EDITOR COMMENTS

Editor: “Clyde gives a very good and lengthy review. I agree very much with his commentary, and think all his points are valid and need to be addressed in a good final paper.”

Author: I have done so as outlined below.

Editor: “I do not fully understand Figure 1/revised Figure 2. There is something either wrong in logic or wrong in presentation. I think it is the latter, and that the red rectangles in “panel a” are not supposed to be the same as the red lines in “panel b”. This has to be amended”

Author: I have removed the red rectangles on the left in Figure 2, which were intended to indicate the ETM2 and H2 isotope excursions, but which I can see now were confusing given the thick, red lines on the right (indicating the level of the biostratigraphic events and C24r-C24n shift). I have modified the Figure 2 caption to define the thick red lines.

Editor: “In any case, H-1/ETM2 and H-2 both DEFINITELY occurred well before (at least >1.0 Myr) the start of EECO but DEFINITELY within the general long-term warming trend from the late Paleocene through the early Eocene. The point here is to get all written correctly and within the framework of current knowledge, all the while realizing there have been some serious miscommunication and stratigraphy problems.”

Author: I have made all changes as suggested by Clyde to clarify this point (outlined below).

Editor: “The link between changes across hyperthermal events and the near future has to be couched very carefully. Not only are there the issues of additional anthropogenic influence as stressed by Clyde, there is the issue of rate. I will be up front: I think the idea of the PETM being initiated in 13 years (Schaller et al., PNAS, 2014) is beyond complete bollocks (Zeebe et al., PNAS, 2014); most of these events likely began over thousands of years. The point here is that rate of change is a crucial component, presumably especially so for mammals that might migrate.”

Author: I have completely removed any speculation about future anthropogenic changes.

Editor: “Abels and Gingerich give a lengthy review that also highlights potential stratigraphic problems. They raise an intriguing point about sedimentation rates, namely that if the two locations had proportional sedimentation, the H-1 and H-2 events should be about 10 m apart at Fifteenmile Creek rather than the 20 m indicated.”

Author: In responding to Abels and Gingerich, I have enhanced discussion of known variation in sediment accumulation rate between faunal events B-1 and B-2.

Editor: “Huber makes some very good points concerning background temperatures for the Early Eocene and rates of temperature change during this time interval. While the PETM and other hyperthermals may be our best analogs for future climate change, they were definitely imperfect analogs. The initial boundary conditions were different; the rates of change in multiple parameters, though very fast from a geological perspective, were very slow compared to those in the modern. As noted above, any linkages between the past and the future need to be written very carefully.”

Author: I have completely removed any speculation about future anthropogenic changes.

Basic Comments:

Editor: “Place references in chronological order as per CoP final papers.”

Author: I followed the Climate of the Past manuscript preparation guidelines, which state: “These references have to be listed alphabetically at the end of the manuscript under the first author's name… In terms of in-text citations, the order can be based on relevance, as well as chronological or alphabetical listing, depending on the author's preference.” I chose alphabetical listing for the in-text citations. Please let me know if this is not acceptable.

Editor: “Some of the writing and referencing is not precise. The referees have given several examples. I give some more below for the first two pages. The manuscript needs a good cleaning before final publication. Please go through the manuscript and make sure all is correct.”

Author: I have attempted to do so.

Introduction – p. 1373

Lines 4-5. First sentence deleted as suggested. Also deleted first sentence of the Abstract, which was similar.

Lines 6-18. Changed to "The late Paleocene and early Eocene (ca. 58–51 Ma) was an interval of global warming and massive inputs of carbon to the ocean and atmosphere (Zachos et al., 2008). Changes in temperature and carbon cycling happened on both long and short time scales. The Earth's surface warmed from the late Paleocene through the Early Eocene, culminating in the Early Eocene Climatic Optimum (EECO), the hottest sustained period of the Cenozoic (~53-50 Ma; Zachos et al., 2001, 2008). Superimposed on this long-term change were several 'hyperthermals', short-term (<100 ka) warming events (Cramer et al., 2003; Lourens et al., 2005). The hyperthermals are marked by large decreases in the δ^{13}C composition of carbon bearing phases in sedimentary strata, which are referred to as carbon isotope excursions (CIEs), and carbonate dissolution in deep-sea sediment. The latter suggests that the hyperthermals were related to massive inputs of reduced carbon to the ocean and atmosphere (Zachos et al., 2005). The most prominent and best known of the hyperthermals is the Paleocene-Eocene Thermal Maximum (PETM) (Zachos et al., 2008; McInerney and Wing, 2011), the onset of which now defines the base of the Eocene (Luterbacher et al., 2000). Comparison of multiple excursions in diverse carbon isotope records from the PETM indicate that several thousand petagrams of reduced carbon were released into the ocean-atmosphere system in <20 ka (review in McInerney and Wing, 2011). This was somehow related to a ~100 ka period of elevated global temperature (5-7 °C warmer) and perturbations in earth surface systems (Bowen et al., 2006; Gingerich, 2006; McInerney and Wing, 2011)" according to suggestion.

Lines 26-27. Changed to "A major advantage of studying records across the late Paleocene-early Eocene interval is the potential to characterize faunal responses to a range of climatic perturbations that occurred over both long and short time scales" according to suggestion.

Introduction – p. 1374

Lines 6-8. Deleted Sexton et al., 2011, and inserted Nicolo et al., 2007, according to suggestion.

Line 10. Changed to "Planktonic assemblages at ETM2 and H2 were somewhat similar to those at the PETM" according to suggestion.

REVIEW BY CLYDE:

1) Major concern: stratigraphic framework of fossils.

Referee: "The Fifteenmile Creek *composite* section (~700 meters thick) used in this study ties together some 410 fossil localities in an area that is roughly 30 km x 40 km by correlating some 44 different local sections (Bown et al., 1994)."

Author: This statement is inaccurate. The entire Fifteenmile Creek (FC) composite stratigraphic section is ~700 meters thick and was created by Bown et al. (1994) from 44 different local sections measured over an area ~3000 km^2. There are more than 1000 localities tied to the composite section. The 410 localities included in this analysis come from a subset of the FC section (290-510m) and are found along the FC (i.e., excluding the Elk Creek area, which is known to be more poorly resolved) in an area that is roughly 40 km by 15 km, although localities and sections only occupy ~300 km^2 of this area. Here, the section is based on 11 major local sections (PD, RWC, RS, RSA, PSB, SD, BW, NF, NFE, S, SF, TM, see Bown et al., 1994, Table 7), and several additional smaller sections that in many cases connect the longer ones. The endpoints of each local section are considerably less than 0.5 km apart in their sequence along the FC, with the exception of a distance of ~5 km between the RSA and SD sections.

Referee: "Although this [the south-central Bighorn Basin] is certainly one of the most densely sampled regions of the world for fossil mammals, the stratigraphic uncertainty in the correlations between local sections and fossil localities must be on the order of at least +/- 10 meters (and probably more) given the difficulty of tracing beds through the low-lying outcrops in this area and the prevalence of "cut and fill" channel structures (Bown et al., 1994). This study, however, assigns a single meter level to each fossil locality with no error."

Author: In fact, in Bown et al. (1994), localities were tied by meter level to the FC stratigraphic section with no error reported. Bown and colleagues' method of sampling and their stratigraphic framework were designed to be resolved to meter-level, as described in their monograph in detail (1994: p. 9-15) It is apparent that great care was undertaken in collecting efforts along the FC from 1975-1994 (and thereafter) to ensure tight stratigraphic control and that the authors believed they were able to achieve meter-level stratigraphic resolution. I asked Bown, the primary author of the FC section, to respond to Clyde's criticism. From his response, it is clear that Bown is strongly convinced that there is no widespread, systematic error in the assessment of the stratigraphic position of localities within the FC section on the order of 10 meters or more. There have been no subsequent studies to test the integrity of the FC section, but nor does Clyde provide any specific evidence to support that there is systematic error in the FC section. Clyde's argument appears to rest on the premise that the FC section is too big and complex (i.e., encompasses a large area and is based on too many local sections) to be resolved to meter level without large errors. I do not believe either size or complexity is a particular barrier to resolution; the FC composite stratigraphic section is the culmination of 20 years of work by a skilled stratigrapher. The local sections are comprehensive, closely spaced and cover all of the area in question.

Referee: "ETM2 and H2 where they have actually been identified by isotopic data in the northern part of the basin are each only ~20 meters thick (and would likely be less than that in the southern part of the basin where sediment accumulation rates are lower)".

Author: This is in fact the case; faunal events B-1 and B-2 are 12-13 meters thick. This coincides closely with expectation, given that the McCullough Peaks section is roughly twice as thick as the FC section in the upper levels, as described by Clyde (2001).

Changes in the manuscript:

Methods – p. 1375

Line 11. Inserted the following "The sampling protocol and resulting stratigraphic section were conceived, designed and implemented with the specific goal of this level of resolution. As described by Bown and colleagues: "Recent collecting operations in the Fifteenmile Creek drainage, beginning under the University of Wyoming auspices in late 1973 and continuing with the U.S. Geological Survey and joint U.S. Geological Survey-Johns Hopkins University School of Medicine expeditions through 1992 [and thereafter], were undertaken, following the

1974 season, with the specific goal of collecting large samples of Willwood vertebrates with tight stratigraphic controls tied to fossil provenances in paleosols. Field collecting began to be consciously restricted to specific stratigraphic intervals that could be related to fossil provenances, and these are almost invariably in paleosols"" to more fully describe the section.

2) Major concern: precise correlation between the isotope and fossil stratigraphic sections.

Referee: "Chew chooses to tie these two frameworks together using the C24r-C24n geomagnetic reversal and the Biohorizon B faunal event. However, there is no discussion of the large uncertainty associated with the correlation of these tie points except to say that "these are rough predictions" (line 14, p. 1376). Can "rough predictions" provide the kind of precise stratigraphic correlation necessary to support the conclusions (and title) of the paper? Unfortunately, I don't think so."

Author: I agree that it is impossible to precisely correlate the McCullough Peaks isotope sections with the FC section given available information. This was not my intention. The hypothesis of this paper can be more clearly stated (borrowing the phrasing of Abels et al., 2012) as follows: two faunal events described in the FC section are hypothesized to be related to the McCullough Peaks isotope excursions based on the proximity of the C24r-C24n.3n magnetic polarity reversal and the Wasatchian 4-Wasatchian 5 biozone boundary, and the pattern of faunal change within each event. Changes in the manuscript described below remove all discussion of, and reference to, the rough correlation I originally attempted to make and restate the hypothesis as described.

Changes in the manuscript:

Abstract – p. 1372

Lines 12-18. Changed to "Two carbon isotope excursions (CIEs) have been described in the northern part of the Bighorn Basin, WY, USA, and related to ETM2 and H2. An ~80-meter thick zone of stratigraphic section in the extraordinarily dense, well-studied terrestrial mammal fossil record along the Fifteenmile Creek (FC) in the south-central part of the basin spans the levels at which the CIEs occur in the northern Bighorn Basin. High-resolution, multi-parameter paleoecological analysis of this part of the FC section reveals two episodes of significant faunal change, faunal events B-1 and B-2, characterized by significant peaks in species diversity and turnover and changes in abundance and relative body size. Faunal events B-1 and B-2 are hypothesized to be related to the CIEs in the northern part of the basin and hence to the climatic and environmental change of ETM2 and H2" to reflect and emphasize the hypothesis as restated above.

Methods – p. 1375-1376

Lines 25-26 and lines 1-17. Changed to "Previous analysis of paleosol carbonates was not sufficiently resolved to demonstrate the CIEs of ETM2 and H2 in the FC section (Fig. 2, Koch et al., 2003).Two CIEs attributed to ETM2 and H2 have been described in two isotope sections in the McCullough Peaks of the northern Bighorn Basin (Abels et al., 2012), where they are found in 60-70 meter thick intervals of mixed geomagnetic polarity between the C24 reversed and C24 normal geomagnetic zones (Fig. 2). Biostratigraphic events at the beginning of Biohorizon B are also tied to the McCullough Peaks isotope sections below the level of the ETM2 and H2 CIEs, including the last appearance of the condylarth *Haplomylus speirianus* and the first appearance of the artiodactyl *Bunophorus etsagicus.* These species co-occur at a single locality (MP 122, ~5 km west of the nearest isotope section) that was traced to near the middle of a ~35 meter thick gap between them in the isotope sections (Fig. 2). The C24r-C24n geomagnetic shift and the nearly simultaneous Biohorizon B biostratigraphic events are also known in the FC section. The C24r-C24n geomagnetic shift occurs at ~455 m in two local paleomagnetic sections measured through the Dorsey and Elk creeks (Clyde et al., 2007). The latter is associated with a 30-meter zone of mixed geomagnetic polarity. The last appearance of *Haplomylus* (and also the condylarth *Ectocion osbornianus* originally described by Schankler (1980) as part of the suite of biostratigraphic events at the beginning of Biohorizon B) and the first appearance of *Bunophorus* occur at ~381 m (this project, Fig. 2) in the FC section. The uncertainties in the stratigraphic position of the C24r-C24n geomagnetic shift and the biostratigrahic events at the beginning of Biohorizon B in the McCullough Peaks isotope sections, as well as pronounced variation in sediment accumulation rate around Biohorizon B in the FC (Bown and Kraus, 1993), preclude precise correlation between the McCullough Peaks isotope sections and the FC fossil record. However, the common occurrence of the C24r-C24n geomagnetic shift and the biostratigrahic events at the beginning of Biohorizon B in both areas indicates that the ~80 meter stretch of the FC section described here documents the interval of Bighorn Basin time in which the CIEs of the McCullough Peaks occur (Fig. 2)." These changes enhance the existing discussion of the uncertainty of the stratigraphic position of events in the McCullough Peaks and FC sections, delete all discussion of rough correlation and explicitly state that precise correlation between the McCullough Peaks and FC sections is not possible but that this part of the FC section includes events also found in the McCullough Peaks isotope sections.

Results – p. 1381-1382

Line 24 and line 1. Deleted the last part of the sentence to remove reference to the rough correlation.

Discussion – p. 1383-1384

Lines 25-27 and line 1. Changed to "Faunal events B-1 and B-2 may be related to the CIEs identified in the McCullough Peaks and thus represent response to the ETM2 and H2 hyperthermals. Faunal events B-1 and B-2 occur above the distinctive biostratigraphic events of Biohorizon B and in close proximity to the C24r-C24n geomagnetic shift, as do the CIEs in the McCullough Peaks (Abels et al., 2012). Faunal events B-1 and B-2 are similar in all aspects of faunal change described here" to reflect and emphasize the hypothesis as restated above.

Lines 11-12 (p. 1384). Changed to "For discussion purposes, it is hypothesized here that there is a relationship between the McCullough Peaks CIEs, ETM2 and H2, and faunal events B-1 and B-2. A critical test of this hypothesis requires directly related isotope data, which are presently unavailable" to reflect and emphasize the hypothesis as restated above.

Discussion – p. 1385-1386

Lines 26-28 and lines 1-6 (p. 1386). "ETM2 and H2" are changed to "Faunal events B-1 and B-2" to reflect and emphasize the hypothesis as restated above.

Discussion – p. 1387

Lines 18-19. Changed to "The turnover within lineages at faunal events B-1 and B-2 suggests that more species were lost through evolutionary transitions at this time" to reflect and emphasize the hypothesis as restated above.

Summary – p. 1389

Lines 16-23. "ETM2 and H2" are changed to "Faunal events B-1 and B-2" to reflect and emphasize the hypothesis as restated above.

Figures – p. 1401-1403

Figures 2 and 4. Modified to explicitly separate the McCullough Peaks and FC records and remove all visual reference to rough correlation and prediction.

Referee: "More recent work in this area has shown clearly that the event labeled H2 in the Gilmore Hill section in Abels et al., 2012 is actually ETM2 (this was presented at the Ferrara 2014 CBEP meeting and is the basis for D'Ambrosia et al., 2014 and Snell et al., 2014 and the details will be part of an upcoming paper by D'Ambrosia based on her Ph.D. thesis work). This pushes the position of Biohorizon B down ~25 meters relative to the hyperthermals and thus fundamentally alters the correlation of the faunal turnover events to the isotopic anomalies (the faunal peaks identified by Chew will now fall below the isotope peaks by ~25 meters)."

Author: I am happy to learn about this unpublished revision of the Gilmore Hill section, information which has evidently been shared with Clyde's student and colleagues but of which I was not aware until now. (Clyde states that this was presented at CBEP but it is not described in either D'Ambrosia et al., 2014, or Snell et al., 2014, which present other research. I attended both talks and took detailed notes, and spoke with Clyde during the meeting, but missed this important information). While certainly relevant to this paper, it does not alter the fundamental relationship of the isotope excursions and faunal events B-1 and B-2 to the biostratigraphic events at the beginning of Biohorizon B. That is, those biostratigraphic events still occur below ETM2 and faunal event B-1. If the biostratigraphic events are now thought to occur ~25 meters lower than the ETM2 isotope excursion in the McCullough Peaks, this translates to a more modest 10-13 meter difference in the FC section, given the differences in section thickness (Clyde, 2001). The additional ~25 meters of thickness between the biostratigraphic events and the ETM2 isotope excursion in the Gilmore Hill section are still less than the ~35 meters of uncertainty associated with the biostratigraphic events in that section.

Referee: “These tie points also have uncertainties in the Fifteen Mile Creek section (unknown for Biohorizon B because it is assigned a single meter level despite previous arguments that it lasted ~300 ky [Chew 2009] and ~13 meters for the C24r-24n reversal [Clyde et al., 2007]).”

Author: Clyde’s concern regarding my assignment of a single meter level to “Biohorizon B” in the FC section stems from a typo on p. 1376. Lines 3-5 on p. 1376 are as follows: “Biostratigraphic events at the beginning of Biohorizon B are also loosely tied to the McCullough Peaks isotope sections, including the last appearance of the condylarth *Haplomylus speirianus* and the first appearance of the artiodactyl *Bunophorus etsagicus.*” I then refer to the “nearly simultaneous Biohorizon B stratigraphic events” in line 9. This should read *biostratigraphic* events. I hope it then becomes clear that the 381-meter level is not assigned to “Biohorizon B”, which I myself have described previously and in this paper as an event spanning 25-40 meters of stratigraphic thickness, but rather to the level at which *Haplomylus* (and *Ectocion*) disappear and *Bunophorus* appears. This does happen nearly simultaneously in the FC section (clearly illustrated in Figure 2) and is documented in the supplementary information. I have corrected the typo.

Referee: “These tie points also have uncertainties in the Fifteen Mile Creek section (unknown for Biohorizon B because it is assigned a single meter level despite previous arguments that it lasted ~300 ky [Chew 2009] and ~13 meters for the C24r-24n reversal [Clyde et al., 2007]).”

Author: I assume that the ~13 meter error for the C24r-24n reversal in the FC section refers to the 30-meter zone of intermediate geomagnetic polarity described in the Elk Creek Rim local paleomagnetic section of Clyde et al. (2007: p. 854). The C24r-24n reversal was assigned to the approximate middle of this zone in the Elk Creek Rim local section to coincide with the level of the reversal in the Dorsey Creek local paleomagnetic section. In the Dorsey Creek local paleomagnetic section, the C24r-24n reversal occurs at “the ~200 m level” with no error described apart from two cryptochrons ~80 m and ~160 m below this level (2007: p. 854). The ~200 m level of the Dorsey Creek local paleomagnetic section corresponds with 455 m in the FC section, whereas there is confusion over the correlation of the Elk Creek and FC sections (Clyde et al., 2007: p. 856-857), which is why no Elk Creek localities are included in this analysis. I chose to describe the C24r-24n reversal as occurring at 455 m (without reported error) in the FC section based on the local paleomagnetic section (Dorsey Creek) that can be directly correlated with the FC section, and to maintain the separation of the Elk and Fifteenmile creeks as clearly advocated in Clyde et al. (2007).

Changes in the manuscript:

Figure – p. 1401

Figure 2. As Clyde here suggests that this zone of mixed polarity in the Elk Creek paleomagnetic section should be interpreted as error in the level of the C24r-24n reversal in the FC section, I have added this zone to Figure 2 accordingly.

Referee: “The easiest and most obvious solution to this problem is to isotopically sample the Fifteenmile Creek localities from which the fossils come so an isotope record showing the precise position of ETM2 and H2 is directly tied to the fossils being analyzed.”

Author: As Clyde is aware, this is a research priority for which I and colleagues have been trying to obtain funding for several years. When we are able to isotopically sample the FC localities, we plan to use the directly related isotope data to test the hypothesis presented herein.

3) Less significant concerns: use of the term EECO.

Referee: “In several places in the paper, Chew suggests that ETM2 and H2 occur during the beginning of the EECO (e.g. line 9 in Abstract, p. 1372) but these events (which are older than 53.5 Ma, Zachos et al. 2010) occur before the EECO (which is 53-51 according to Chew – line 10, p. 1373 - and are considered even younger by many others). This misstatement is repeated many times in the paper and I suggest rewording to align with Line 8 in Introduction (p. 1373) that says “in the approach to the Early Eocene Climate Optimum (EECO)”.”

Author: Following the editor’s discussion of the uncertainty surrounding the characterization of the EECO, I have modified all discussion in the text to reflect least objectionable description of these events as occurring in the “approach to” and “lead-up to” the EECO.

Changes in the manuscript:

Abstract – p. 1372

Lines 9-10. Changed to “The later hyperthermals occurred during warming that resulted in the Early Eocene Climatic Optimum (EECO), the hottest sustained period of the Cenozoic.”

Lines 21-23. Changed to “Response at faunal events B-1 and B-2 is distinctive in its high proportion of species losses potentially related to heightened species vulnerability in response to the changes already underway in the lead-up to the EECO.”

Introduction – p. 1374

Lines 18-20. Changed to “The dense, highly-resolved, well-documented mammal record from the Fifteenmile Creek (FC) in the south-central part of the Bighorn Basin (Fig. 1) chronicles almost the entire early Eocene from the PETM to the beginning of the EECO (Bown et al., 1994b).”

Lines 23-26. Changed to “Biohorizon B marks a major turning point in faunal diversity (Chew and Oheim, 2013) that has been correlated with paleoecological change across North America attributed to the onset of warming in the lead-up to the EECO (Woodburne et al., 2009).”

Methods and materials – p. 1375

Lines 14-16. Changed to “the ^{40}Ar/^{39}Ar date of a volcanic ash indicates that the upper levels are within the beginning of the EECO (Smith et al., 2004; Tsukui and Clyde, 2012).”

Discussion – p. 1386

Lines 2-4. Changed to “Faunal events B-1 and B-2 are set in the context of pronounced climatic, environmental and faunal change attributed to warming in the approach to the EECO (Chew, 2009a; Woodburne et al., 2009).”

Discussion – p. 1387

Lines 14-16. Changed to “In contrast, the CIEs indicating the rapid warming of ETM2 and H2 occurred soon after the onset of the climatic and environmental disturbance at Biohorizon B in the lead-up to the EECO.”

Summary – p. 1389

Lines 18-22. Changed to “Fauanl events B-1 and B-2 are set in the context of pronounced climatic, environmental and faunal change related to warming in the lead-up to the EECO. Faunal events B-1 and B-2 are distinctive in their high proportions of species losses potentially related to heightened species vulnerability in response to the changes already underway in the approach to the EECO.”

4) Less significant concerns: future projections for biotic change.

Referee: “Chew suggests that the changes observed here and at the PETM “will probably occur” in response to current and future anthropogenic warming. I think this discussion needs to at least acknowledge the huge impact that other human activities (e.g. widespread habitat/landscape changes and human controlled dispersal [e.g. invasive species]) have already had on “natural” mammal populations and how those factors could very well swamp any response to climate change. Also, the 12_C temperature change in Wyoming (from 8°C – 20°C MAT) over the next 300 years quoted in this section (Line 15, p. 1388) is way beyond typical predictions. I believe this is due to confusion between Celsius and Fahrenheit temperature scales.”

Author: Clyde’s concern was echoed in Huber’s online review and discussed in our back and forth exchanges. Huber points out that warming of the magnitude of the early Eocene hyperthermals is not likely to be replicated in our future. Thus, the changes documented here are not directly analogous for the future, although as Huber points out they may pertain to other areas under certain scenarios of future warming. In response to Huber’s comments and clarifications, I have removed all discussion of implications for future change.

Changes in the manuscript:

Deleted:

Abstract - p. 1372, lines 26-27

Abstract - p. 1373, lines 1-2

Introduction – p. 1373, lines 23-25

Introduction – p. 1374, lines 1-3

Discussion - section 4.3, p. 1388-1389

Summary - p. 1389, line 26

Summary - p. 1390, lines 1-2

5) Technical corrections.

Those corrections addressed in the previous sections are not repeated here.

Title. Changed to "Mammal faunal change in the zone of the Paleogene hyperthermals ETM2 and H2" according to suggestion.

Abstract – p. 1372
Line 12. Changed to "relatively unknown" according to suggestion.
Line 19. Changed to "is not driven by immigration" according to suggestion.

Introduction - p. 1373
Line 21. Inserted Clyde and Gingerich, 1998 reference according to suggestion.

Introduction - p. 1374
Lines 13-14. Changed to "relatively unknown" according to previous suggestion.

Methods and materials - p. 1375
Line 12. See description of "red 1" in Rose et al. (2012: p. 9 and Fig. 6). No change required.

Methods and materials - p. 1376
Line 4: Deleted "loosely" according to suggestion.
Line 21. Inserted "(as advocated in Clyde et al., 2007)" according to suggestion.

Methods and materials - p. 1377

Line 20. Referee: "More explanation is needed to explain how this analysis of randomly overlapping time bins of different length artificially increases the temporal resolution of the data when the raw data are not sufficiently resolved to begin with. A simple simulation would be helpful to illustrate the point. In essence, it seems to be arguing that you can get better temporal resolution than your original data set by a moving window averaging method but that sounds like a free lunch :)."

Author: The method does not increase the resolution, which I can see I have mistakenly implied in the wording of line 21, p. 1377: "to approximate meter level resolution" and lines 13-14, p. 1381 "indicating an appropriate level of resolution in the averaged parameters (Fig. 4)." This wording has been deleted. The underlying parameter pattern is extrapolated from multiple, overlapping bins. This is now more clearly explained as follows: p. 1377, lines 20-24 "One alternative is to combine the signals of a series of overlapping bins of different lengths (Fig. 3). Bin values are assigned to all meter levels within each bin in each series and then averaged by meter level across all bins. When multiple series are averaged in this way, the average closely approximates the original pattern (e.g., four series of all possible bins of each given bin length are averaged in the binning simulation in Fig. 3)" and p. 1377 lines 26-28 and p. 1378, lines 1-2 "This results in a total of 26 separate binning series, which is prohibitive for the calculation of all parameters. An exhaustive search to minimize gaps and maximize bin sample sizes identified an 'optimal' series at each bin length to be used in the calculation of averaged, standardized parameters. Basing the parameter averages on this subset of optimal binning series slightly reduces the accuracy of the resultant curve (equivalent to the dashed line in Fig. 3)". This is also illustrated with a simulation in Figure 3 as suggested.

Methods and materials - p. 1379
Line 1. Replaced "algorithmic" with "subsampled" according to suggestion.

Methods and materials - p. 1380

Line 23. Referee: "Why sum these metrics instead of just plotting them separately to see if they agree? It seems like summing them unnecessarily masks them (and same question on Line 9, P. 1381)."

Author: All metrics, including alpha and beta richness, evenness and dominance, and rates of first and last appearance, are plotted separately in Figure 4 (and also in the revised Fig. 4) and discussed extensively (both individually and summed) in the Results section, p. 1381-1382 and Discussion section, p. 1386-1388.

Results - p. 1381

Line 18. Referee: “It is absolutely not possible to say with confidence that this 40 meter interval is the same as the ETM2 and H2 interval without having isotope data tied directly to the fossil localities (see detailed discussion above).”

Author: The sentence is: “This analysis demonstrates two distinct events within that 40 m zone, separated by ~10 m (~60 ka) of pre-event parameter values.” The “40m zone” referred to in this sentence has nothing to do with the McCullough Peaks ETM2 and H2 interval. It refers to the previous sentence (lines 14-17): “Three overlapping peaks occur in both sets of parameters (370–394, 405–417 and 435–448m), significantly refining previous work at a coarser resolution (20m thick intervals, =~100 ka), in which a single, 40m thick interval (370–410 m) of biotic change was identified in this part of the FC section (Chew, 2009a).”

Results - p. 1382

Line 28. Referee: “What is meant by “aligned” here. I am assuming it means independently correlated but it sounds like the patterns were wiggle matched which of course would not be appropriate. Assuming independent correlation, there are still all of the issues mentioned above (especially with respect to the updated position of Biohorizon B relative to ETM2 in McCullough Peaks sections).”

Author: The faunal events are independently correlated with the CIEs in the Upper Deer Creek section using the range end-points of species in this part of the section to delimit the stratigraphic range of faunal events B-1 and B-2. I modeled this particular correlation analysis on Clyde and colleagues' alignment of the CIEs from the Bighorn Basin and Walvis Ridge in order to illustrate “the close similarity between the large-scale carbon isotope changes across both hyperthermals” (Abels et al., 2012: p. 2, Fig. 2). Once aligned, I tested the correlation between the parameters calculated from averaged, resampled specimen data and the isotope data to determine whether the variation in the parameters and offsets in their peaks undermine the interpretation of coincident change. The unpublished data pertaining to the Gilmore Hill section and the position of Biohorizon B has no bearing on this alignment. I have changed the wording on p. 1382, line 28 from “aligned” to “independently correlated with the FC section using the stratigraphic ranges of faunal events B-1 and B-2 as determined from species range end-points.”

Results - p. 1383

Line 3. Inserted D'Ambrosia et al. (2014) in the Discussion section, p. 1385, lines 2-4, rather than here as suggested.

Discussion - p. 1384

Line 1. Referee: “Similar to each other?”

Author: The sentence on line 1 seems fairly self-explanatory: faunal events B-1 and B-2 are “similar in all aspects of faunal change described here.” As exhaustively described in the Results section, p. 1381-1383, faunal events B-1 and B-2 exhibit similar changes in richness, evenness, turnover and body size that are in many cases distinct from Biohorizon B.

Line 4. Referee: “Except earlier you indicated that immigration was not important at ETM2 and H2 but it certainly was at PETM.”

Author: The sentence on line 4 seems fairly self-explanatory: “Change at faunal events B-1 and B-2 is superficially similar to that described at the only other well-known early Eocene hyperthermal, the PETM (Gingerich, 1989; Rose et al., 2012; Secord et al., 2012), including increases in diversity and turnover and a general shift towards smaller body size.” The *superficial* similarities include increases in diversity and turnover and smaller body sizes. In the very next paragraph, I describe in detail the differences between the PETM and faunal events B-1 and B-2, focusing on immigration and the extent of body size decrease.

Discussion - p. 1385

Line 1. Inserted Clyde and Gingerich, 1998 reference here according to suggestion.

Line 15. Referee: “Snell et al., 2014 should be cited here as it is the first to give absolute temp estimates for these hyperthermals in the Bighorn Basin.”

Author: Snell et al. (2014) dispute the scaling of CIE and temperature change as discussed in this sentence. I insert this reference as “(but see Snell et al., 2014).”

Discussion - p. 1386

Line 7: Referee: “Not clear what this means given these are the sections where the CIEs are actually documented.”

Author: The sentence is: “there is no evidence of a CIE in the McCullough Peaks isotope sections of Abels et al. (2012) to suggest a hyperthermal mechanism”. I have added “at Biohorizon B” to the end of the sentence to clarify.

Line 16: Referee: “Onset of what change? To be clear, Biohorizon B does not correlate to ETM2 or H2 just as Abels et al 2012 argued and is further supported in this analysis.”

Author: The sentence is: “Biohorizon B, the largest faunal event in the FC record after the PETM, coincides with the onset of this change”. I have added “with the onset of this warming, lithological and floral change”, which are described in detail in the preceding part of the paragraph, p. 1386, lines 1-15 and which constitute the change to which this sentence refers.

Discussion - p. 1387

Line 10. Inserted “in this basin” according to suggestion.

Summary - p. 1389

Line 17. Changed to “is not fueled by immigration” according to suggestion.

Tables - p. 1398

Table 1 caption. Inserted “what are thought to be” according to suggestion.

Figures p. 1401

Figure 2. Referee: “Could the peaks in abundance be driving your peaks in turnover? These should be shown side-by-side or correlated to make sure that sampling is still not influencing the turnover results.”

Author: I have revised Fig. 2 to show the entire size distribution of the binning series, rather than the subset that was originally pictured. I have revised Fig. 4 to show the averaged, binned sampling distribution (prior to standardization) side-by-side with the results to illustrate that there is no significant correlation except for richness. The correlation with alpha richness is weak (r=0.28, p=0) and with beta richness is strong (r=0.91, p=0). Previous analysis (Chew and Oheim, 2013) demonstrated significantly higher beta richness in this part of the section even in samples that were rigorously standardized for both sample size and area. Given the lack of correlation in the other parameters, the weak correlation with alpha richness, and the results of previous work just described, I do not believe that the significant correlation between the original sampling distribution and the beta richness parameter indicates uncorrected sample size bias but rather independent increases in preservation (sampling) and differentiation across the landscape (beta richness).

Changes in the manuscript:

Results – p. 1382

Line 25. Inserted “Only the richness parameters are significantly correlated with the averaged, binned sampling distribution, which might suggest lingering sample size bias in spite of the extensive standardization instituted here. The correlation between alpha richness and the averaged, binned sampling distribution is weak (Spearman’s $\rho=0.28$, $p=0.00$), with many of the peaks in alpha richness corresponding to lows in sampling. The correlation between beta richness and the original sampling distribution is strong (Spearman’s $\rho=0.91$, $p=0.00$), but previous work (Chew and Oheim, 2013) demonstrated an increase in beta richness in this part of the FC section in samples that were rigorously standardized for both sampling and area variation, to the latter of which beta richness is particularly susceptible. Combined with the lack of correlation with the other parameters and weak correlation with alpha richness, this suggests that the strong correlation between beta richness and the averaged, binned sampling distribution reflects independent trends of an increase in preservation (sampling) and differentiation across the landscape (beta richness)” to clarify the relationship of sample size.

Figures - p. 1403

Figure 4. Referee: “The relative spacing between ETM2 and H2 and the tie points shifts between the bottom bar (which I assume represents the McCullough Peaks record?) and the upper graphs. Why would that be if the McCullough Peaks spacing of these events is being used as the independent guide to

interpreting the turnover curves? The caption needs a lot more detail to explain this as well as what all of the different color curves represent."

Author: The first part of Clyde's concern has been addressed in previous revisions. For increased clarity, the parameters have been color coded and this color coding is described in the revised figure caption as suggested.

REVIEW BY ABELS AND GINGERICH:

Additional comments not addressed in my response to the review by Clyde:

Referees: “For these correlations, the position of the first normal polarity related to C24n.3n at McCullough Peaks is used, which is however preceded by an interval of nearly 60m of uncertain polarity at McCullough Peaks. For the correlation, the magnetochron boundary should thus be positioned in the middle of this uncertain polarity interval with ~30 m of uncertainty above and below,”

Author: In one of the two geomagnetic sections in the south-central part of the Bighorn Basin (Elk Creek Rim local section, Clyde et al., 2007), the shift to C24n.3n occurs in an analogous zone of ~30m of uncertain polarity. Both zones encompass the H2 CIE and the B-2 faunal event and do not alter the clear proximity of this geomagnetic event to them.

Referees: “In the correlations made by Chew, ETM2 and H2 are placed between 410–420 m and between 430–440 m, respectively. This results in sedimentation rates of 0.165 m/kyr at Fifteenmile Creek.”

Author: The 0.165 m/kyr sediment accumulation rate is an average over ~450 meters of stratigraphic thickness from the PETM to the C24r-C24n geomagnetic polarity shift. In the next paragraph (lines 16-17, p. 1376), I point out that there is “variation in sediment accumulation rates [in the FC] over time, especially around Biohorizon B (Bown and Kraus, 1993; Clyde, 2001).” This variation is described in Bown and Kraus (1993: p. 73) as both long-term and punctuated at the 75-150 m, 200-250 m, 375-425 m and 600-625 m intervals. The third of these punctuated episodes of increasing sediment accumulation rate encompasses Biohorizon B and faunal event B-1. This variation, averaged over several hundred meters of section, severely limits the utility of the 0.165 m/kyr sediment accumulation rate in reconstructing time in this part of the FC section.

Referees: “The B-1 and B-2 events are however tied to diversity peaks at about 410 and 440 m, respectively, meaning that they are separated by about about 30 m and 181 kyr. Both separations at Fifteenmile Creek are substantially longer than the 100-kyr eccentricity-cycle spacing of the ETM2 and H2 hyperthermals.”

Author: In fact, this overestimation is to be expected, given the marked acceleration in sediment accumulation rate near the beginning of, or between, faunal events B-1 and B-2. I did not go into accumulation rates and the temporal separation of faunal events B-1 and B-2 in the paper because I thought it was apparent from the published work describing rate variation, especially around Biohorizon B, that this exercise would be futile.

Changes in the manuscript:

Methods – p. 1375

Lines 22-24. Inserted “although variation in sediment accumulation rate, particularly in this part of the FC section (Bown and Kraus, 1993), severely limits the utility of such estimates” to the end of the last sentence in the first paragraph of the methods to clarify and emphasize the variation in sediment accumulation rates.

Results – p. 1381-1382

Lines 16, 19 and lines 2, 16 (p. 1382). Deleted the estimates of event durations based on the 0.165 m/kyr sediment accumulation rate and removed the absolute ages from the scale bar in Fig. 2 in order to eliminate any misleading impression of reliance on this rate.

Referees: “These are the two narrow stratigraphic intervals that have yielded some 15–20 times more specimens than others in the broader Fifteenmile Creek interval being correlated to McCullough Peaks.”

Author: I do not deny that there is great sampling discrepancy. It is why I instituted such exhaustive standardization procedures (binning, resampling, rarefaction, instantaneous, per-taxon rates, etc.). Nevertheless, Abels and Gingerich exaggerate. The “narrow stratigraphic intervals” documenting faunal events B-1 and B-2 are each ~13 meters thick and their average sample size (3728 specimens) is seven times greater than the average sample size (506 specimens) of all 13-meter intervals in the series beginning directly below faunal event B-1 (range of 4-9 times greater for all but two of the individual 13-meter intervals below faunal event B-1). The average sample size of the B-1 and B-2 intervals is twice that of the 13-meter intervals between them (1959 specimens), and the average sample size of all 13-meter intervals in the series beginning directly above faunal event B-2 (4746 specimens) is actually 30% larger than the average sample size of the B-1 and B-2 intervals. All but one of the 13-meter intervals above faunal event B-2 is between 1.2 and 1.8 times greater than the average sample size of the B-1 and B-2 intervals. From this, it should be clear that there is a long-term trend of increasing sample size of which faunal events B-1 and B-2 are part. As indicated in my response to Clyde's review, I have added the entire sampling distribution of the binning series to Fig. 2, which demonstrates this variation more clearly.

Referees: "A discrepancy in sampling this large is difficult to overcome statistically because standardized comparison requires degrading the better samples for comparison with the poorer ones, and the poorer samples in this case are biased in lacking many of the smaller and rarer taxa that only appear when samples are large."

Author: Yes, this is unfortunately necessary and the explicit point of the resampling and rarefaction techniques used in this paper. The alternative is that paleoecological (or other) analysis can only be done when all samples are equally well (or poorly) represented, which is not practical in paleontological scenarios. The FC fossil record is widely regarded as exceptional. I am not aware of any better records with which to attempt just such an analysis as this.

Referees: "The intervals identified as B-1 and B-2 are exceptionally fossiliferous, have been more intensely sampled than other intervals, or both (collectors naturally focus on productive intervals). B-1 and B-2 stand out for being rich and well sampled, but this does not make them biotic events. And the presence of two rich, well-sampled intervals at Fifteenmile Creek does not mean the intervals coincide with ETM2 and H2."

Author: I have demonstrated that the B-1 and B-2 intervals are not exceptionally fossiliferous relative to the intervals above, and are clearly part of a long-term trend of increasing sample size. In my response to Clyde's review and related revisions, I have further demonstrated that the standardization techniques used in this paper were adequate to remove sample size bias from the averaged, binned paleoecological parameters.

Referees: "The new postulates, that ETM2 was the driver of B-1 and that H2 was the driver of B-2, are testable hypotheses, but the postulates will only be tested when ETM2 and H2 δ13C anomalies are found in the same stratigraphic section as B-1 and B-2. Pending documentation of the ETM2 and H2 δ13C anomalies at Fifteenmile Creek, it seems too premature to claim B-1 and B-2 as faunal responses to the hyperthermals ETM2 and H2."

Author: In response to Clyde's review, I have explicitly restated my hypothesis as follows: two faunal events described in the FC section are hypothesized to be related to the McCullough Peaks isotope excursions based on the proximity of geomagnetic and biostratigraphic events, and the pattern of faunal change within each event. Within a brief (~450 kyr) interval of Bighorn Basin time, there were two pronounced CIEs interpreted to represent significant climatic and environmental change *AND* two pronounced, rapid, and appropriately scaled (in terms of section thickness) events of significant faunal change. The hypothesis that they are related is more reasonable and parsimonious than the alternative, which is that the faunas were immune to the climatic and environmental change indicated by the isotope excursions, instead experiencing within this brief interval two other, unassociated episodes of significant change related to some as-yet unknown external perturbations or to intrinsic controls. Abels and Gingerich suggest that this hypothesis is not sufficiently supported without directly-related isotope data. I argue that directly-related isotope data would constitute a critical test of the hypothesis presented herein, but such data are not currently available.

REVIEW BY GUNNELL

Additional comments not addressed in my response to the review by Clyde:

Referee: “Beyond that the complex data manipulation, rarefying, and resampling involved in producing ’comparable’ faunal sample bins makes one wonder what actual biological reality is being compared and contrasted.”

Author: The concepts of species richness, evenness, turnover and body size change are widely employed in paleoecological analysis and are defined and described in detail in the Methods section 2.3 (and references therein). The ‘manipulated’ data are also plotted against non-standardized (i.e., non-manipulated) rates of species first and last appearances, turnover and range-through species richness in Fig. 4.

Referee: “This is especially true given that no central basin localities are precisely stratigraphically controlled enough to be able to eliminate or minimize time averaging in these surface collected samples. It may be a case of trying to look too closely at data that simply can’t answer the questions being asked, at least at the resolution required to test the potential correlations between these two hyperthermal events and these two potential faunal turnovers, if that is, in fact, what they are.”

Author: The precision of the stratigraphic framework of the FC fossil localities was also one of Clyde’s main criticisms and was addressed extensively in my response to his review. In regards to time averaging, which is an issue here and in all surface lag deposits throughout the Bighorn Basin, it apparently did not interfere with the recovery of the ETM2 and H2 CIEs in the McCullough Peaks (Abels et al., 2012). I see no reason to believe that it is any worse in the FC or would preclude recovery of a related faunal signal in the FC.

Technical corrections:

Introduction – p. 1374
Line 2. Corrected spelling.

Methods and materials – p. 1380
Line 16. The Caron and Jackson reference is added to the reference list and provided here:
Caron, J. B., and Jackson, D. A.: Paleoecology of the Greater Phyllopod Bed community, Burgess Shale: Palaeogeogr. Palaeocl., 258(3), 222-256, 2008.

Referee: “I found most of the Figures to be adequate but difficult to decipher based on the minimal captions.”

Author: I have expanded all figure captions.

REVIEW BY HUBER

Referee: “So, I would argue that the various elements of the argument (extreme warmth/high heat stress conditions relative to modern, impact on fauna’s and ecosystems) presented in this paper hold up, just not on a time scale or climate change magnitude relevant to the near-future of Earth. The far future, perhaps.”

Author: I have completely removed any speculation about future anthropogenic changes.

Mammal faunal ~~response to~~ change in the zone of the Paleogene hyperthermals ETM2 and H2.

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Abstract.

~~Scientists are increasingly turning to deep-time fossil records to decipher the long-term consequences of climate change in the race to preserve modern biotas from anthropogenically driven global warming.~~ ‘Hyperthermals’ are past intervals of geologically rapid global warming that provide the opportunity to study the effects of climate change on existing faunas over thousands of years. A series hyperthermals is known from the early Eocene (~56-54 million years ago), including the Paleocene-Eocene Thermal Maximum (PETM) and two subsequent hyperthermals, Eocene Thermal Maximum 2 (ETM2) and H2. The later hyperthermals occurred ~~following the onset of~~during warming ~~at~~ ~~leading~~that resulted in ~~to~~ the Early Eocene Climatic Optimum (EECO), the hottest sustained period of the Cenozoic. The PETM has been comprehensively studied in marine and terrestrial settings, but the terrestrial biotic effects of ETM2 and H2 are relatively unknown. ~~Their~~ Two carbon isotope excursions (CIEs) ~~geochemical signatures~~ have been ~~located~~ described in the northern part of the Bighorn Basin, WY, USA, and related to ETM2 and H2~~,~~. ~~and their levels can be extrapolated to~~An ~8~~5~~0-meter thick zone of stratigraphic section in ~~an~~ the extraordinarily dense, well-studied terrestrial mammal fossil record along the Fifteenmile Creek (FC) in the south-central part of the basin spans the levels at which the CIEs occur in the northern Bighorn Basin. High-resolution, multi-parameter paleoecological analysis of this part of the FC section reveals two episodes of significant faunal change, faunal events B-1 and B-2, characterized by significant peaks in species diversity and turnover and changes in abundance and relative body size ~~at the levels of ETM2 and H2 in the south-central Bighorn Basin record~~. Faunal events B-1 and B-2 are hypothesized to be related to the CIEs in the northern part of the basin and hence to the climatic and environmental change of ETM2 and H2. In contrast with the PETM, ~~faunal~~ change at ~~the later hyperthermals~~faunal events B-1 and B-2 is less extreme, ~~does not include~~is not driven by immigration and involves a proliferation of body sizes, although abundance shifts tend to favor smaller congeners. ~~Faunal r~~Response at ~~ETM2 and H2~~faunal events B-1 and B-2 is distinctive in its high proportion of species losses potentially related to heightened species vulnerability in response to ~~the~~ changes already underway ~~at the beginning of~~in the lead-up to the EECO. Faunal response at ~~ETM2 and H2~~faunal events B-1 and B-2 is also distinctive in high proportions of beta richness, suggestive of increased geographic dispersal related to transient increases in habitat (floral) complexity

and/or precipitation or seasonality of precipitation. ~~These results suggest that rapid ecological changes, increased heterogeneity in species incidence, and heightened species vulnerability and loss may be expected across most of North America in the near future in response to anthropogenically-driven climate change.~~

1 Introduction

~~Contemporary scientific priorities include the study of past geobiological systems to predict Earth system response to climate forcing (National Research Council, 2011).~~ The late Paleocene and early Eocene (ca. 58–51 Ma) was an interval of global warming and massive inputs of carbon to the ocean and atmosphere (Zachos et al., 2008). Changes in temperature and carbon cycling happened on both long and short time scales. The Earth's surface warmed from the late Paleocene through the Early Eocene, culminating in the Early Eocene Climatic Optimum (EECO), the hottest sustained period of the Cenozoic (~53-50 Ma; Zachos et al., 2001, 2008). Superimposed on this long-term change were several 'hyperthermals', short-term (<100 ka) warming events (Cramer et al., 2003; Lourens et al., 2005). The hyperthermals are marked by large decreases in the δ^{13}C composition of carbon bearing phases in sedimentary strata, which are referred to as carbon isotope excursions (CIEs), and carbonate dissolution in deep-sea sediment. The latter suggests that the hyperthermals were related to massive inputs of reduced carbon to the ocean and atmosphere (Zachos et al., 2005)~~The early Eocene (~56-52 Ma) is particularly relevant for understanding modern anthropogenic warming as it witnessed global temperature fluctuation including several hyperthermals (intervals of geologically rapid global warming) in the approach to the Early Eocene Climatic Optimum (EECO), the hottest sustained period of the Cenozoic (53-51 Ma, Zachos et al., 2008)~~. The ~~largest~~ most prominent and best known of the hyperthermals is the Paleocene-Eocene Thermal Maximum (PETM) (Zachos et al., 2008; McInerney and Wing, 2011), the onset of which now defines~~ at~~ the base of the Eocene ~~(Kennett and Stott, 1991; Zachos et al., 1993)~~ (Luterbacher et al., 2000). Comparison of multiple e~~E~~xcursions in ~~multiple~~ diverse carbon isotope records ~~(carbon isotope excursions, CIEs) at~~from the PETM indicate that several thousand petagrams of reduced carbon were released into the ocean-atmosphere system in <20 ka (review in McInerney and Wing, 2011). This ~~initiated~~ was somehow related to a ~100 ka period of elevated global temperature (5-7 °C warmer) and perturbations in ~~Earth's carbon cycling, ocean chemistry and plankton communities~~ earth surface systems (Bowen et al., 2006; Gingerich, 2006; McInerney and Wing, 2011). On land, biotic response to the PETM is best known from the fossil record of the Bighorn Basin in northwestern Wyoming, which documents major intra- and intercontinental immigration, widespread temporary dwarfing, and changes in the diversity, trophic structure and physiology of floras and faunas (Clyde and Gingerich, 1998; Currano et al., 2008; Gingerich, 1989; Gingerich and Smith, 2006; Rose et al., 2012; Secord et al., 2012; Smith et al., 2009; Wing et al., 2005; Yans et al., 2006). ~~The PETM has been described as the best deep-time analogue for anthropogenic climate warming (Bowen et al., 2006; Gingerich, 2006; McInerney and Wing, 2011).~~

A major advantage of studying records across the late Paleocene-early Eocene interval is the potential to characterize faunal responses to a range of climatic perturbations that occurred over both long and short time scales~~deep-time records is the potential for documentation of multiple events, providing the opportunity to characterize faunal response to climate change of varying rate and magnitude against different background conditions. Consistencies in faunal respsonse under specific conditions strengthen the case for causality and can be used for predictive purposes.~~

Two additional early Eocene hyperthermals, Eocene Thermal Maximum 2 (ETM2=H1) and H2 (Cramer et al., 2003; Lourens et al., 2005), occurred ~2 ma after the PETM, constituting what is effectively a set of *repeated* natural experiments in climate change. The CIEs of ETM2 and H2 are similar but one half to one third the magnitude of the PETM CIE (Lourens et al., 2005; Nicolo et al., 2007; Stap et al., 2010)~~(Lourens et al., 2005; Sexton et al., 2011; Stap et al., 2010)~~. They occurred when the Earth was warmer and may have pushed high-latitude temperatures to greater extremes than the PETM (Sluijs et al., 2009). ~~Changes in plankton~~Planktonic assemblages at ETM2 and H2 were somewhat similar to those at the PETM, ~~with~~ and the degree of response was proportionate to the magnitude of the CIEs (Foster et al., 2013; Gibbs et al., 2012; Sluijs et al., 2009; Stassen et al., 2012). However, in stark contrast with the well-studied PETM, terrestrial biotic response to ETM2 and H2 is ~~currently~~ relatively unknown. The ETM2 and H2 CIEs have been documented in the northern part of the Bighorn Basin (Abels et al., 2012) and from one other terrestrial sequence in India (Clementz et al., 2011), but neither record includes sufficient fossils to permit testing of faunal response.

The dense, highly-resolved, well-documented mammal record from the Fifteenmile Creek (FC) in the south-central part of the Bighorn Basin (Fig. 1) chronicles almost the entire early Eocene from the PETM to the beginning of the EECO (Bown et al., 1994b). The largest sample of PETM mammals has been studied and described from the FC record (Rose et al., 2012) along with other faunal events or ‘biohorizons’, the largest of which after the PETM is Biohorizon B (Chew, 2009a; Schankler, 1980). Biohorizon B marks a major turning point in faunal diversity (Chew and Oheim, 2013) that has been correlated with paleoecological change across North America attributed to the onset of warming in the lead-up to~~at~~ the EECO (Woodburne et al., 2009). In the northern Bighorn Basin isotope record, the CIEs of ETM2 and H2 occur ~60-80 ka after biostratigraphic events at the beginning of Biohorizon B (Abels et al., 2012) but there is no obviously correlated faunal change after Biohorizon B in the FC record (Chew, 2009a, b; Chew and Oheim, 2009). This lack was interpreted as biotic insensitivity to ETM2 and H2 (Abels et al., 2012). However, no previous analysis of the FC record achieved sufficient resolution to detect faunal perturbation at the scale of the hyperthermals (~40 ka). This report describes the first high-resolution, multi-parameter paleoecological analysis of the exceptional FC record ~~to test mammal faunal response to ETM2 and H2~~to characterize mammal faunal change in the zone of the ETM2 and H2 hyperthermals.

2 Methods and Materials

2.1 Collections

The low angle of dip and wide area of exposure along the Fifteenmile Creek (FC) in the south-central part of the Bighorn Basin (Fig. 1) ~~allows~~ has permitted tying Willwood Formation (early Eocene) fossil localities ~~to be tied~~ by meter level to a composite stratigraphic section of ~700 m (Bown et al., 1994b). The sampling protocol and stratigraphic section were conceived, designed and implemented with the specific goal of this accuracy of resolution. As described by Bown and colleagues: "Recent collecting operations in the Fifteenmile Creek drainage, beginning under the University of Wyoming auspices in late 1973 and continuing with the U.S. Geological Survey and joint U.S. Geological Survey-Johns Hopkins University School of Medicine expeditions through 1992 [and thereafter], were undertaken, following the 1974 season, with the specific goal of collecting large samples of Willwood vertebrates with tight stratigraphic controls tied to fossil provenances in paleosols. Field collecting began to be consciously restricted to specific stratigraphic intervals that could be related to fossil provenances, and these are almost invariably in paleosols." The base of the FC section (0 m) rests on a distinctive red bed that marks the beginning of the PETM at Sand Creek Divide on the eastern edge of the study area (Rose et al., 2012). The C24r-C24n geomagnetic polarity shift has been located near the middle of the section (~455 m, Clyde et al., 2007). Near the top of the section (634 m), the ^{40}Ar/^{39}Ar date of a volcanic ash indicates that the upper levels are within the beginning of the EECO (Smith et al., 2004; Tsukui and Clyde, 2012) ~~(Smith et al., 2004)~~. Numerical ages (56.33 Ma, 53.57 Ma, and 52.9 Ma, respectively) are assigned to these three tie points following the recent regional recalibration of Tsukui and Clyde (2012). Average sediment accumulation rates between the tie points increase from 0.165 m·ka^{-1} to 0.267 m·ka^{-1} above the C24r-C24n geomagnetic polarity shift~~,~~ ~~which is in broad agreement with previous analysis of depositional rates based on paleosols (Bown and Kraus, 1993)~~. These rates suggest that one meter of FC section thickness represents ~6 ka in the lower levels and ~4 ka above the C24r-C24n geomagnetic polarity shift although variation in sediment accumulation rate, particularly in this part of the FC section (Bown and Kraus, 1993), severely limits the utility of such estimates.

Previous analysis of paleosol carbonates was not sufficiently resolved to demonstrate the CIEs of ETM2 and H2 in the FC section (Fig. 2, Koch et al., 2003).~~ but their levels can be extrapolated~~Two CIEs attributed to ETM2 and H2 have been described in ~~from isotopic work~~two isotope sections in the McCullough Peaks of the northern Bighorn Basin (Abels et al., 2012), where they are found ~~. Abels et al. (2012) identified the CIEs of ETM2 and H2 within an~~ in 60-70 meter thick intervals of mixed geomagnetic polarity ~~below the shift from~~between the C24 reversed ~~to~~ and C24 normal geomagnetic zones (Fig. 2). Biostratigraphic events at the beginning of Biohorizon B are also ~~loosely~~ tied to the McCullough Peaks isotope sections below the level of the ETM2 and H2 CIEs, including the last appearance of the condylarth *Haplomylus speirianus* and the first appearance of the artiodactyl *Bunophorus etsagicus*. These species co-occur at a single locality (MP 122, ~5 km west of the nearest isotope section) that was traced to near the middle of a ~35 meter thick gap between them in the isotope sections (Fig. 2). The C24r-C24n geomagnetic shift and the nearly simultaneous Biohorizon B biostratigraphic events ~~bracket the ETM2 and H2 CIEs and~~ are also known in the FC section. The C24r-C24n geomagnetic shift occurs at ~455 m in two local paleomagnetic sections measured through the Dorsey and Elk creeks (Clyde et al., 2007). The latter is associated with a 30-meter zone of mixed geomagnetic polarity. The last appearance of *Haplomylus* (and also the condylarth *Ectocion osbornianus* originally described by Schankler (1980) as part of the suite of biostratigraphic events at the beginning of Biohorizon B) and the first appearance of *Bunophorus* occur at~~ and~~ ~381 m (this project, Fig. 2) in the FC section. ~~Between these tie points, the McCullough Peaks sediments are roughly 42% thicker than the FC sediments. Scaling the McCullough Peaks sections by x0.68 allows the extrapolation of ETM2 and H2 to the 410-420 m and 430-440 m levels, respectively, of the FC section. These are rough predictions due to the uncertainty associated with the level of the biostratigraphic events in the McCullough Peaks and to variation in sediment accumulation rates over time, especially around Biohorizon B (Bown~~

~~and Kraus, 1993; Clyde, 2001).~~ The uncertainties in the stratigraphic position of the C24r-C24n geomagnetic shift and the biostratigrahic events at the beginning of Biohorizon B in the McCullough Peaks isotope sections, as well as pronounced variation in sediment accumulation rate around Biohorizon B in the FC (Bown and Kraus, 1993), preclude precise correlation between the McCullough Peaks isotope sections and the FC fossil record. However, the common occurrence of the C24r-C24n geomagnetic shift and the biostratigrahic events at the beginning of Biohorizon B in both areas indicates that the ~80 meter stretch of the FC section described here documents the interval of Bighorn Basin time in which the CIEs of the McCullough Peaks occur (Fig. 2).

All specimens included in this project were collected from 410 fossil localities spanning 290-510 m in the FC section. Neighboring localities along the Elk Creek (Fig. 1) have also been tied to the FC section but are excluded from this analysis (as advocated in Clyde et al., 2007) because of differences in section thickness (up to 70 m, Bown et al., 1994b) that would compromise resolution. This exclusion results in comparatively limited sample sizes below ~370 m (Fig. 2). More than 32,000 specimens are included in this study (Table S1), representing 103 lineages and species (Table S2, 68 genera, 27 families, 16 orders). Of these, >1100 are recently collected specimens (2004-2011 field seasons) not included in previous paleoecological analyses (Chew, 2009a, b; Chew and Oheim, 2009; Chew and Oheim, 2013). Specimens are identified to species level (as in Chew, 2009a). Singleton taxa and stratigraphic outliers are excluded to avoid inflation of paleoecological parameters and loss of resolution. Species with single occurrences in this dataset that are not excluded (Table S2) are known to have existed below 290 m and/or above 510 m. A stratigraphic outlier is defined as a well-documented, clearly identifiable individual recovered ~50-~100 m outside of the stratigraphic range of the species. Seven stratigraphic outliers were identified and excluded (*Anacodon ursidens* - Condylarthra, *Apatemys rodens* - Apatotheria, *Bunophorus etsagicus* and *Bunophorus grangeri* - Artiodactyla, *Lambdotherium* - Perissodactyla, *Pachyaena ossifraga* – Mesonychia, *Palaeictops bicuspis* – Leptictida).

2.2 Specimen data binning

The specimen data are binned by meter level, providing the maximum possible resolution (~4-~6 ka). At this resolution, stratigraphic gaps constitute ~40% of the record and there are large disparities in sample size (0-~3000 specimens/meter) and a trend of increasing sample size over time (Spearman's ρ=0.19, $p<0.05$), all of which complicate the calculation and interpretation of paleoecological parameters. Although longer data bins decrease resolution, they eliminate gaps and allow extensive sample size standardization, permitting the calculation of multiple, complimentary and unbiased paleoecological parameters. Five meters is the minimum bin thickness that eliminates all gaps in the zone in which ETM2 and H2 must occur (370-455 m) in the FC section. However, each five-meter bin represents ~30 ka, which approaches the length of the hyperthermals under investigation and makes it impossible to construct a single binning series that divides the section appropriately to capture each event. One alternative is to ~~approximate meter-level resolution through the combination of~~combine the signals of a series of ~~randomly~~ overlapping bins of different lengths (Fig. 3). Bin values are assigned to all meter levels within each bin in each series and then averaged by meter level across all bins. When multiple series are averaged in this way, the average closely approximates the original pattern (e.g., four series of all possible bins of each bin length are averaged in the binning simulation in Fig. 3). Four series of equal-time data bins are created here ~~through an exhaustive search to eliminate gaps and maximize sample sizes~~ at five-, six-, seven- and eight-meter bin lengths (Table S3). (To accommodate increasing sediment accumulation rate above ~455 m, the bins in each series are lengthened accordingly; 5-7 m, 6-8 m, 7-10 m, and 8-11 m). This results in a total of 26 separate binning series, which is prohibitive for the calculation of all parameters. An exhaustive search to minimize gaps and maximize bin sample sizes identified an 'optimal' series at each bin length to be used in the calculation of averaged, standardized parameters. ~~Collectively, the binning series provide continuous coverage and sample sizes >100 specimens from 376-505 m in the FC section. Paleoecological parameters are calculated for each series. Parameter values are assigned to all meter levels within each bin in each series and then averaged by meter level across all bins.~~ Basing the parameter averages on this subset of optimal binning series slightly reduces the accuracy of the resultant curve (equivalent to the dashed line in Fig. 3). To test the accuracy ~~of resolution~~ of the binning protocol, the binned, averaged parameters are compared with (sample-size biased) parameters calculated from specimen data binned by meter level where possible.

Each binning series provides species abundance data and the levels of species first and last appearances within the stratigraphic range of this dataset. An algorithm is used to standardize these data by randomly sampling (without replacement) each bin to a sample size of 100 specimens. This process is repeated a specified number of times. From each run through each binning series the algorithm tabulates species first and last appearances and the total number of range-through species per bin (assumed present if found in bins above and below a gap). The algorithm is modified from a previous version (Chew, 2009a) to discount first and last appearances that occur outside of the stratigraphic range of this dataset to reduce edge effects (Foote, 2000). From each set of repeated runs for each binning series, average first and last appearance and range-through species data are produced per bin, as well as the average number of times each species occurs in each bin. The latter are multiplied by the species' relative abundance in each bin to create standardized proportional relative abundances.

2.3 Paleoecological parameters

To characterize the FC mammal fauna, fundamental concepts in paleoecology are parameterized, including diversity, the interplay between species richness and the evenness of abundance distributions, and turnover, compositional change through evolution and migration. These are complex, multifactorial concepts and diversity in particular is often oversimplified (Magurran, 2004). Here, diversity is represented as variation in the average number of species in assemblages (alpha richness), the differentiation in richness between assemblages (beta richness), the equality of species relative abundances (evenness) and the commonness of one or a few species (dominance). Turnover is characterized by rates of species first and last appearances. Most of the parameters are dependent on sample size and are standardized or calculated from the standardized appearances and relative abundances provided by the ~~algorithmic~~ subsampled treatment of the binned data.

2.3.1 Richness. Richness is the number of species present in a sample and is highly dependent on sample size. Where samples allow (>100 specimens, continuously distributed), rarefaction is used to produce standardized estimates of richness (Colwell, 2013; Holland, 2003). Alpha (average, within-sample) richness is estimated using conventional, individual-based rarefaction (IR, Fig. 3), which plots the number of species found through the accumulation of individuals (Hurlburt, 1971; Sanders, 1968). Point estimates of alpha richness at a sample size of 100 specimens are directly comparable between samples. To estimate beta (differentiation between sample) richness, sample-based rarefaction (SR, Fig. 3) is used, which plots the number of species that are found through the accumulation of samples (Chiarucci et al., 2008; Colwell et al., 2004; Gotelli and Colwell, 2001). SR is dependent upon the spatial distribution of specimens. In the presence of distributional heterogeneity, SR richness estimates are lower than IR richness estimates, as IR assumes a random distribution of individuals and produces a curve of maximal, theoretical richness (Colwell et al., 2004; Foote, 1992; Gotelli and Colwell, 2001; Olszewski, 2004). The difference between IR and SR curves reflects beta richness (Crist and Veech, 2006; Gotelli and Colwell, 2001; Olszewski, 2004) and is largest near the base of the SR curve (Fig. 3). Comparable IR and SR point richness estimates from the base of each SR curve are used to estimate beta richness (as in Chew and Oheim, 2013). Gamma (total landscape) richness is the sum of alpha and beta richness.

2.3.2 Evenness. Aspects of evenness are independent of sample size, but evenness is difficult to characterize (Magurran, 2004). Two indices are used here, both calculated from standardized proprotional relative abundances. The first is the well-known Probability of Interspecific Encounter, *PIE*, index (Hurlburt, 1971), which is the inverse of Simpson's dominance index standardized for finite collection size.

$$PIE = 1 - \left[\sum_{i=1}^{s} n_i(n_i - 1)/N(N - 1)\right], \qquad (1)$$

where n_i is the number of specimens of species 'i' and N is the total number of specimens in a sample. Though widely employed as a descriptor of the "evenness" of species abundance distributions, PIE is strongly correlated with the proportional relative abundance of the two most common species in these data (mainly equid and hyopsodontid species; Spearman's ρ=-0.49 to -0.84, p=0.00). To avoid confusion, it is referred to here as an index of 'inverse dominance'. The second index is a modification of rank-abundance analysis (Fig. 3), in which species are ranked from most to least abundant and their natural-log transformed relative abundances are plotted against ranks (Magurran, 2004). Rank-abundance curves provide a visual representation of an abundance distribution that is shaped by the majority of the species present in a sample. The slopes of exponential trendlines fitted to the curves are directly comparable between samples (Fig. 3, as in Caron and Jackson, 2008). The fit of the trendlines for these data is high (R^2>0.75) and the slopes of the trendlines are shallow and negative (<-0.1). The reciprocal of the absolute value of the slopes is used to transform them into an index of 'inclusive abundance'. The two indices have values between zero and one. Higher values of inverse dominance indicate higher evenness through decreased dominance of the sample by a few taxa. Higher values of inclusive abundance indicate higher evenness through a more equal distribution of the abundances of the majority of the species in the sample. The two indices are summed as an index of evenness.

2.3.3 Turnover. Rates of species first, *F*, and last, *L*, appearances are highly dependent on sample size. Standardized, instantaneous per-taxon rates are calculated for series of consecutive samples of equal time (as in Alroy, 2000; Chew, 2009a; Foote, 2000).

$$F = -ln[(RS - FA - LA)/(RS - LA)] \qquad (2)$$

and

$$L = -ln[(RS - FA - LA)/(RS - FA)], \qquad (3)$$

where *FA* is the number of first appearances, *LA* is the number of last appearances and *RS* is the range-through richness of each sample. Turnover is the sum of these rates.

3 Results

The parameters calculated from the one-meter bins and averaged from the coarser binning series correspond closely~~, indicating an appropriate level of resolution in the averaged parameters~~ (Fig. 4). Three overlapping peaks occur in both sets of parameters (370-394 m, 405-417 m and 435-448 m), significantly refining previous work at a coarser resolution (20-meter thick intervals~~, =~100 ka~~), in which a single, 40-meter thick interval (370-410 m) of biotic change was identified in this part of the FC section (Chew, 2009a). This analysis demonstrates two distinct events within that 40 meter zone, separated by ~10 m ~~(~60 ka)~~ of pre-event parameter values. The lowest peak is the longest ~~(~150 ka)~~ and is distinguished by high turnover driven by many species first appearances (Fig. 4). It contains the distinctive biostratigraphic events conventionally referred to Biohorizon B (Bown et al., 1994b; Chew, 2009a; Schankler, 1980), including the last appearances of the condylarth genera *Haplomylus* and *Ectocion* and the first appearance of the artiodactyl *Bunophorus* (Table 1). The middle and upper peaks ~~correspond closely (within <10 m, Fig. 4) to the predicted levels of the ETM2 and H2 CIEs,~~ are comparatively short~~ (~60-~70 ka)~~, and are distinguished by increases in diversity driven by beta richness (Fig. 4). The middle peak was previously thought to be part of Biohorizon B and the upper peak falls within a longer interval of previously recognized, heightened and fluctuant diversity after Biohorizon B (Chew, 2009a; Chew and Oheim, 2013; Schankler, 1980). The middle and upper peaks are referred to here as faunal events B-1 and B-2 given their close association with Biohorizon B. Although faunal event B-1 encompasses more species first and last appearances than Biohorizon B (Table 1), appearance rates (Fig. 4) demonstrate that turnover is less pronounced at the faunal events in relation to higher standing richness and neither event appears to warrant the term ‘biohorizon’.

Focusing on the averaged parameters from the binned data, the turnover and diversity changes at faunal events B-1 and B-2 are highly significant. Two-sample Kolmogorov-Smirnov tests of the evenness and turnover parameters indicate that the parameter distributions above (and excluding) Biohorizon B vary significantly from their distributions in the ~~~2~~40 ~~ka~~m prior to Biohorizon B (Table S4, K-S p values <0.000). Mann-Kendal tests indicate significant trends in a number of the parameters, but the absolute value of all trend slopes is <0.001 (Table S4) and it is unlikely that these trends influence the significance of the differences. Alpha richness is not significantly different after Biohorizon B compared with before, but the peaks in gamma richness at ETM2 and H2 are driven by beta richness (Fig. 4), which is significantly different (Table S4, K-S $p=0.002$). Mann-Kendal tests indicate significant and opposing trends from before-to-after Biohorizon B in beta richness, but these also have absolute slope values of ~0.01 (Table S4) that are unlikely to greatly influence the significance of the differences in parameter distribution.

Only the richness parameters are significantly correlated with the averaged, binned sampling distribution, which might suggest lingering sample size bias in spite of the extensive standardization instituted here. The correlation between alpha richness and the averaged, binned sampling distribution is weak (Spearman’s $\rho=0.28$, $p=0.00$), with many of the peaks in alpha richness (e.g., Biohorizon B) corresponding to lows in sampling. The correlation between beta richness and the original sampling distribution is strong (Spearman’s $\rho=0.91$, $p=0.00$), but previous work (Chew and Oheim, 2013) demonstrated an increase in beta richness in this part of the FC section in samples that were rigorously standardized for both sampling and area variation, to the latter of which beta richness is particularly susceptible. Combined with the lack of correlation with the other parameters and weak correlation with alpha richness, this suggests that the strong correlation between beta richness and the averaged, binned sampling distribution reflects independent trends of an increase in preservation (sampling) and differentiation across the landscape (beta richness). Finally, ~~A~~apart from inclusive abundance, the averaged parameters are significantly correlated with average carbon isotope value (Spearman's ρ=0.35-0.83, $p \leq 0.04$) when the McCullough Peaks isotope record (Abels et al., 2012) is ~~aligned~~ independently correlated with the FC section ~~between~~ using the stratigraphic ranges of faunal events B-1 and B-2 as determined from species range end-points.

Ten families constitute >90% of the Willwood fauna and are sufficiently common to assess proportional relative abundance and body size trends across the part of the FC section under investigation here (Fig. 5). Abundance changes are most pronounced at Biohorizon B but many appear to play out across the subsequent faunal events B-1 and B-2. There is a proliferation of body sizes at and above Biohorizon B, but abundance changes appear to favor smaller relative sizes. In two of the four most common families (Hyopsodontidae and Adapidae), closely related species that are smaller than the common lineage representing each family appear in high abundance across Biohorizon B and faunal events B-1 and B-2. This includes the largest abundance change in this part of the FC section, in which the small hyopsodontid *Hyopsodus minor* almost completely displaces the common hyopsodontid lineage between Biohorizon B and faunal event B-2 (proportional relative abundance of 30-40% decreases to ~7% after faunal event B-2). In three of the remaining families (Phenacodontidae, Isectolophidae, Viverravidae), a common, large species disappears or markedly decreases in abundance across Biohorizon B and faunal events B-1 and B-2. In two other families (Esthonychidae, Oxyaenidae) a comparatively large lineage increases in abundance after faunal event B-2. Finally, the microsyopids experience a dramatic decrease in abundance at Biohorizon B that is maintained to some extent across faunal events B-1 and B-2, which is probably associated with a temporary reduction in body mass (Silcox et al., 2014).

4 Discussion

High-resolution, multiparameter paleoecological analysis of the superb FC fossil record from the south-central part of the Bighorn Basin demonstrates two previously unrecognized intervals of change, faunal events B-1 and B-2. These events immediately follow Biohorizon B but differ notably from it, suggesting different underlying causes and that their differentiation from Biohorizon B is warranted. ~~There are several indications that f~~Faunal events B-1 and B-2 may be related to the CIEs identified in the McCullough Peaks and thus represent response to the ETM2 and H2 hyperthermals. ~~They~~ Faunal events B-1 and B-2 occur above the distinctive biostratigraphic events of Biohorizon B and in close proximity to the C24r-C24n geomagnetic shift, as do the CIEs in the McCullough Peaks (Abels et al., 2012). ~~correspond closely to the predicted stratigraphic levels of the ETM2 and H2 CIEs and~~ Faunal events B-1 and B-2 are similar in all aspects of faunal change described here. The simplest explanation for their similarity is a comparable trigger, and ETM2 and H2 are akin (Abels et al., 2012; Sexton et al., 2011; Stap et al., 2010). Change at faunal events B-1 and B-2 is superficially similar to that described at the only other well-known early Eocene hyperthermal, the PETM (Gingerich, 1989; Rose et al., 2012; Secord et al., 2012), including increases in diversity and turnover and a general shift towards smaller body size. In addition, the increases in (alpha) richness and turnover are less pronounced at faunal events B-1 and B-2 than at the PETM (Table 2), which is also the case in marine plankton across the hyperthermals (Foster et al., 2013; Gibbs et al., 2012; Stassen et al., 2012) and conforms with the expectation that ETM2 and H2 were smaller events. For discussion purposes, i~~I~~t is ~~assumed~~ hypothesized here that there is a ~~causal~~ relationship between the McCullough Peaks CIEs, ETM2 and H2, and faunal events B-1 and B-2. A critical test of this hypothesis requires directly related isotope data, which are presently unavailable.

4.1 Comparison with the PETM

Turnover and changes in body size at the PETM are dramatic compared with faunal events B-1 and B-2 (Table 2). Pronounced turnover at the PETM was recognized long before the hyperthermal was known by the placement of the first major boundary (Clarkforkian / Wasatchian) in the North American Land Mammal Age sequence (Wood, 1941). Nearly half of the Bighorn Basin mammal genera and ~80% of the species that existed during the PETM are new (Rose et al., 2012; Woodburne et al., 2009). This turnover was fueled by immigration; up to ~40% of new genera at the PETM were immigrants (Rose et al., 2012; Woodburne et al., 2009) from the southern part of the continent (Burger, 2012; Gingerich, 2001) and from the Holarctic continents via northern land bridges (Bowen et al., 2002; Gingerich, 2006; Rose et al., 2011). In comparison, <10% of genera at faunal events B-1 and B-2 are new (Table 2) and none of these are documented immigrants (Woodburne et al., 2009). Decreases in body size at the PETM are widespread (e.g., Smith et al., 2009) including ~40% of all mammal genera (Secord et al., 2012). These decreases occurred through temporary dwarfing of lineages and species via metabolic effects, or through the immigration of closely related, smaller species (Burger, 2012; Clyde and Gingerich, 1998; Gingerich, 2001; Secord et al., 2012; Smith et al., 2009)~~(Burger, 2012; Clyde and Gingerich, 1998; Gingerich, 2001; Secord et al., 2012; Smith et al., 2009)~~. In comparison, <20% of genera at faunal events B-1 and B-2 experience decreases in body size and there is preliminary evidence of dwarfing in only ~~one primate~~ a few primate lineages (D'Ambrosia et al., 2014; Silcox et al., 2014). Smaller body sizes at faunal events B-1 and B-2 are primarily the result of abundance shifts and appearance events that are not related to significant migration, although they could represent range shifts of smaller regional congeners (Fig. 4, see also Bown et al., 1994a). There are no genera that increase in body size at the PETM, whereas this proportion is ≥20% at faunal events B-1 and B-2 (Table 2).

Specific conditions of the hyperthermals may account for these differences. In the Bighorn Basin, mean annual temperature (MAT) increased 5-10 °C in ≤10 ka at the beginning of the PETM (Fricke and Wing, 2004; Koch et al., 2003; Secord et al., 2010; Wing et al., 2005). There are no MAT estimates for the predicted levels of ETM2 and H2 in the Bighorn Basin, but the proportionality of warming and CIE magnitude in regional comparisons (Abels et al., 2012) suggests that MAT increased at about one half to one third the rate of PETM warming (3-6 °C and 2-5 °C, respectively, in ~10 ka, but see Snell et al., 2014). Continental precipitation varied regionally at the PETM (Collinson et al., 2003; Foreman et al., 2012; Samanta et al., 2013; VanDeVelde et al., 2013), but in the Bigorn Basin there was notable drying related to a ~40% decrease in mean annual precipitation (Kraus et al., 2013; Kraus and Riggins, 2007; Wing et al., 2005). In contrast, the distinct lithology of the ETM2 and H2 levels in the McCullough Peaks record, including thick purple paleosols, increased channel sandstones and mud-filled scours (Abels et al., 2012) are suggestive of moist conditions (as in Foreman et al., 2012; Kraus et al., 2013; Kraus and Riggins, 2007) and there is no evidence of drying in floras at this time (Wilf, 2000; Wing et al., 2000). Rapid range shifts and dwarfing have been linked with both moisture limitation and high rates of warming in modern terrestrial organisms (Chen et al., 2011; Foden et al., 2007; Sheridan and Bickford, 2011). It may be the combination of rapid warming and significant drying at the PETM that led to disproportionate immigration and dwarfing compared with ~~ETM2 and H2~~faunal events B-1 and B-2.

4.2 Characteristics of ~~ETM2 and H2~~faunal events B-1 and B-2

~~ETM2 and H2~~Faunal events B-1 and B-2 are set in the context of pronounced climatic, environmental and faunal change attributed to ~~the onset of~~ warming ~~at~~ in the approach to the EECO (Chew, 2009a; Woodburne et al., 2009). Leaf margin analysis of scattered floras (Wing et al., 1991) and isotope ratios of paleosol hematites (Bao et al., 1999; Wing et al., 2000) indicate that MAT rose from a low of ~11 °C to ~16 °C around the time of ~~H2~~faunal event B-2. Although the rate of this temperature increase is unknown, there is no evidence of a CIE in the McCullough Peaks isotope sections of Abels et al. (2012) to suggest a hyperthermal mechanism at Biohorizon B. Coincident lithological changes, such as increased sediment accumulation rate and common channel sandstones and mud-filled scours, may reflect tectonic activity on the southern edge of the basin (Bown and Kraus, 1993) and/or marked increases in temperature, precipitation and/or seasonality of precipitation (as in Foreman, 2014; Foreman et al., 2012). At the same time, floras began to transition to subtropical and tropical species (Wilf, 2000; Wing et al., 2000), indicating the possible development of a canopy that would account for coincident changes in soil moisture (Bown and Kraus, 1993) and temperature (Snell et al., 2013). Biohorizon B, the largest faunal event in the FC record after the PETM, coincides with the onset of this ~~change~~ warming, lithological and floral change, and marks a major turning point in faunal diversity that has been correlated with jumps in generic alpha richness and turnover across North America (Chew and Oheim, 2013; Woodburne et al., 2009). In the FC record, Biohorizon B is distinguished by a burst of new species that were not immigrants, heralding long-term increases in alpha richness and evenness (Fig. 4, Chew and Oheim, 2013). There is also a proliferation of body sizes at this time, although abundance shifts tend to favor relatively smaller species (Fig. 5, Bown et al., 1994a). These results support the interpretation of Woodburne et al. (2009) that there was major evolutionary innovation in the lead-up to the EECO.

Faunal events B-1 and B-2 are distinct intervals of change set within the context of Biohorizon B. Abundance, evenness, dominance and body size trends were initiated at, or before, Biohorizon B (e.g., some long-term increases in size and the relative abundance of dominant species, see Chew, 2009a, b; Chew and Oheim, 2013) and carried through faunal events B-1 and B-2. However, faunal events B-1 and B-2 are unique in their higher proportions of species loss, which nearly equal the proportions of new species at each event (Table 2). Nearly half of the turnover at faunal events B-1 and B-2 occurs within lineages, with correspondingly small proportions (≤6%) of generic events. In contrast, and in spite of their widely different mechanisms, both the PETM and Biohorizon B are characterized by bursts of new species, including many new genera, and comparatively few losses. The PETM was a transient episode of ecological change, including immigration and body size adjustment, whereas Biohorizon B involved marked evolutionary change in this basin ~~(Woodburne et al., 2009)~~ (Chew and Oheim, 2013). Both events were initiated by significant climatic and environmental disturbance that ended ≥1 ma periods of relatively static conditions; warm and moist before the PETM and cool and dry before Biohorizon B (Kraus et al., 2013; Kraus and Riggins, 2007; Snell et al., 2013; Wilf, 2000; Wing et al., 2000). In contrast, the CIEs indicating the rapid warming of ETM2 and H2 occurred soon after the onset of the climatic and environmental disturbance ~~related~~ at Biohorizon B in the lead-up to the EECO ~~and Biohorizon B~~. Faunal structure may have been comparatively unstable as communities were adjusting to changing conditions, perhaps leaving more species vulnerable to further change. The turnover within lineages at faunal events B-1 and B-2 suggests that more species were lost through evolutionary transitions at ~~ETM2 and H2~~this time.

Faunal events B-1 and B-2 are also unique in their high proportions of beta richness (Table 2). Beta richness reflects heterogeneity in species incidence patterns (Collins and Simberloff, 2009; Colwell et al., 2004; Gotelli and Colwell, 2001) that may occur through specialization for dispersed microhabitats and/or heightened ecological interactions that prompt species to seek out or avoid each other (e.g., competition, predation). Previous analysis identified a rise in beta richness in the ~2 ma after Biohorizon B to which both mechanisms may have contributed (Fig. 3, Chew and Oheim, 2013; Woodburne et al., 2009). A coincident long-term increase in alpha richness (Fig. 3, Chew and Oheim, 2013; Woodburne et al., 2009) implies that there were more species packed into the available space of the landscape, increasing the potential for ecological interactions. Increased habitat complexity as subtropical and tropical floras became more established implies more opportunities for microhabitat specialization (Chew and Oheim, 2013; Wing et al., 2000; Woodburne et al., 2009). The proportions of new species and alpha richness are not particularly high at faunal events B-1 and B-2, suggesting that the temporary peaks in beta richness at ETM2 and H2 are probably not related to an acceleration of species packing and heightened ecological interactions. Instead, they may represent increased microhabitat specialization in response to transient increases floral complexity, perhaps heightened by the more seasonal, possibly more intense and episodic, precipitation suggested by transient lithological changes (Abels et al., 2012).

~~4.3 Implications for modern anthropogenic change~~

~~Aspects of faunal change in the Bighorn Basin record of the early Eocene are relevant for predicting modern anthropogenic effects. The PETM, ETM2 and H2 raised MAT in the Bighorn Basin to nearly the same absolute value (~20 °C given the proportionality of CIE and temperature, and long-term temperature trends at ETM2 and H2, Abels et al., 2012; Fricke and Wing, 2004; Wing et al., 2000). Extrapolating from current and projected regional rates of change, Wyoming's MAT (~8 °C according to US climate data) will approach this value in ~300 years even if emissions are stabilized before then, given the time scale of climate processes and feedbacks (Pachauri and Reisinger, 2007). This rate of warming far exceeds those of the past, implying that species-specific, rapid ecological adjustments (e.g., geographic range and body size changes) will probably occur in the near future as they did at the PETM, the interval with the highest rate of warming. River runoff and water availability are expected to decrease in the dry areas of western North America with ongoing climate change but precipitiation and the frequency of heavy precipitation events are expected to increase across the rest of the continent with the contraction of the Greenland ice sheet (Pachauri and Reisinger, 2007). The latter changes are more consistent with the Bighorn Basin record of the beginning ofapproach to the EECO. In addition, human activities such as urbanization, habitat degradation and fragmentation, and human controlled dispersal (e.g., invasive species) have already stressed many of the Earth's terrestrial faunas. Such stresses may be considered analogous to the faunal changes underway in the Bighorn Basin when ETM2 and H2 occurred. This suggests that increased heterogeneity in species incidence and heightened species vulnerability and loss may be expected across most of North America in the near future as occurred at ETM2 and H2 in the remote past.~~

5 Summary

This analysis highlights the importance of analytical resolution and the use of multiple parameters in the paleoecological analysis of whole communities. Two previously unsuspected episodes of faunal change ~~most likely~~potentially related to the ETM2 and H2 hyperthermals are identified. Comparison of diverse and complementary lines of evidence summarizing different functional and ecological groups allows the differentiation of superficially similar faunal response to these hyperthermals and the PETM. Faunal change at the PETM is characterized by pronounced turnover fueled by immigration and widespread decreases in body size. These changes are probably related to the combination of rapid warming and drying at the PETM. In contrast, faunal change at ~~ETM2 and H2~~faunal events B-1 and B-2 is less extreme, ~~does~~ is not ~~include~~ fueled by immigration, and involves a proliferation of body sizes, although abundance shifts tend to favor smaller sizes. ~~ETM2 and H2~~Fauanl events B-1 and B-2 are set in the context of pronounced climatic, environmental and faunal change related to ~~the onset of~~warming in the lead-up to the EECO. Faunal events B-1 and B-2~~response at ETM2 and H2 is~~ are distinctive in ~~its~~ their high proportions of species losses potentially related to heightened species vulnerability in response to the changes already underway ~~at the beginning of the EECO~~in the approach to the EECO. Faunal ~~response at ETM2 and H2 is~~events B-1 and B-2 are also distinctive in high proportions of beta richness, suggestive of increased geographic dispersal related to transient increases in habitat (floral) complexity and/or precipitation or seasonality of precipitation. ~~These results suggest that rapid ecological changes, increased heterogeneity in species incidence, and heightened species vulnerability and loss may be expected across most of North America in the near future in response to anthropogenically-driven climate change.~~

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Table 1. First and last appearances of species at Biohorizons B and faunal events B-1 and B-2. Paired species represent segments of what are thought to be individual lineages. Taxa in parentheses did not have first or last appearances within the significant intervals but are probably related to the event. Bold-faced taxa indicate the appearance or disappearance of a genus.

Biohorizon B	
Disappearances – 379-392 m	Appearances – 370-394 m
Ectocion, Haplomylus, Plagiomene	***Ambloctonus***, *Anemorhysis pattersoni*, ***Bunophorus*** *grangeri*, *Bunophorus etsagicus*, *Cantius* new sp., *Chriacus gallinae*, ***Copelemur***, *Homogalax* sp., *Hyopsodus minor*, ***Minnipus, Palaeictops, Systemodon, Vulpavus*** *australis*
Cantius trigonodus –	*Cantius abditus*
Hyopsodus wortmani –	*Hyopsodus latidens*
Prototomus martis –	***Tritemnodon*** *gigantea*
Prototomus sp –	*Prototomus secundarius*
Faunal event B-1	
Disappearances – 409-417 m	Appearances – 405-417 m
Cardiolophus, *Dissacus sp., Miacis exiguus, Microparamys scopaiodon, Pachyaena ossifraga*, ***Pseudotetonius***, *Viverravus politis, Viverravus rosei*	***Anacodon***, *Apatemys rodens, Hyopsodus powellianus, Oxyaena forcipata, Phenacodus sp., Prolimnocyon sp.*, ***Steinius***, *Uintacyon new sp. 1, Xenicohippus grangeri*
Apheliscus insidiosus –	(*Apheliscus* sp. 423 m)
Arenahippus pernix –	***Eohippus*** *angustidens*
Diacodexis metsiacus –	*Diacodexis secans*
Didymictis protenus –	*Didymictis lysitensis*
(*Galecyon mordax* 357 m) –	*Galecyon* sp.
(*Thryptacodon antiguus* 360 m) –	*Thryptacodon loisi*
Faunal event B-2	
Disappearances – 435-448 m	Appearances – 438-442 m
Oxyaena intermedia, Prolimnocyon sp., Uintacyon rudis	*Absarokius abbotti*, ***Hexacodus***, *Phenacolemur willwoodensis*
Esthonyx spatularius –	Esthonyx sp.
Arenahippus *aemulor* –	***Protorohippus*** *venticolum*
Prolimnocyon atavus –	*Prolimnocyon antiquus*

Table 2. Comparison of faunal change at the PETM and faunal events B-1 and B-2. Summary paleoecological parameter values are calculated for the entire PETM sample (Rose et al., 2012) and the entire faunal event B-1 and B-2 samples. Proportions of taxa lost at the PETM are based on the Clarkforkian (late Paleocene) Bighorn Basin mammal fauna described in Rose (1981). Proportions of change in body size at the PETM are from Secord et al. (2012). Proportions of change in body size at faunal events B-1 and B-2 are based on the total number of taxa for which body size can be assessed.

Parameter		PETM	B-1	B-2	Biohorizon B
Diversity					
	Proportion of alpha richness	$\frac{29}{39}$	$\frac{24}{39}$	$\frac{23}{39}$	$\frac{26}{34}$
	Proportion of beta richness	$\frac{10}{39}$	$\frac{15}{39}$	$\frac{16}{39}$	$\frac{8}{34}$
	Proportion of evenness (inclusive abundance)	$\frac{0.92}{1.84}$	$\frac{0.92}{1.8}$	$\frac{0.91}{1.78}$	$\frac{0.92}{1.78}$
	Proportion of dominance (inverse dominance)	$\frac{0.92}{1.84}$	$\frac{0.88}{1.8}$	$\frac{0.87}{1.78}$	$\frac{0.86}{1.87}$
Turnover					
	Proportion of new species	$\frac{46}{58}$	$\frac{14}{78}$	$\frac{6}{77}$	$\frac{13}{70}$
	Proportion of new genera	$\frac{20}{42}$	$\frac{3}{53}$	$\frac{2}{53}$	$\frac{8}{51}$
	Proportion of species lost	$\frac{18}{39}$	$\frac{12}{78}$	$\frac{6}{77}$	$\frac{7}{70}$
	Proportion of genera lost	$\frac{7}{39}$	$\frac{2}{53}$	$\frac{1}{53}$	$\frac{3}{51}$
Body size					
	Proportion of genera in which body size decreases	$\frac{10}{26}$	$\frac{6}{35}$	$\frac{2}{35}$	$\frac{6}{32}$
	Proportion of genera in which body size increases	$\frac{0}{26}$	$\frac{7}{35}$	$\frac{9}{35}$	$\frac{4}{32}$

Figure 1. Fossil localities in the south-central part of the Bighorn Basin. Colored localities have been tied by meter level to the Fifteenmile Creek composite stratigraphic section of Bown et al. (1994). Circled localities span the ETM2 and H2 hyperthermal levels (290-510 m) in the Fifteenmile Creek section. Isotope sections recording the ETM2 and H2 CIEs in the McCullough Peaks are from Abels et al. (2012).

Figure 2. Available fossil samples and carbon isotope data from the northern and south-central parts of the Bighorn Basin. ~~Absolute ages are based on Tsukui and Clyde (2012).~~ Both t~~T~~he McCullough Peaks isotope sections (Abels et al., 2012) ~~are tied to~~and this part of the Fifteenmile Creek (FC) section (Bown et al., 1994b) ~~between two tie points indicated by thick red lines:~~ include distinctive biostratigraphic events: the first (FAD) and last (LAD) appearances of *Bunophorus etsagicus* (B), *Haplomylus speirianus* (H), *Ectocion osbornianus* (E) and *Anacodon ursidens* (A)~~distinctive taxa and~~. The McCullough Peaks isotope sections and this part of the FC section also include the C24r-C24n.3n geomagnetic shift (gray shading indicates intervals of mixed polarity). ~~Distinctive taxa include *Bunophorus etsagicus* (B), *Haplomylus speirianus* (H), *Ectocion osbornianus* (E) and *Anacodon ursidens* (A)~~. The common occurrence of the biostratigraphic and geomagnetic events (indicated by thick, red lines in the FC section) shows that this part of the FC section corresponds to the McCullough Peaks isotopes sections. Previous isotope analysis of FC soil carbonates (Koch et al., 2003) was not sufficiently resolved to identify CIEs as in the McCullough Peaks, but those results do not preclude the possibility of CIEs in this part of the section. FC mammal fossils are binned into four series of overlapping, equal-length intervals for ~~high-resolution~~ paleoecological analysis.

Figure 3. Illustration of the ~~calculation of richness and evenness parameters~~methods. The binning simulation illustrates a series of all possible bins at 5-, 6-, 7- and 8-meters thickness (thin lines) created for a hypothetical parameter distribution (purple squares) with a ten meter peak. Parameter values are assigned to all meter levels within each bin and averaged by meter level across all bins (solid black line). Because calculation of parameters for all possible binning series is prohibitive, this project uses the average of the optimal binning series (least number of gaps and maximum sample sizes) at each thickness (dashed black line). The richness and evenness

parameters are calculated from a representative binned sample (407-413 m). Alpha richness is the individual-based rarefaction estimate of the number of species in a sample of 100 specimens. Beta richness is the difference between the individual- and sample-based rarefaction curves at the base of the sample-based rarefaction curve. Inclusive abundance is the reciprocal of the absolute value of the slope of the exponential trendline of the rank-abundance curve. Inverse dominance is the Probability of Interspecific Encounter index.

Figure 4. ~~High-resolution p~~Paleoecological parameters calculated for the ~~south-central Bighorn Basin~~FC fossil mammal fauna. The individual turnover, richness and evenness parameters ~~are~~ averaged from the ~~coarser~~ optimal 5-, 6-, 7-, and 8-meters thick binning series (blue lines) and individual bin values (diamonds) are shown along with summative turnover, richness and evenness parameters (black lines). ~~and~~ The averaged, binned parameters are compared with the original (prior to standardization) average, binned sample sizes (purple lines) to demonstrate little likelihood of lingering sample size bias. The averaged, binned parameters are also compared with turnover and range-through richness (S) parameters (sample-size biased) calculated from the data binned by meter-level ~~(gray lines)~~ to demonstrate the congruence of parameter peaks.

Figure 5. Changes in proportional relative abundance of species and comparative body sizes in the ten most abundant families in the ~~south-central Bighorn Basin~~FC fossil mammal fauna. Equidae: small – *Minippus index*; medium – *Arenahippus pernix* lineage, *Xenicohippus grangeri*; large – *Arenahippus aemulor* lineage, *Xenicohippus craspedotum*. Hyopsodontidae: small – *Haplomylus speirianus*, *Hyopsodus minor*; medium – *Hyopsodus wortmani* lineage; large – *Hyopsodus lysitensis*, *Hyopsodus powellianus*. Diacodexidae: small – *Diacodexis gracilis*; medium – *Diacodexis metsiacus* lineage; large – *Diacodexis robustus*, *Bunophorus grangeri*, *Bunophorus etsagicus*, *Hexacodus* sp. Adapidae: small – *Copelemur feretutus*; medium – *Cantius trigonodus* lineage; large – *Cantius* new sp. Phenacodontidae – small: *Copecion brachypternus*, *Ectocion osbornianus*; medium – *Phenacodus vortmani*, *Phenacodus* sp.; large – *Phenacodus intermedius*, *Phenacodus trilobatus*. Isectolophidae: small – *Cardiolophus radinskyi*, *Homogalax* sp.; medium – *Systemodon tapirinus*; large – *Homogalax protapirinus*. Esthonychidae: medium – *Esthonyx bisulcatus*, *Esthonyx spatularius* lineage; large – *Esthonyx*

acutidens. Viverravidae: small – *Viverravus acutus*; large – *Didymictis protenus* lineage. Oxyaenidae: medium – *Oxyaena intermedia*; large – *Oxyaena forcipata*. Microsyopidae: *Microsyops angustidens* lineage.

Figure 1.

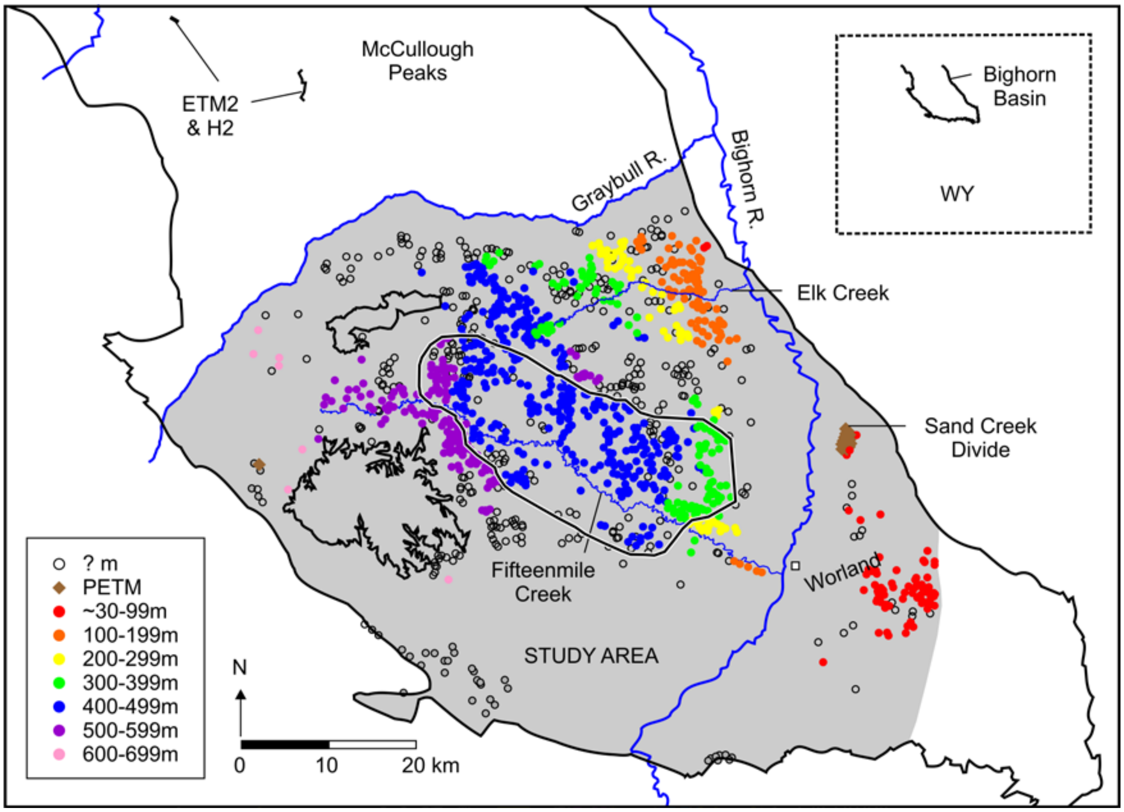

McCullough Peaks
ETM2 & H2
Graybull R.
Bighorn R.
Bighorn Basin
WY
Elk Creek
Sand Creek Divide
Worland
Fifteenmile Creek
STUDY AREA
○ ? m
◆ PETM
● ~30-99m
● 100-199m
● 200-299m
● 300-399m
● 400-499m
● 500-599m
● 600-699m
N
0
10
20 km

Figure 2

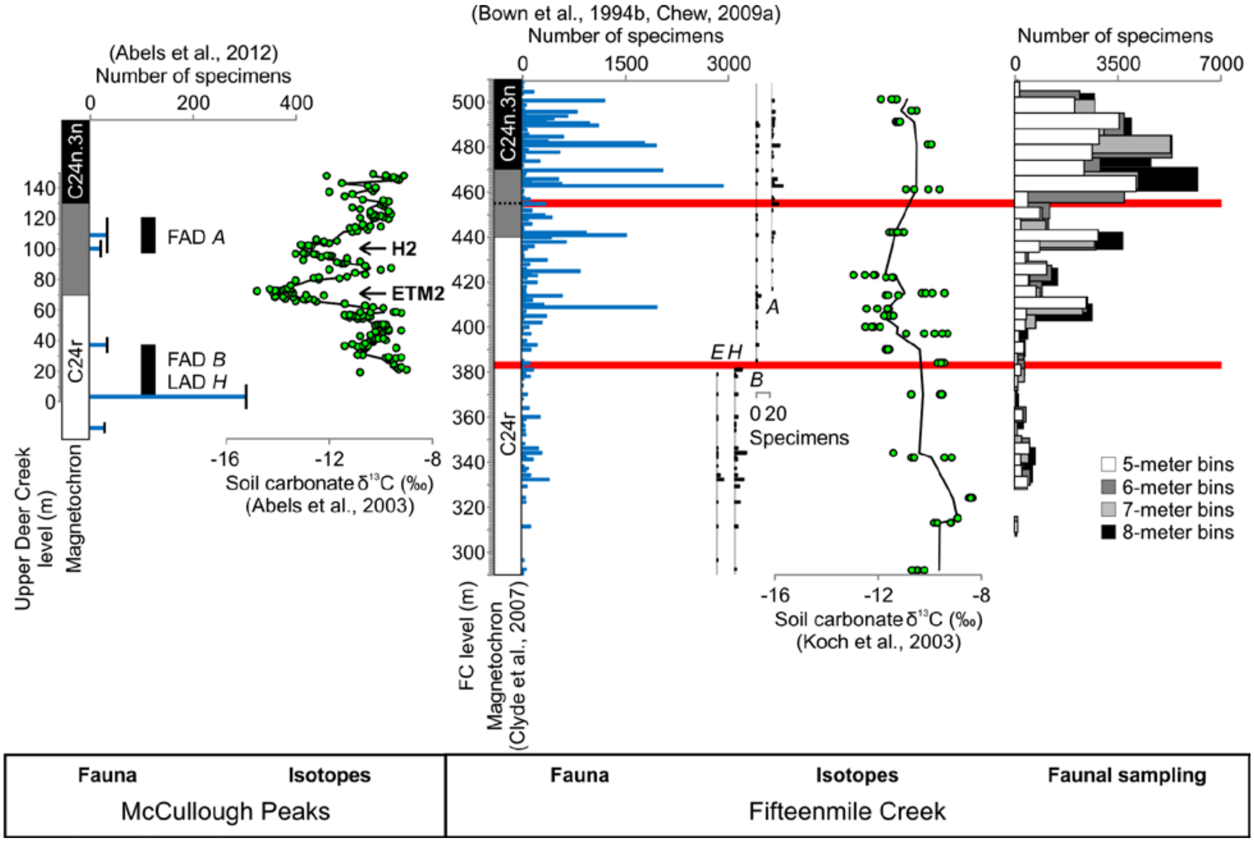
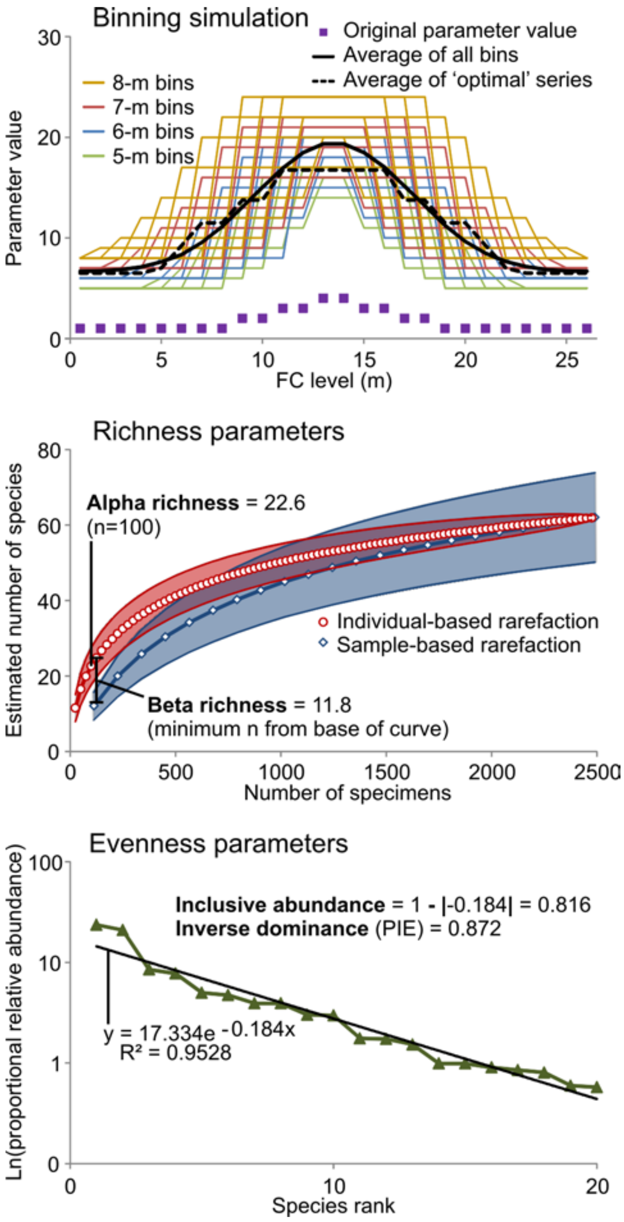
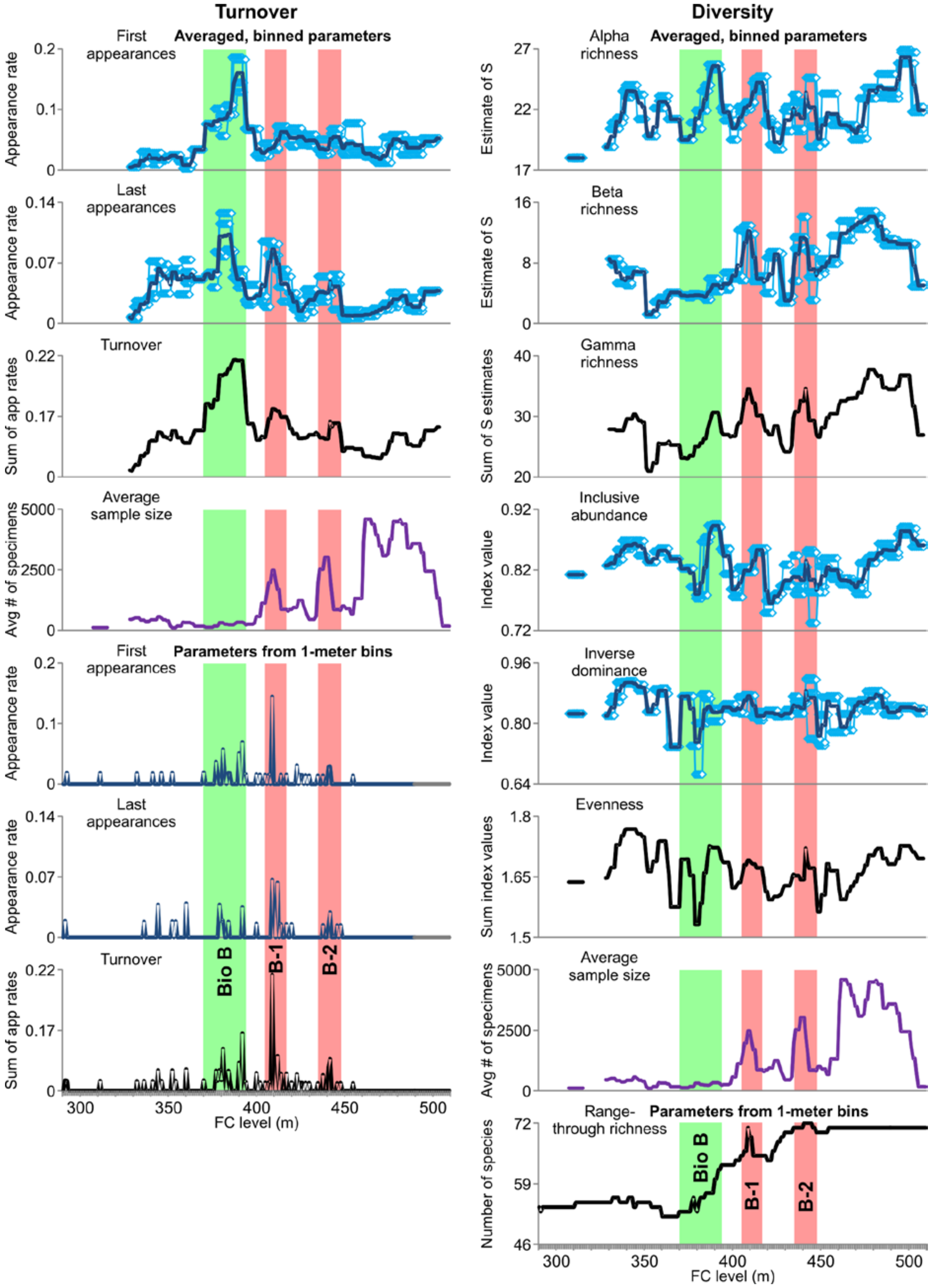

(Abels et al., 2012)
Number of specimens
0
200
400
C24n.3n
C24r
140
120
100
80
60
40
20
0
FAD A
FAD B
LAD H
H2
ETM2
-16
-12
-8
Soil carbonate δ13C (‰)
(Abels et al., 2003)
Upper Deer Creek level (m)
Magnetochron
(Bown et al., 1994b, Chew, 2009a)
Number of specimens
0
1500
3000
500
480
460
440
420
400
380
360
340
320
300
A
E H
B
0 20
Specimens
-16
-12
-8
Soil carbonate δ13C (‰)
(Koch et al., 2003)
FC level (m)
Magnetochron (Clyde et al., 2007)
Number of specimens
0
3500
7000
☐ 5-meter bins
▨ 6-meter bins
▨ 7-meter bins
■ 8-meter bins
Fauna
Isotopes
McCullough Peaks
Fauna
Isotopes
Faunal sampling
Fifteenmile Creek

Figure 3.

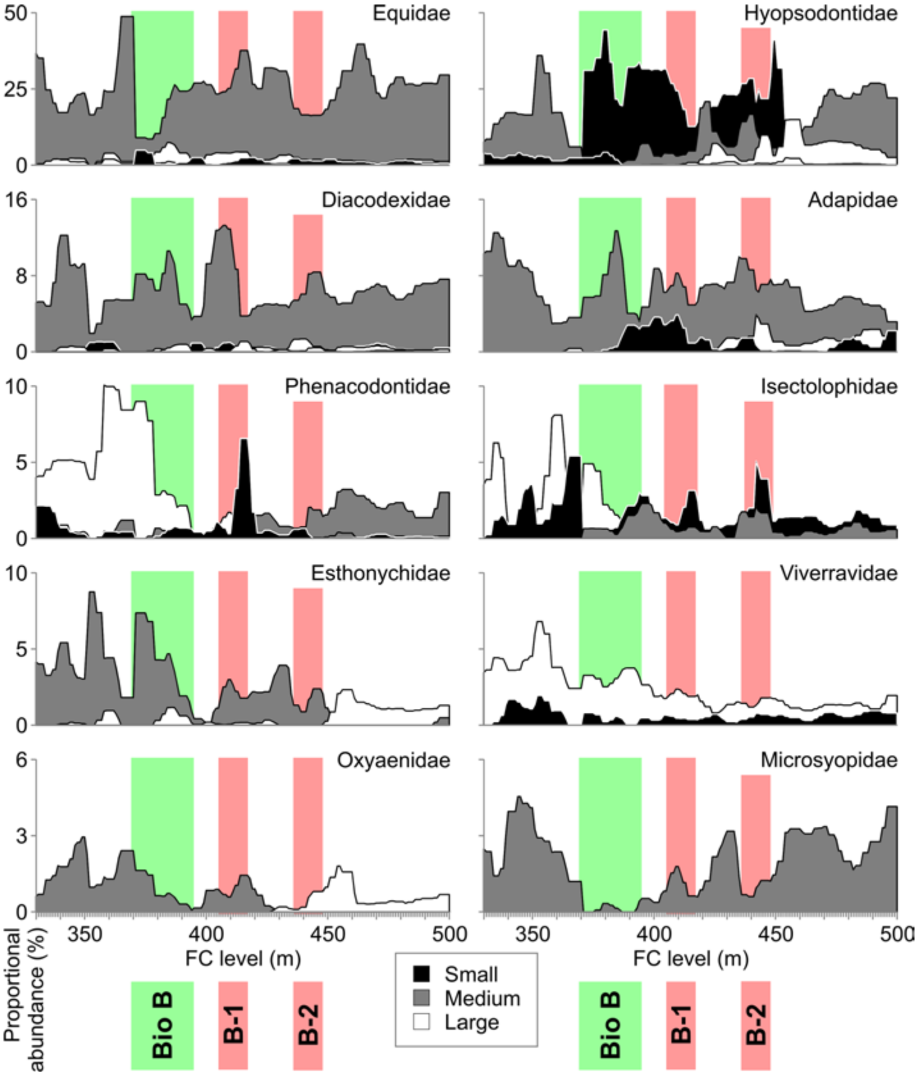

Binning simulation
Original parameter value
Average of all bins
Average of 'optimal' series
8-m bins
7-m bins
6-m bins
5-m bins
Parameter value
30
20
10
0
0
5
10
15
20
25
FC level (m)
Richness parameters
Estimated number of species
80
60
40
20
0
Alpha richness = 22.6
(n=100)
Individual-based rarefaction
Sample-based rarefaction
Beta richness = 11.8
(minimum n from base of curve)
0
500
1000
1500
2000
2500
Number of specimens
Evenness parameters
Ln(proportional relative abundance)
100
10
1
0
Inclusive abundance = 1 - |-0.184| = 0.816
Inverse dominance (PIE) = 0.872
y = 17.334e -0.184x
R² = 0.9528
0
10
20
Species rank

1596 Figure 4.



1597

Figure 5.


Equidae
Hyopsodontidae
Diacodexidae
Adapidae
Phenacodontidae
Isectolophidae
Esthonychidae
Viverravidae
Oxyaenidae
Microsyopidae
50
25
0
16
8
0
10
5
0
10
5
0
6
3
0
350
400
450
500
350
400
450
500
FC level (m)
FC level (m)
Proportional abundance (%)
Small
Medium
Large
Bio B
B-1
B-2
Bio B
B-1
B-2