.L., Touma, D., Charland, A.,  
555 Liu, Y., Haugen, M., Tsiang, M., and Rajaratnam, B.: Quantifying the influence of global  
556 warming on unprecedented extreme climate events, *P. Natl. Acad. Sci. USA*, 114, 4881–4886,  
557 2017.

558 Driese, S.G., Peppe, D.J., Beverly, E.J., DiPietro, L.M., Arellano, L.N., and Lehmann, T.:  
559 Paleosols and paleoenvironments of the early Miocene deposits near Karunga, Lake Victoria,  
560 Kenya, *Palaeogeogr. Palaeoclimatol.*, 443, 167–182, 2016.

561 Eiler, J.M.: Clumped-isotope geochemistry – The study of naturally-occurring, multiply-  
562 substituted isotopologues, *Earth Planet. Sci. Lett.*, 262, 309–327, 2007.

563 Eiler, J.M.: Paleoclimate reconstruction using carbonate clumped isotope thermometry: *Quat.*  
564 *Sci. Rev.*, 30, 3575–3588, 2011.

565 Eldrett, J.S., Greenwood, D.R., Polling, M., Brinkhuis, H., and Sluijs, A.: A seasonality trigger  
566 for carbon injection at the Paleocene-Eocene Thermal Maximum, *Clim. Past*, 10, 759–769, 2014.

567 Evans, D., Sagoo, N., Renema, W., Cotton, L.J., Muller, W., Todd, J.A., Saraswati, P.K.,  
568 Stassen, P., Ziegler, M., Pearson, P.N., Valdes, P.J., and Affek, H.P.: Eocene greenhouse climate  
569 revealed by coupled clumped isotope-Mg/Ca thermometry, *P. Natl. Acad. Sci. USA*, 115, 1174–  
570 1179, 2018.

571 Fang, J., Wang, Z., and Tang, Z.: *Atlas of woody plants in China: Distribution and climate*,  
572 Springer-Verlag (Beijing, CH), 1909 pp., 2011.

573 Frantz, C.M., Petryshyn, V.A., Marengo, P.J., Tripatic, A., Berelson, W.M., and Corsetti, F.A.:  
574 Dramatic local environmental change during the Early Eocene Climatic Optimum detected using  
575 high-resolution chemical analyses of Green River stromatolites, *Palaeogeogr. Palaeoclimatol.*, 405, 1-  
576 15, 2014.

577 Gallagher, T.M., and Sheldon, N.D.: A new paleothermometer for forest paleosols and its  
578 implications for Cenozoic climate, *Geology*, 41, 647–650, 2013.

579 Gallagher, T.M., and Sheldon, N.D.: Combining soil water balance and clumped isotopes to  
580 understand the nature and timing of pedogenic carbonate formation, *Chem. Geol.*, 435, 79–91,  
581 2016.

582 Garzzone, C.A., Auerbach, D.J., Smith, J.J., Rosario, J.J., Passey, B.H., Jordan, T.E., and Eiler,  
583 J.M.: Clumped isotope evidence for diachronous surface cooling of the Altiplano and pulsed  
584 surface uplift of the Central Andes, *Earth Planet. Sci. Lett.*, 393, 173–181, 2014.

585 Ghosh, P., Adkins, J., Affek, H., Balta, B., Guo, W., Schauble, E., Schrag, D., and Eiler, J.:  $^{13}\text{C}$ -  
586  $^{18}\text{O}$  bonds in carbonate minerals: a new kind of paleothermometer, *Geochim. Cosmochim. Ac.*,  
587 70, 1439–1456, 2006.

588 Global Biodiversity Information Facility (GBIF): Open Access Biodiversity Data: <http://gbif.org>  
589 (last accessed July 2016).

590 Greenwood, D.R., and Wing, S.L.: Eocene continental climates and latitudinal temperature  
591 gradients, *Geology*, 23, 1044–1048, 1995.

592 Greenwood, D.R., Archibald, S.B., Mathewes, R.W., and Moss, P.T.: Fossil biotas from the  
593 Okanagan Highlands, southern British Columbia and northeastern Washington State: Climates  
594 and ecosystems across an Eocene landscape, *Can. J. Earth Sci.*, 42, 167–185, 2005.

595 Greenwood, D.R., Keefe, R.L., Reichgelt, T., and Webb, J.A.: Eocene paleobotanical altimetry  
596 of Victoria's Eastern Uplands, *Aus. J. Earth Sci.*, 64, 625–637, 2017.

597 Grimm, G.W., and Denk, T.: Reliability and resolution of the coexistence approach- A  
598 revalidation using modern day data, *Rev. Palaeobot. Palyno.*, 172, 33–47, 2012.

599 Grimm, G.W., and Potts, A.: Fallacies and fantasies: the theoretical underpinnings of the  
600 coexistence approach for paleoclimate reconstructions, *Clim. Past*, 12, 611–622, 2016.

601 Guo, W., and Eiler, J.M.: Temperatures of aqueous alteration and evidence for methane  
602 generation on the parent bodies of the CM chondrites, *Geochim. Cosmochim. Ac.*, 71, 5565–  
603 5575, 2007.

604 Harbert, R., and Nixon, K.: Climate reconstruction analysis using coexistence likelihood  
605 estimation (CRACLE): A method for the estimation of climate using vegetation, *Am. J. Bot.*,  
606 102, 1277–1289, 2015.

607 He, B., Olack, G., and Colman, A.: Pressure baseline correction and high-precision CO<sub>2</sub> clumped  
608 isotope ( $\Delta_{47}$ ) analysis by gas-source isotope ratio mass spectrometry, *J. Mass Spectrom.*, 44,  
609 1318–1329, 2012.

610 Hickey, L.: Stratigraphy and paleobotany of the Golden Valley Formation (early Tertiary) of  
611 western North Dakota, *Geol. Soc. Am. Mem.*, 150, 183 pp., 1977.

612 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., and Jarvis, A.: Very high resolution  
613 interpolated climate surfaces for global land areas, *Intl. J. Climatol.*, 25, 1965–1978, 2005.

614 Hough, B.G., Fan, M., and Passey, B.H.: Calibration of the clumped isotope geothermometer in  
615 soil carbonate in Wyoming and Nebraska, USA: Implications for paleoelevation and  
616 paleoclimate reconstruction, *Earth Planet. Sc. Lett.*, 391, 110–120, 2014.

617 Huber, M., and Caballero, R.: The early Eocene equable climate problem revisited, *Clim. Past*, 7,  
618 603–633, 2011.

619 Huntington, K.W., Eiler, J.M., Affek, H.P., Guo, W., Bonifacie, M., Yeung, L.Y., Thiagarajan,  
620 N., Passey, B., Tripathi, A., Daeron, M., and Came, R.: Methods and limitations of clumped CO<sub>2</sub>  
621 isotope ( $\Delta_{47}$ ) analysis by gas-source isotope ratio mass spectrometry, *J. Mass Spectrom.*, 44,  
622 1318–1329, 2009.

623 Hyland, E.G., and Sheldon, N.D.: Coupled CO<sub>2</sub>-climate response during the Early Eocene  
624 Climatic Optimum, *Palaeogeogr. Palaeoclim.*, 369, 125–135, 2013.

625 Hyland, E.G., and Sheldon, N.D.: [Examining the spatial consistency of palaeosol proxies:  
626 Implications for palaeoclimatic and palaeoenvironmental reconstructions in terrestrial  
627 sedimentary basins, \*Sedimentology\*, 63, 959–971, 2016.](#)

628 [Hyland, E.G.](#), Sheldon, N.D., and Cotton, J.M.: Constraining the early Eocene climatic optimum:  
629 A terrestrial interhemispheric comparison: *Geol. Soc. Am. Bull.*, 129, 244–252, 2017.

630 Intergovernmental Panel on Climate Change (IPCC): Fourth Assessment Report: Climate  
 631 Change (AR4), In Pachuari, R.K., and Reisinger, A. (Eds.), IPCC (Geneva, SWI), 104 pp., 2007.

632 Intergovernmental Panel on Climate Change (IPCC): Fifth Assessment Report: Climate Change  
 633 (AR5), In Pachuari, R.K., and Meyer, L.A. (Eds.), IPCC (Geneva, SWI), 151 pp., 2014.

634 Jagniecki, E.A., Lowenstein, T.K., Jenkins, D.M., and Demicco, R.V.: Eocene atmospheric CO<sub>2</sub>  
 635 from the nahcolite proxy, *Geology*, 43, 1075–1078, 2015.

636 Jordan, G.J.: Uncertainty in paleoclimatic reconstructions based on leaf physiognomy, *Aus. J.*  
 637 *Bot.*, 45, 527–547, 1997.

638 Kelson, J., Huntington, K.W., Schauer, A., Saenger, C., and Lechler, A.: Toward a universal  
 639 carbonate clumped isotope calibration: Diverse synthesis and preparatory methods suggest a  
 640 single temperature relationship, *Geochim. Cosmochim. Ac.*, 197, 104–131, 2017.

641 Kluge, T., John, C., Jourdan, A., Davis, S., and Crawshaw, J.: Laboratory calibration of the  
 642 calcium carbonate clumped isotope thermometer in the 25 - 250°C temperature range, *Geochim.*  
 643 *Cosmochim. Ac.*, 157, 213–227, 2015.

644 Koch, P.L.: Isotopic reconstruction of past continental environments, *Annu. Rev. Earth Plant.*  
 645 *Sci.*, 26, 573–623, 1998.

646 Lunt, D., Jones, T., Heinemann, M., Huber, M., LeGrande, A., Winguth, A., Loptson, C.,  
 647 Marotzke, J., Roberts, C., Tindall, J., Valdes, P., and Winguth, C.: A model-data comparison for  
 648 a multi-model ensemble of early Eocene atmosphere-ocean simulations: EoMIP, *Clim. Past*, 8,  
 649 1717–1736, 2012.

650 MacGinitie, H.D.: The Eocene Green River Flora of northwestern Colorado and northeastern  
 651 Utah, University of California Press (Berkeley, CA), 201 pp., 1969.

652 Manchester, S., and Dilcher, D.: Pterocaryoid fruits in the Paleogene of North America and their  
 653 evolutionary and biogeographic significance, *Am. J. Bot.*, 69, 275–286, 1982.

654 Manchester, S.R.: Revisions to Roland Brown's North American Paleocene flora, *Ac. Mus. Natl.*  
 655 *Prag.*, 70, 153–210, 2014.

656 McInerney, F.A., and Wing, S.L.: The Paleocene-Eocene Thermal Maximum: A perturbation of  
 657 carbon cycle, climate and biosphere with implications for the future, *Ann. Rev. Earth Planet.*  
 658 *Sci.*, 39, 489–516, 2011.

659 Michel, L.A., Peppe, D.J., Lutz, J.A., Driese, S.G., Dunsworth, H.M., Harcourt-Smith, W.,  
 660 Horner, W.H., Lehmann, T., Nightingale, S., and McNulty, K.P.: Remnants of an ancient forest  
 661 provide ecological context for Early Miocene fossil apes, *Nat. Commun.*, 5, 3236, 2014.

662 Mosbrugger, V., and Utescher, T.: The coexistence approach- a method for quantitative  
 663 reconstructions of tertiary terrestrial palaeoclimate data using plant fossils, *Palaeogeogr.*  
 664 *Palaeoclim.*, 134, 61–86, 1997.

665 National Climatic Data Center (NCDC): United States Climate Normals, 1981–2010:  
 666 Climatology of the US, National Oceanic and Atmospheric Administration,  
 667 <http://www.ncdc.noaa.gov/data#normals> (last accessed April 2015).

668 Pal, J.S., et al. (19 others): The ICTP RegCM3 and RegCNET: Regional climate modeling for  
 669 the developing world, *Bull. Am. Meteorol. Soc.*, 88, 1395–1409, 2007.

670 Passey, B.H., Levin, N., Cerling, T.E., Brown, F., and Eiler, J.: High-temperature environments  
 671 of human evolution in East Africa based on bond ordering in paleosol carbonates, *P. Natl. Acad.*  
 672 *Sci. USA*, 107, 11245–11249, 2010.

673 Peppe, D.J., Royer, D.L., Wilf, P., and Kowalski, E.: Quantification of large uncertainties in  
 674 fossil leaf paleoaltimetry, *Tectonics*, 29, TC3015, 2010.

675 Peppe, D.J.: Hot summers in continental interiors: The case against equability during the early  
 676 Paleogene, *Geology*, 41, 95–96, 2013.

677 Peters, N., Huntington, K.W., and Hoke, G.: Hot or not? Impact of seasonally variable soil  
 678 carbonate formation on paleotemperature and O-isotope records from clumped isotope  
 679 thermometry, *Earth Planet. Sc. Lett.*, 361, 208–218, 2013.

680 Program for Climate Model Diagnosis and Intercomparison (PCMDI): Bias corrected and  
 681 downscaled World Climate Research Programme’s Coupled Model Intercomparison Project  
 682 phase 5 (CMIP5) climate projections, [http://gdo-dcp.ucllnl.org/downscaled\\_cmip\\_projections/](http://gdo-dcp.ucllnl.org/downscaled_cmip_projections/),  
 683 2014.

684 Quade, J., Eiler, J., Daeron, M., and Achyuthan, H.: The clumped isotope geothermometer in soil  
 685 and paleosol carbonate, *Geochim. Cosmochim. Ac.*, 105, 92–100, 2013.

686 R Core Team: R: A language and environment for statistical computing: Foundation for  
 687 Statistical Computing (Vienna, AT), <https://www.r-project.org>, 2013.

688 Reichgelt, T., Kennedy, E.M., Conran, J.G., Mildenhall, D.C., and Lee, D.E.: The early Miocene  
 689 paleolake Manuherikia: vegetation heterogeneity and warm-temperate to subtropical climate in  
 690 southern New Zealand, *J. Paleolimnol.*, 53, 349–365, 2015.

691 [Retallack, G.J.: Cenozoic paleoclimate on land in North America, \*J. Geol.\*, 115, 271-294, 2007.](#)

692 Ringham, M.C., Hoke, G.D., Huntington, K.W., and Aranibar, J.N.: Influence of vegetation type  
 693 and site-to-site variability on soil carbonate clumped isotope records, Andean piedmont of  
 694 Central Argentina (32–34 °S), *Earth Planet. Sc. Lett.*, 440, 1–11, 2016.

695 Roe, G.H., and Baker, M.B.: Why is climate sensitivity so unpredictable?, *Science*, 318, 629–  
 696 632, 2007.

697 Sarg, J.F., Suriamin, H., Tanavsuu-Milkeviciene, K., and Humphrey, J.D.: Lithofacies, stable  
 698 isotopic composition, and stratigraphic evolution of microbial and associated carbonates, Green  
 699 River Formation (Eocene), *Am. Assc. Petr. Geol. Bull.*, 97, 1937–1966, 2013.

700 Schauble, E.A., Ghosh, P., and Eiler, J.M.: Preferential formation of  $^{13}\text{C}$ - $^{18}\text{O}$  bonds in carbonate  
701 materials estimated using first-principle lattice dynamics, *Geochim. Cosmochim. Ac.*, 70, 2510–  
702 2529, 2006.

703 Schauer, A.J., Kelson, J., Saenger, C., and Huntington, K.W.: Choice of  $^{17}\text{O}$  correction affects  
704 clumped isotope ( $\Delta_{47}$ ) values of  $\text{CO}_2$  measured with mass spectrometry, *R. Comm. Mass*  
705 *Spectrom.*, 30, 2607–2616, 2016.

706 Sewall, J., and Sloan, L.: Come a little bit closer: A high-resolution climate study of the early  
707 Paleogene Laramide foreland, *Geology*, 34, 81–84, 2006.

708 Sheldon, N.D., and Tabor, N.J.: Quantitative paleoenvironmental and paleoclimatic  
709 reconstruction using paleosols, *Earth Sci. Rev.*, 95, 1–52, 2009.

710 Sheldon, N.D., Retallack, G.J., and Tanaka, S.: Geochemical climofunctions from North  
711 American soils and application to paleosols across the Eocene-Oligocene boundary in Oregon, *J.*  
712 *Geol.*, 110, 687–696, 2002.

713 Sloan, L.C.: Equable climates during the early Eocene: Significance of regional paleogeography  
714 for North American climate, *Geology*, 22, 881–884, 1994.

715 Sloan, L.C., and Barron, E.: “Equable” climates during Earth history, *Geology*, 18, 489–492,  
716 1990.

717 Smith, M.E., Carroll, A.R., and Singer, B.S.: Synoptic reconstruction of a major ancient lake  
718 system: Eocene Green River, western United States, *Geol. Soc. Am. Bull.*, 120, 54–84, 2008.

719 Smith, M.E., Chamberlain, K.R., Singer, B.S., and Carroll, A.R.: Eocene clocks agree: coeval  
720  $^{40}\text{Ar}/^{39}\text{Ar}$ , U-Pb, and astronomical ages from the Green River Formation, *Geology*, 38, 527–530,  
721 2010.

722 Smith, M.E., Carroll, A.R., Scott, J.J., and Singer, B.S.: Early Eocene carbon isotope excursions  
723 and landscape destabilization at eccentricity minima: Green River Formation of Wyoming, *Earth*  
724 *Planet. Sc. Lett.*, 403, 393–406, 2014.

725 Smith, M.E., Carroll, A.R., and Scott, J.J.: Stratigraphic expression of climate tectonism, and  
726 geomorphic forcing in an underfilled lake basin: Wilkins Peak Member of the Green River  
727 Formation, In Smith, M.E. and Carroll, A.R. (Eds.), *Stratigraphy and Paleolimnology of the*  
728 *Green River Formation*, Springer (Dordrecht, NE), 61–102, 2015.

729 Smithsonian Institution Museum of Natural History Paleobiology (SIMNHP): Paleobiology  
730 Database, Smithsonian Institution (Washington, DC), <http://www.nmnh.si.edu/>, 2015.

731 Snell, K.E., Thrasher, B.L., Eiler, J.M., Koch, P.L., Sloan, L.C., and Tabor, N.J.: Hot summers in  
732 the Bighorn Basin during the early Paleogene, *Geology*, 41, 55–58, 2013.

733 Suarez, M.B., Passey, B.H., and Kaakinen, A.: Paleosol carbonate multiple isotopologue  
734 signature of active East Asian summer monsoons during the late Miocene and Pliocene,  
735 *Geology*, 39, 1151–1154, 2011.

736 Spicer, R.A., and Parrish, J.T.: Late Cretaceous–early Tertiary paleoclimates of northern high  
737 latitude: a quantitative view, *J. Geol. Soc.*, 147, 329–341, 1990.

738 Spicer, R.A., Herman, A.B., Liao, W., Spicer, T.E.V., Kodrul, T.M., Yang, J., and Jin, J.: Cool  
739 tropics in the Middle Eocene: Evidence from the Changchang Flora, Hainan Island, China,  
740 *Palaeogeogr. Palaeocl.*, 412, 1–16, 2014.

741 Stinchcomb, G.E., Nordt, L.C., Driese, S.G., Lukens, W.E., Williamson, F.C., and Tubbs, J.D.:  
742 A data-driven spline model designed to predict paleoclimate using paleosol geochemistry, *Am. J.*  
743 *Sci.*, 316, 746–777, 2016.

744 Takeuchi, A., Larson, P.B., and Suzuki, K.: Influence of paleorelief on the Mid-Miocene climate  
745 variation in southeastern Washington, northeastern Oregon, and western Idaho, USA,  
746 *Palaeogeogr. Palaeocl.*, 254, 462–476, 2007.

747 Thompson, R.S., Anderson, K.H., Pelltier, R.T., Strickland, L.E., Bartlein, P.J., and Shafer, S.L.:  
748 Quantitative estimation of climatic parameters from vegetation data in North America by the  
749 mutual climatic range technique, *Quat. Sci. Rev.*, 51, 18–39, 2012.

750 Thrasher, B.L., and Sloan, L.C.: Carbon dioxide and the early Eocene climate of western North  
751 America, *Geology*, 37, 807–810, 2009.

752 Thrasher, B.L., and Sloan, L.C.: Land cover influences on the regional climate of western North  
753 America during the early Eocene, *Global Planet. Change*, 72, 25–31, 2010.

754 TROPICOS: Global Plant Database: Missouri Botanical Garden (St. Louis, MO),  
755 <http://www.tropicos.org/>, 2015.

756 United States Department of Agriculture (USDA): The PLANTS Database: NRCS National  
757 Plant Data Team (Greensboro, NC), <http://plants.usda.gov>, 2015.

758 Utescher, T., Bruch, A., Erdei, B., Francois, L., Ivanov, D., Jacques, F., Kern, A., Liu, Y.,  
759 Mossbrugger, V., and Spicer, R.: The Coexistence Approach- Theoretical background and  
760 practical considerations of using plant fossils for climate quantification, *Palaeogeogr. Palaeocl.*,  
761 10, 58–73, 2014.

762 Wang, Q., Ferguson, D.K., Feng, G., Ablav, A.G., Wang, Y., Yang, J., Li, Y., and Li, C.:  
763 Climatic change during the Palaeocene to Eocene based on fossil plants from Fushun China,  
764 *Palaeogeogr. Palaeocl.*, 295, 323–331, 2010.

765 West, C.K., Greenwood, D.R., and Basinger, J.F.: Was the Arctic Eocene 'rainforest' monsoonal?  
766 Estimates of seasonal precipitation from early Eocene megaflores from Ellesmere Island,  
767 Nunavut, *Earth Planet. Sc. Lett.*, 427, 18–30, 2015.

768 Wilf, P.: Using fossil plants to understand global change: Evidence for Paleocene-Eocene  
769 warming in the greater Green River Basin of southwestern Wyoming, University of  
770 Pennsylvania (Philadelphia, PA), 384 pp., 1998.

771 Wilf, P.: Late Paleocene-early Eocene climate changes in southwestern Wyoming:  
772 Paleobotanical analysis, *Geol. Soc. Am. Bull.*, 112, 292–307, 2000.

773 Wing, S.L.: Late Paleocene-early Eocene floral and climatic change in the Bighorn Basin,  
 774 Wyoming, In Aubrey, M., Lucas, S., and Berggren, W. (Eds.), Columbia University Press (New  
 775 York, NY), 380–400, 1998.

776 Wolfe, J.A.: A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere,  
 777 *Am. J. Sci.*, 66, 691–703, 1978.

778 Wolfe, J.A.: Paleoclimatic estimates from Tertiary leaf assemblages: *Ann. Rev. Earth Planet.*  
 779 *Sci.*, 23, 119–142, 1995.

780 Wolfe, J.A., and Wehr, W.: Middle Eocene dicotyledonous plants from Republic, northeastern  
 781 Washington, *USGS Bull.*, 1597, 67 pp., 1987.

782 Wolfe, J.A., Forest, C.E., and Molnar, P.: Paleobotanical evidence of Eocene and Oligocene  
 783 paleoaltitudes in midlatitude western North America, *Geol. Soc. Am. Bull.*, 110, 664–678, 1998.

784 [World Climate Research Programme: Climate Model Intercomparison Project \(Phase 5\),](https://cmip.llnl.gov/)  
 785 [https://cmip.llnl.gov/, 2011.](https://cmip.llnl.gov/)

786 Zaarur, S., Affek, H.P., and Brandon, M.: A revised calibration of the clumped isotope  
 787 thermometer, *Earth Planet. Sc. Lett.*, 382, 47–57, 2013.

788 Zachos, J., Pagani, M., Sloan, L., Thomas, E., and Billups, K.: Trends, rhythms, and aberrations  
 789 in global climate 65 Ma to Present, *Science*, 292, 686–693, 2001.

790 Zachos, J.C., Dickens, G.R., and Zeebe, R.E.: An early Cenozoic perspective on greenhouse  
 791 warming and carbon-cycle dynamics, *Nature*, 451, 279–283, 2008.

792 Zamanian, K., Pustovoytov, K., and Kuzyakov, Y.: Pedogenic carbonates: Forms and formation  
 793 processes, *Earth Sci. Rev.*, 157, 1–17, 2016.



794 **Figure Captions.**

795 **Figure 1.** Map and stratigraphy of the Green River Basin. A) Map of the region, showing major  
796 sedimentary basins and topographic highs. Stars show proxy record sampling sites (paleosols in  
797 yellow, paleoflora in red), and dashed box is the sampling region for modern climate stations and  
798 the downscaling domain for both models. CF = Cordilleran fold-thrust belt, UU = Uinta uplift,  
799 WR = Wind River uplift, OC = Owl Creek uplift, GM = Granite Mountains, FR = Front Range.  
800 B) Simplified stratigraphy of the central to eastern GRB, showing facies for the Green River  
801 Formation (GRF) and the equivalent and interfingering Wasatch Formation (WF) based on the  
802 work of Smith et al. (2015) and Hyland and Sheldon (2013). LY = Lysitean, BF = Blackforkian,  
803 LU = Luman Member, NT = Niland Tongue, TM = Tipton Member, WPM = Wilkins Peak  
804 Member, LA = Laney Member, RR = Ramsey Ranch Member, CB = Cathedral Bluffs Member.

806 **Figure 2.** Paleosol carbonate descriptions. A) Paired transmitted light and cathodoluminescence  
807 (CL) images of carbonate nodules showing primary micrite in sampled nodules (I-II) and  
808 diagenetically altered material in unsampled nodules (III-IV). Images taken on a Premier ELM-  
809 3R Luminoscope at 8–10 kV, 0.5 mA, and 6.6–13.3 Pa with preset 1 s exposure; scale bars ~50  
810 µm. B) Clumped isotope-based soil temperature profiles from discrete layers sampled within  
811 analyzed paleosol exemplars. [SampleProfile](#) HB-129 contained nodular carbonate layers at 20–  
812 30 cm, 50–65 cm, and 80–100 cm; [SampleProfile](#) HB-187 contained nodular carbonate layers at  
813 150–170 cm, 190–205 cm, and 240–260 cm.

814  
815 **Figure 3.** Floral methods description. A) Probability density functions of hypothetical Taxa A  
816 and B along climatic variable X to form a PDF representative of the maximum likelihood of co-

817 occurrence. B) Hypothetical climatic envelope of Taxon Q with climatic variables X and Y,  
818 where point R occurs outside the envelope of Taxon Q but within its range of both variables  
819 (creating a false inclusion of point R). C) Probability density function distributions for seasonal  
820 temperatures from sampled paleofloral sites, where arrows indicate calculated mean  
821 temperatures for each parameter, and  $n$  = number of morphotypes included in assemblage.  
822

823 **Figure 4.** Temperature proxy estimates of CMMT (white), MAT (gray), and WMMT (black)  
824 through the early Eocene. Triangles represent paleobotanical coexistence estimates, squares  
825 represent paleosol geochemistry estimates, stars represent revised paleobotanical physiognomy  
826 estimates, and circles represent clumped isotope estimates. Error bars represent PDF  $2\sigma$   
827 (paleobotanical coexistence), root mean squared error (PPM<sub>1.0</sub> paleosol geochemistry),  
828 calibration standard error (paleobotanical physiognomy), and propagated analytical/calibration  
829 error (clumped isotopes). Shading highlights peak EECO conditions based on previous work  
830 (e.g., Hyland et al., 2017), and long dashed line highlights possible aliasing due to a long  
831 sampling interval, and short dashed line highlights exclusion of two clumped isotope data points  
832 (see Discussion). Estimates of peak EECO (51  $\pm$ 0.5 Ma) and non-peak EECO MART are defined  
833 as described in Table 1 and the Discussion, with MAT shown by vertical lines. Modern MART  
834 and MAT are from averaged climate normals for NOAA weather stations in the GRB (NCDC,  
835 2010).

836

837 **Figure 5.** Averaged monthly mean temperatures in the GRB, including: modern instrumental  
838 data (filled black circles; NCDC, 2010); high (red squares; RCP8.5) and low (red circles;  
839 RCP4.5) future emissions scenarios (PCDMI, 2014); high (blue squares; HiCO) and low (blue

840 circles; LoCO) early Eocene  $p\text{CO}_2$  scenarios (Thrasher and Sloan, 2009; 2010); and proxy  
841 reconstructions of WMMT and CMMT for non-peak (filled triangles) and peak EECO (open  
842 triangles) from this study. Method-averaged MART estimates shown for each category  
843 (symbols/colors match main panel).

844  
845 **Table 1.** Comparison of Eocene MART estimates using different constraining temperatures and  
846 calculation methods.

847

848

849 **Supplement.**

850 **A. Paleosol Data**

851 *Table A.1.* Paleosol geochemistry data

852 **B. Isotope Data**

853 *Table B.1.* Clumped isotope data summary

854 *Table B.2* Clumped isotope data full

855 **C. Floral Data**

856 *Table C.1.* Floral lists and NLR data

857 *Table C.2.* Climatic envelopes for plant taxa

858 *Table C.3.* Mean annual temperature estimates

859 **D. Modeling Data**

860 *Table D.1.* Modern climate data and model outputs