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Mammal faunal response to 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 warming at 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 unknown. Their geochemical signatures have been located in the northern part of the Bighorn Basin, WY, USA, and their levels can be extrapolated to an extraordinarily dense, well-studied terrestrial mammal fossil record in the south-central part of the basin. High-resolution, multi-parameter paleoecological analysis reveals 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. In contrast with the PETM, faunal change at the later hyperthermals is less extreme, does not include immigration and involves a proliferation of body sizes, although abundance shifts tend to favor smaller congeners. Faunal response at ETM2 and H2 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 the EECO. Faunal response at ETM2 and H2 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

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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 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 and best known of the hyperthermals is the Paleocene-Eocene Thermal Maximum (PETM) at the base of the Eocene (Kennett and Stott, 1991; Zachos et al., 1993). Excursions in multiple carbon isotope records (carbon isotope excursions, CIEs) at 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 a ~100 ka period of elevated global temperature (5–7°C warmer) and perturbations in Earth’s carbon cycling, ocean chemistry and plankton communities (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 (Curran 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 deep-time records is the potential for documentation of multiple events, providing the opportunity to characterize faunal response to climate change

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of varying rate and magnitude against different background conditions. Consistencies in faunal response 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; 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 at ETM2 and H2 were similar to those at the PETM with the degree of response 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 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 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 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

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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.

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 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 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 $^{40}\text{Ar}/^{39}\text{Ar}$ date of a volcanic ash indicates that the upper levels are within the EECO (Smith et al., 2004). Numerical ages (56.33, 53.57, 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 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.

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 from isotopic work in the McCullough Peaks of the north-

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ern Bighorn Basin. Abels et al. (2012) identified the CIEs of ETM2 and H2 within an interval of mixed geomagnetic polarity below the shift from the C24 reversed to C24 normal geomagnetic zones (Fig. 2). 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*. 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 m thick gap between them in the isotope sections (Fig. 2). The C24r-C24n geomagnetic shift and the nearly simultaneous Biohorizon B stratigraphic events bracket the ETM2 and H2 CIEs and are also known at ~ 455 m (Clyde et al., 2007) and 381 m (this project) 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 ×0.68 allows the extrapolation of ETM2 and H2 to the 410–420 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).

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 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, 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

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(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*–
 5 *Apatotheria*, *Bunophorus etsagicus* and *Bunophorus grangeri* – Artiodactyla, *Lambdotherium* – Perissodactyla, *Pachyaena ossifraga* – Mesonychia, *Palaeictops bicuspsis* – 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
 10 and there are large disparities in sample size (0–~ 3000 specimens m⁻¹) and a trend of increasing sample size over time (Spearman's $\rho = 0.19$, $p < 0.05$), 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
 15 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
 20 series that divides the section appropriately to capture each event. One alternative is to approximate meter-level resolution through the combination of a series of randomly overlapping bins of different lengths. Four series of equal-time data bins are created 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 sedi-
 25 ment accumulation rate above ~ 455 m, the bins in each series are lengthened accordingly; 5–7, 6–8, 7–10, and 8–11 m). Collectively, the binning series provide continuous coverage and sample sizes > 100 specimens from 376–505 m in the FC section. Paleoeological parameters are calculated for each series. Parameter values are assigned

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to all meter levels within each bin in each series and then averaged by meter level across all bins. 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.

5 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
 10 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
 15 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 Paleoeological 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
 20 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
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the standardized appearances and relative abundances provided by the algorithmic 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 standard-

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ized proportional relative abundances. The first is the well-known Probability of Inter-specific Encounter, PIE, index (Hurlburt, 1971), which is the inverse of Simpson's dominance index standardized for finite collection size.

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

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 hyposodontid species; Spearman's $\rho = -0.49$ 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.

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 faunal events B-1 and B-2 represent response to the ETM2 and H2 hyperthermals. They correspond closely to the predicted stratigraphic levels of the ETM2 and H2 CIEs

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and 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. It is assumed here that there is a causal relationship between ETM2 and H2 and faunal events B-1 and B-2.

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

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related, smaller species (Burger, 2012; 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 evidence of dwarfing in only one primate lineage (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 $\geq 20\%$ 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 and 2–5 °C, respectively, in ~ 10 ka). 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 Bighorn Basin there was notable drying related to a $\sim 40\%$ 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.

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4.2 Characteristics of ETM2 and H2

ETM2 and H2 are set in the context of pronounced climatic, environmental and faunal change attributed to the onset of warming at 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 to ~ 16 °C around the time of H2. 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. 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 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

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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 ($\leq 6\%$) 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 (Woodburne et al., 2009). 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 rapid warming of ETM2 and H2 occurred soon after the onset of the climatic and environmental disturbance related 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.

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

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cal 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 ($\sim 20^\circ\text{C}$ 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 ($\sim 8^\circ\text{C}$ 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 precipitation 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 of the EECO. In addition, human activities such as urbanization, habi-

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tat degradation and fragmentation 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 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 is less extreme, does not include immigration, and involves a proliferation of body sizes, although abundance shifts tend to favor smaller sizes. ETM2 and H2 are set in the context of pronounced climatic, environmental and faunal change related to the onset of the EECO. Faunal response at ETM2 and H2 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 the EECO. Faunal response at ETM2 and H2 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,

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

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

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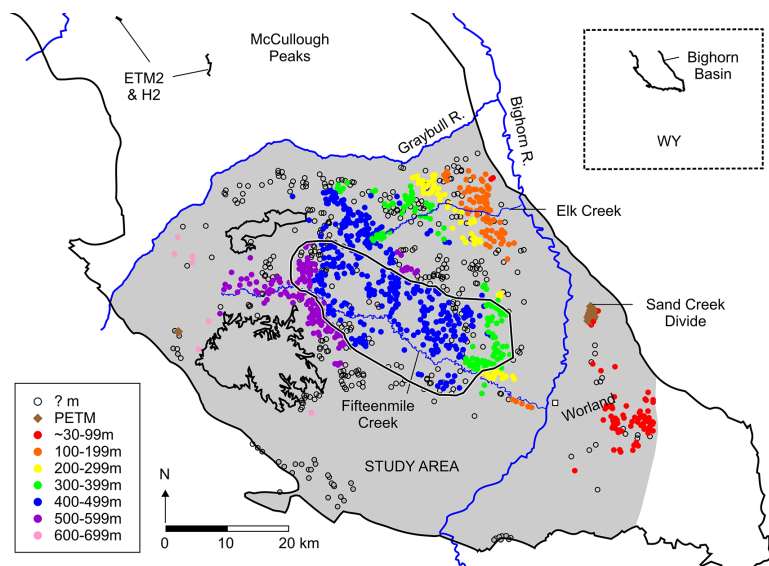


Figure 1. Fossil localities in the south-central part of the Bighorn Basin. Colored localities have been tied by meter level to the Fifteenmile Creek composite stratigraphic section of Bown et al. (1994b). Circled localities span the ETM2 and H2 hyperthermal levels (290–510 m) in the Fifteenmile Creek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

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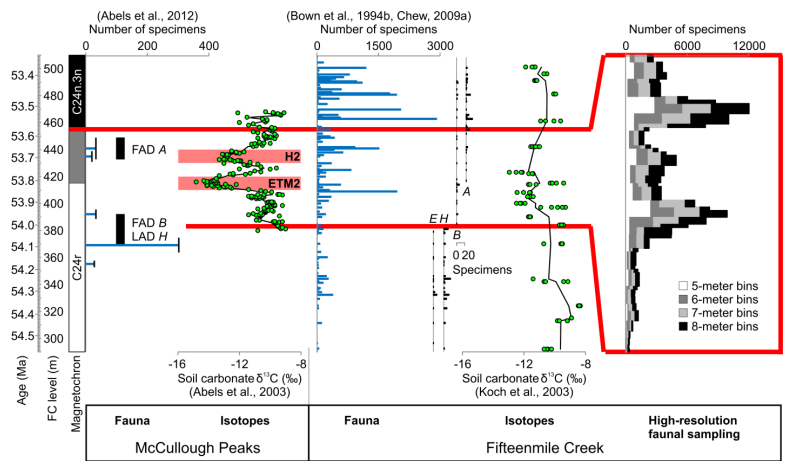


Figure 2. Available fossil samples and carbon isotope data from the northern and south-central parts of the Bighorn Basin. Absolute ages are based on Tsukui and Clyde (2012). The McCullough Peaks sections (Abels et al., 2012) are tied to the Fifteenmile Creek (FC) section (Bown et al., 1994b) between two tie points indicated by thick red lines: the first (FAD) and last (LAD) appearances of distinctive taxa and the C24r-C24n geomagnetic shift. Distinctive taxa include *Bunophorus etsagicus* (*B*), *Haplomylus speirianus* (*H*), *Ectocion osbornianus* (*E*) and *Anacodon ursidens* (*A*). FC mammal fossils are binned into overlapping intervals for high-resolution paleoecological analysis.

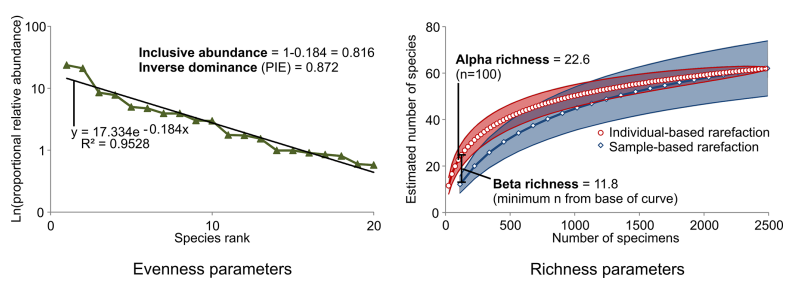
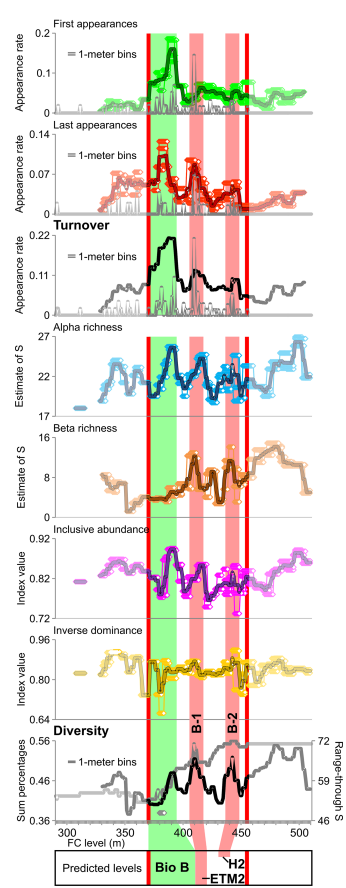


Figure 3. Illustration of the calculation of richness and evenness parameters from a representative binned sample (407–413 m).



1403

Figure 4. High-resolution paleoecological parameters calculated for the south-central Bighorn Basin fossil mammal fauna. The parameters are averaged from the coarser binning series and compared with turnover and range-through richness (*S*) parameters calculated from the data binned by meter-level (gray lines).

1404

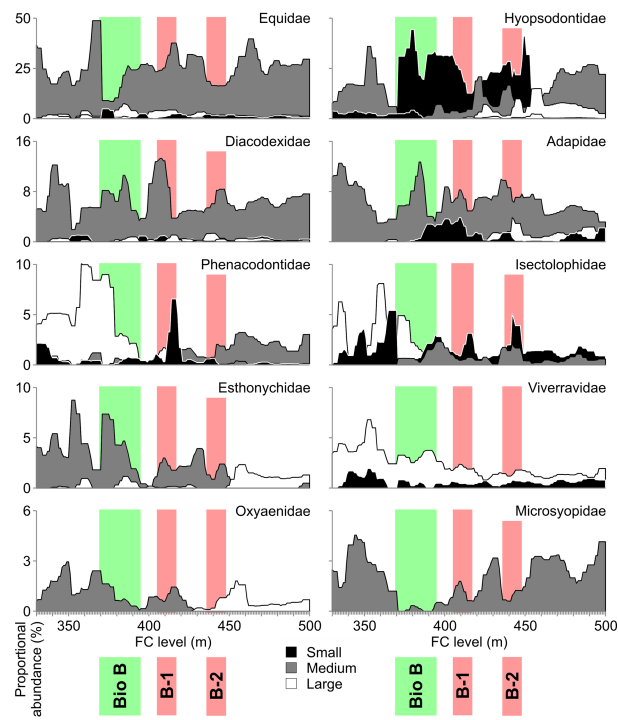


Figure 5. Changes in proportional relative abundance of species and comparative body sizes in the south-central Bighorn Basin fossil mammal fauna.