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Middle Eocene habitat shifts in the North American western interior: A case study

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ABSTRACT

There has been great interest in the global warming events that heralded the onset of the Eocene and particularly the response of mammalian faunas to these events. However, little information is available on the subsequent deterioration of tropical habitats in the interior of North America after these major warming episodes. The decline of tropical habitats is thought to have begun during the middle Eocene in the interior of North America, but until now, no studies have been able to document the details of this event. Recent fossil collection and stratigraphic studies from sites in southwestern Wyoming and northeastern Utah that span the middle Eocene offer a unique opportunity to evaluate changes in habitat in the western interior. Using a discriminant function analysis, habitats were reconstructed for a sequence of eight stratigraphically controlled middle Eocene assemblages. Adaptive profiles (diets, substrate use, and body masses) of fossil mammal communities were statistically compared to those of extant faunas from a variety of Neotropical habitats. Previously published magnetostratigraphic data from Utah provided a means to correlate our stratigraphic sections to the geomagnetic polarity time scale and the oxygen isotope record. The discriminant model shows that there was a significant change in the mammalian community ecology near the end of the late middle Eocene that is likely reflective of a habitat shift. When correlated to the time scale and oxygen isotope record, this key transition from forested habitats typical of the tropical early Eocene to more open woodlands began about 42 million years ago in this region of the Rocky Mountains.

1. Introduction

The Eocene epoch (55–34 Ma) is bookended by two major climatic and organismal transition events that have been popularized in the scientific literature by terming this epoch a global greenhouse that subsequently transitioned into the Oligocene icehouse (Fischer, 1984). Recently, intensive interdisciplinary focus on the global warming events that occurred at the Paleocene–Eocene boundary, the Paleocene Eocene Thermal Maximum (PETM) and the following early Eocene Climatic Optimum (EECO) has illustrated a strong relationship between these two climatic events and the restructuring of mammalian faunas that characterize the early Eocene (Clyde and Gingerich, 1998; Zachos et al., 2001; Bowen et al., 2002; Gingerich, 2006; Woodburne et al., 2009). During the middle Eocene, after a brief peak in global temperatures, these tropical conditions began to wane (Janis, 1993; Zachos et al., 2001; Ivany et al., 2003). In Europe, these declining tropical conditions ended during the early Oligocene and is marked by a faunal event referred to as the Grand Coupure, when tropically adapted mammals (primates, bats, and some rodents) were greatly reduced or eliminated (Janis, 1993; Kohler and Moyà–Solà, 1999; Hooker et al., 2004; Mosbrugger et al., 2005).

Unlike the dramatic pattern seen in Europe, the transition from tropical to temperate environments in North America was not defined by a single faunal event. In North America, the loss of tropical, forested conditions occurred earlier and probably at a more gradual rate beginning in the middle Eocene (Frederiksen, 1988; Janis, 1993; Prothero, 1998; Wing, 1998; Wolfe et al., 1998). The climatic conditions associated with this trend were driven by temperature change and the development of Antarctic glaciers and polar sea ice that began to form sometime in the middle Eocene (Prothero, 1998; Barbieri et al., 2004; Hurley and Fluegeman, 2003; Ivany et al., 2003).

Multiple lines of evidence (e.g., palynofloral, fish otoliths, nannoplankton, and $\delta^{18}O$ from gastropod shells) indicate that cooling began during the middle Eocene in coastal regions of North America (Frederiksen, 1988; Ivany et al., 2003). In addition to this microfossil record, the local paleobotanical records of both the Gulf Coast and coastal San Diego County have been shown to have experienced an increase in seasonal drought and seasonally dry savanna vegetation during the middle Eocene (Wolfe, 1978; Frederiksen, 1988; Myers, 2004). Such a trend towards more open habitats due to a decline of closed canopied forests is in line with our understanding of Oligocene environments in the northern latitudes that were typified by more

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open woodlands (Wolfe, 1978; Janis, 1993; Wing, 1998; Prothero, 1998; Woodburne et al., 2009). However, knowledge of precisely when this cooling took place in the continental interior during the Eocene has not been achieved.

The present study will attempt to rectify this problem of understanding the timing of local habitat transition for the continental western interior. This study is an integrated analysis of biostratigraphic, faunal assemblage, and ecomorphological data, of eight stratigraphically correlated middle Eocene mammalian assemblages from a single geographic region in northeastern Utah and southwestern Wyoming, U.S.A. With these data, the timing of the cessation of tropical conditions in the interior of North America was evaluated. The location, stratigraphic association, and age of these assemblages offer a unique opportunity to investigate the decline of tropical conditions during the middle Eocene in the western interior. Of the eight middle Eocene assemblages used in this study, four represent early middle Eocene time (Bridgerian North American Land Mammal Age [NALMA]) and one temporally transitional unit from the Bridger Formation, Green River Basin, Wyoming, and three represent later middle Eocene assemblages from the Uintan NALMA, Uinta Formation, Uinta Basin, Utah (Fig. 1).

Fossil mammals from the Bridger Formation have been the subject of numerous studies and large collections from this formation have been made since before the 20th Century (Matthew, 1909; Woodburne, 2004). In contrast to the preceding Bridgerian NALMA, the Uintan NALMA is characterized by the first appearance of selenodont cetartiodactyls and cursorial rhinocerotoids, an increase in rodent species diversity, and a marked decline in primate abundance and diversity, especially in the continental western interior (Prothero, 1996, 1998; Rasmussen et al., 1999; Woodburne et al., 2009). The distinctive composition of Uintan faunas has suggested to numerous scholars that a period of significant climatic change within the Rocky Mountain region towards more arid, likely cooler, and less forested conditions possibly existed during this time (Gazin, 1955; Gingerich, 1979; Stucky, 1990; Woodburne, 2004; Woodburne et al., 2009). The precise timing and character of these hypothetical changes, however, has remained unknown. The beginning of the Uintan NALMA, its end, or the time of transition between early and late Uintan faunas, have all been hypothesized as possible intervals that were associated with major ecological shifts away from canopy forested, tropical conditions to more open habitats in the Rocky Mountain region (Stucky, 1990; Woodburne, 2004).

Until recently, it has not been possible to detect major shifts in climate or habitat during the middle Eocene, particularly for Uintan-age sediments, in the North American continental interior because: (1) high resolution biostratigraphically and geochronologically controlled fossil

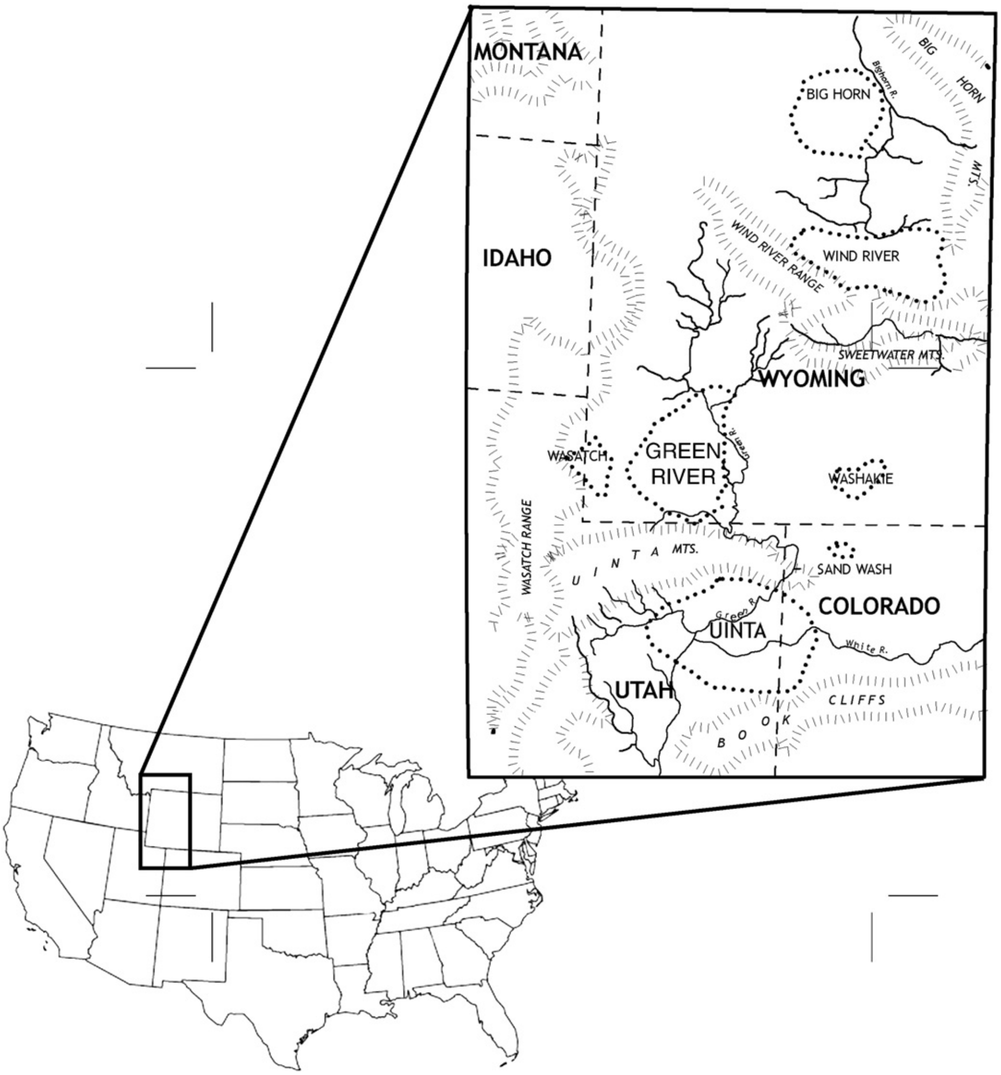

Fig. 1. Location of the Bridger Formation, Green River Basin, Wyoming and the Uinta Formation, Uinta Basin, Utah. The map illustrates the approximate relationship of each formation to the associated mountain ranges and the more northerly Eocene sedimentary basins (outlined in dotted lines). Adapted from Gazin (1962).

collections from rocks of this age were lacking; (2) time-specific habitat reconstructions have been difficult due largely to the small and stratigraphically sparse floral assemblages associated with specific formations; and (3) detailed comparisons between the faunas of the Uintan and the Bridgerian NALMA have not been made. Such studies are necessary to establish the presence or magnitude of any changes in paleofauna and inferred habitat. These issues were addressed by: (1) measuring a stratigraphic section through a portion of the Uinta Formation to which over 200 fossil mammal localities are tied and have produced thousands of mammalian specimens (Townsend, 2004; Townsend et al., 2006); (2) conducting an ecomorphological analysis of three stratigraphically restricted mammalian faunal zones from the Uinta Formation using modern Neotropical mammals as analogs for the purpose of reconstructing habitat types (Townsend, 2004); and (3) applying the comparative ecomorphological analysis to five stratigraphically documented faunal assemblages from the upper Bridger Formation (Twin Buttes and Turtle Bluffs members) (Townsend, 2004; Murphey and Evanoff, 2007).

In this paper, habitats were reconstructed for eight stratigraphic collection units from the middle Eocene Bridger Formation, Green River Basin, Wyoming and Uinta Formation, Uinta Basin, Utah (Fig. 1). These results were then applied to the geomagnetic polarity time scale (GPTS) to assess the timing of local habitat change in the Uinta Basin. This is the first study to reconstruct local habitats using a stratigraphic approach for the Uinta Formation. These data provide information on the evolving regional habitats in both the Bridger Formation and the Uinta Formation and allow for an environmental context for the evolution of fossil mammals found in these formations.

2. Hypotheses

This study has two components: to reconstruct and evaluate the habitats for the Bridgerian–Uintan NALMA habitat transition at a local scale (Hypothesis 1) and to evaluate the timing of the any habitat transition event based upon correlation of the units of study with the appropriate stratigraphic sections, Bridgerian or Uintan (Hypothesis 2). To reconstruct the habitats of both Bridgerian and Uintan faunas, the correlation between extinct mammalian ecological diversity of stratigraphically defined assemblages to that of modern mammals with established ecological diversity relationships to their local habitats was evaluated (Townsend, 2004). To assess the timing of the habitat transition, the stratigraphic section from the Uinta Formation was related to the GPTS through marker bed correlation with the published stratigraphic section of Prothero (1996). Previous interpretations of the Bridgerian to Uintan NALMA transition suggested that habitats changed substantially at the beginning of the Uintan NALMA from more tropical Bridgerian habitats to habitats more open and less tropical during the Uintan (Gazin, 1955, 1958; Gingerich, 1979; Prothero, 1998; Robinson et al., 2004; Woodburne, 2004; Woodburne et al., 2009).

2.1. Hypothesis 1 (H1)

The ecological adaptations (diet, body size, and substrate use) of fossil mammals can correctly classify stratigraphically defined assemblages into one of four habitat categories: forest, savanna-woodland, chaco, or open country. For H1 to be supported, the following prediction must hold true:

Prediction 1.1. The proportions of ecological adaptations for the fossil assemblages must be similar to those of modern mammalian assemblages in specific habitat categories as reported by Townsend (2004).

2.2. Hypothesis 2 (H2)

All Bridgerian mammal assemblages will have ecological diversity profiles that correlate to closed forest habitats. All Uintan mammal assemblages will have an ecological diversity profile that correlate to dry woodlands, such as Neotropical savanna woodland or Chaco localities. For H2 to be supported the following two predictions must hold true:

Prediction 2.1. The proportions of ecological adaptations for the Bridgerian assemblages must be similar to those of Neotropical modern mammal assemblages from closed forested habitats.

Prediction 2.2. The proportions of ecological adaptations for the Uintan assemblages must be similar to those of Neotropical modern mammal assemblages from either savanna woodland or Chaco habitats.

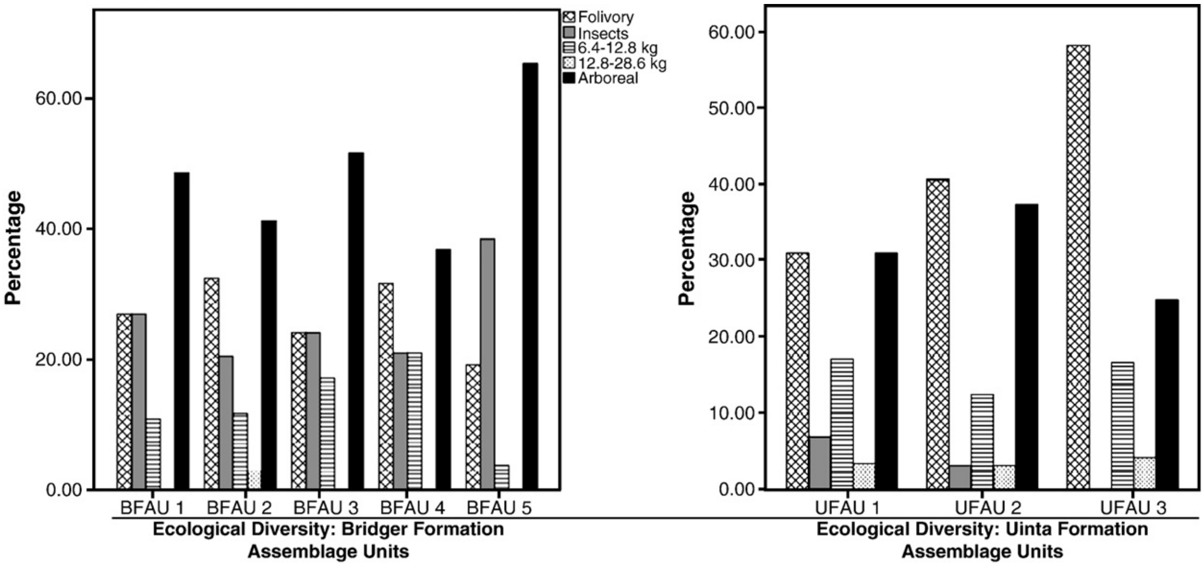

Fig. 2. Bar chart illustrating results of the ecological diversity for both middle Eocene faunas: Bridger Formation assemblage units and Uinta Formation assemblage units. The adaptations are identified by the legend at the top left of the Bridger assemblage chart.

3. Background

3.1. Bridger Formation

The deposition of the Bridger Formation is both of fluvial and lacustrine origin and has produced the largest assemblage of Bridgerian NALMA mammals from the western interior (Matthew, 1909; Murphey and Evanoff, 2007). Matthew (1909) initially divided the formation into five fossiliferous and geologically distinct units (Bridger A, B, C, D, and E). Murphey and Evanoff (2007) subdivided the Bridger C and D units through extensive stratigraphic work, fossil collection, and facies description. Based on radiometric dates from tuffs in the upper Bridger B, Bridger C, lower Bridger D and the Bridger E units, the Bridger Formation is estimated to have been deposited over a period of 3.52 million years between 49.09 and 45.57 Ma (Murphey and Evanoff, 2007).

3.2. Uinta Formation

The sediments of the Uinta Formation are primarily fluvial in origin and much like the older Bridger Formation, has also yielded the largest assemblage of Uintan NALMA fossil mammals from the western interior. The Uinta Formation has been divided into two geologic members (Wagonhound and Myton) and four fossiliferous sedimentary sequences (Uinta A, B1, B2, and C) none of which have been radiometrically dated with any confidence (Osborn, 1929; Wood et al., 1941; Mauger, 1977; Prothero and Swisher, 1992; Prothero, 1996). However, magnetic correlations have proved exceedingly useful in establishing the relative position of the Uinta Formation to the GPTS at Chrons C21n–C18n.2n (Prothero and Swisher, 1992; Prothero, 1996; Robinson et al., 2004). Concerning the Uinta Formation, a great deal of stratigraphic fieldwork needs to be completed in order to evaluate the extent of marker beds and ash units before a finer division of the formation can be achieved (Townsend et al., 2006).

Historically, most of the fossils from the Uinta Formation come from two areas within the Uinta Basin: White River Pocket and Myton Pocket, which, respectively, have produced early (Ui2) and late (Ui3) Uintan mammals (Osborn, 1895; Black and Dawson, 1966; Rasmussen et al., 1999; Robinson et al., 2004; Gunnell et al., 2009). Recent collecting efforts have recovered fossils from the eastern half of the Uinta Basin in Coyote Basin, Devil's Playground, Chipeta Wells, and Wonsits–Wonsits regions (Rasmussen et al., 1999; Townsend, 2004; Townsend et al., 2006). The sediments in these regions correlate to the Uinta B2 and C fossiliferous intervals and lower intervals (A and B1) will not be discussed as they are not abundant in fossils.

3.3. Ecological diversity analyses of the middle Eocene of North America

Ecological diversity analyses have been previously used to reconstruct ancient habitats and trophic relationships among both Paleogene and Neogene fossil mammal assemblages, primarily from Africa (Andrews et al., 1979; Gunnell et al., 1995; Reed, 1997, 1998, 2008). Many of these studies have noted that it is essential to utilize modern comparative faunas from the same continent as the fossil fauna that is under study (e.g., Reed, 1998). The range of modern habitats available in North America are not appropriate for this study considering the highly tropical nature of middle Eocene mammalian faunas (Janis, 1993; Gunnell, 1997; Prothero, 1998; Wing, 1998; Robinson et al., 2004; Townsend, 2004; Woodburne et al., 2009). In this study, we have chosen to use modern Neotropical macrohabitats (including some from the southern latitudes of the North American continent) and their associated faunas for these reasons: 1) available macrohabitats present in the Neotropics are comparable to those that have been reconstructed for the middle Eocene (Wing, 1998; Wolfe et al., 1998; Woodburne, 2004); 2) body size and other adaptations of the mammals associated with these habitats are similar to what is currently known about middle Eocene mammals; and 3) range of habitats are contiguous (i.e., not comparing extant mammals from different, non-adjacent continents) and represent the climatic conditions of a unified geographic area. Extant Neotropical macrohabitats range from closed canopy primary rainforest (typical of the Amazon region) to dry Caatinga or Chaco woodlands and open high-altitude grasslands of the Andes. These sites were chosen as a representation of degree of tree cover, thus, in reconstructing these ancient habitats this study does not provide a great deal of information on the climate of the region during the middle Eocene. Descriptions of the modern Neotropical habitats used in this study are found in Townsend (2004).

4. Materials and methods

4.1. Comparative sample of modern sites

Twenty modern Neotropical sites consisting of national parks and conservation areas spanning a geographic area that covers central Mexico to central Chile were used. The comparative mammalian community database was developed with the mammalian faunal lists from these 20 Neotropical sites. Each habitat locality was assigned a general habitat structure based upon written accounts of the area (Table 1). The general habitat structure assigned to these communities is based on the dominant vegetation structure. The broad categories for the Neotropical communities are based off of Eiten (1974) and Stotz et al. (1996).

The substrate, trophic, and body mass adaptations for each mammalian species from each modern locality was recorded based on published, behavioral observations and examination of stomach contents (e.g., Eisenberg, 1990; Redford and Eisenberg, 1992; Emmons and Feer, 1997; Eisenberg and Redford, 1999; Nowak, 1999; Townsend, 2004). There are 386 species of mammals from these 20 Neotropical sites.

The fossil collections from both the Bridger and Uinta Formations are biased against large mammals and are primarily composed of medium and small-bodied forms, typical of most Eocene mammalian

Table 1
Twenty Neotropical mammal localities organized by macrohabitat.

Localities	Tree cover	Mean annual rainfall	Country
Forests			
Manu	100%	2100 mm	Peru
Sian Ka'an	100%	1128 mm	Mexico
Iguazu	100%	1600 mm	Argentina
Beni	100%	1900 mm	Bolivia
La Selva	100%	3962 mm	Costa Rica
Yasuni	100%	3500 mm	Ecuador
Rio Platano	100%	4000 mm	Peru
La Amistad	100%	2500 mm	Costa Rica
Sierra Gorda	100%	2500 mm	Mexico
Maya Mountains	100%	1500 mm	Belize
Savanna-woodlands			
Cerradao	30–40%	1270 mm	Brazil
Caatinga	30–40%	600 mm	Brazil
Panatanal	30–40%	1600 mm	Brazil
Bañados del Este	10–20%	1000 mm	Uruguay
Chaco			
Estancia Toledo	10–20%	865 mm	Paraguay (Chaco)
Estancia Zalazar	10–20%	900 mm	Paraguay (Chaco)
Open habitat			
Ulla Ulla	0–5%	635 mm	Bolivia
Laguna Pozuelos	0–5%	300 mm	Argentina
Lauca	0–5%	335 mm	Chile
Huascaran	0–5%	884 mm	Peru

Tree cover percentage estimates from Eiten (1978).

faunas (Matthew, 1909; Peterson, 1919; Rose, 1981; Rasmussen et al., 1999; Gunnell and Bartels, 1999; Murphey, 2001; Townsend, 2004). The comparative dataset of modern habitats from the Neotropics is an appropriate series of analogs as a similar size bias is present (Eisenberg, 1990; Redford and Eisenberg, 1992; Emmons and Feer, 1997; Eisenberg and Redford, 1999; Nowak, 1999; Townsend, 2004). Twenty-six ecological adaptations were initially evaluated in this study. These adaptations fell into the ecological categories of diet, substrate use, or body mass class. The adaptations used in this analysis are very broad so that they can accommodate the level of detail provided by the results of ecomorphological analyses of the fossil mammals found in both middle Eocene formations (Table 2).

4.1.1. Ecological variables and macrohabitat designations

All ecological variables were defined broadly in order to accommodate the level of information potentially available from the fossil record. Dietary designations were defined by the long-term dietary adaptation seen in the gross morphology of the tooth and masticatory morphology, which allows for only general dietary assignment (Table 2, see Fortelius and Solounias, 2000). Locomotor assignments were divided into broad categories that would reflect basic substrate use (Table 2). Twelve body mass categories (BMC 1–12) were designated (Table 2). Neotropical macrohabitat designations were defined as forest (continuous canopy), savanna woodland (mixed savannas, woody plants, and non-continuous canopy), open country (mostly grasslands, and few trees), Chaco (arid grasslands, woody plants, and non-continuous canopy; Table 1).

4.2. Formation assemblage units, fossil mammals, and taphonomic bias

The use of generally recognized biochronologic or biostratigraphic units poses a number of problems for subdividing the faunal assemblages in this study. In both the Bridger and Uinta Formations, established biochronological units (Br1–3 and Ui1–3) are associated with stratigraphic columns that are too broad and cover multiple depositional environments and facies changes (Robinson et al., 2004; Murphey and Evanoff, 2007; Gunnell et al., 2009; Woodburne et al., 2009). Second, local fauna assemblages are not well established in the Uinta Formation, as the fossil collection is comprised of specimens that were found at localities with maybe only one or two specimens from varying stratigraphic levels. However, in the Bridger Formation, assemblages are well correlated stratigraphically and facies changes are documented (Townsend et al., 2006; Murphey and Evanoff, 2007).

The assemblages could not be separated according to recognized biochronologic units, they were divided into “formation assemblage units” that correlated to the two stratigraphic sections (Townsend et al., 2006; Murphey and Evanoff, 2007). Formation assemblage units are here defined as those assemblages of fossil mammals associated with previously identified stratigraphic intervals, they are not assemblage zones and do not have any biostratigraphic meaning for correlative purposes. In the Bridger Formation these units correlated to five subdivisions of the upper Bridger Formation: middle Bridger C, upper Bridger C, lower Bridger D, a combined middle and upper Bridger D, and Bridger E (Townsend, 2004; Murphey and Evanoff, 2007). Bridger Formation assemblage units (BFAU) are hereafter referred to as BFAU 1–5 and are defined further in Table 3. Similarly, from the Uinta Formation, the intervals are termed Uinta Formation assemblage units (UFAU) to identify the assemblages from three intervals in the stratigraphic section (Townsend et al., 2006; Table 3).

The collection used for this analysis includes 869 fossils from both the Bridger Formation held at the University of Colorado Museum and the Uinta Formation collected by parties from Washington University and held at the Carnegie Museum of Natural History (Table 4). Literally thousands of fossil specimens are known from both formations, however, only fossil specimens tied to the stratigraphic section were used in the present analysis to derive taxon lists for each BFAU and UFAU. For all analyses, the presence of a taxon, rather than its abundance was used. All taxa used were identified to genus level only.

Table 2
Descriptions of ecological variables: substrate use, diet, body mass.

Category	Behavior
Substrate use: terrestrial	Species that spend most of the time on the ground foraging, nesting. Most often found on the ground by researchers.
Substrate use: arboreal	Obligate arboreal species, rarely if ever found on the ground. Forage, rest, and engage in all behaviors in the trees.
Substrate use: cursorial	Obligate terrestrial species, they may be runners as suggested by the category name, but they do not have the morphology to ascend into the trees or burrow into the ground.
Substrate use: scansorial	Move easily in the trees and on the ground. Rest and forage in both milieus.
Substrate use: fossorial	Burrow into the ground for nesting or foraging. Live almost entire life-cycle in the earth.
Substrate use: aquatic	Forage in and around water and travel in the water.
Substrate use: all arboreal mammals	All mammals that spend any time in trees: committed arborealists and scansorial taxa.
Substrate use: all terrestrial mammals	All mammals that spend all time on ground and cannot go into trees: general terrestrial, fossorial, cursorial, aquatic taxa.
Diet: frugivore	Fruits and seeds are main dietary staple. Includes seed predation and exudate feeding. Other forms of nutrition may be ingested but in smaller proportions.
Diet: folivore	Leaves and the fibrous parts of plants are the main dietary staple. This includes grazers and browsers. Other forms of nutrition may be ingested but in smaller proportions.
Diet: insectivore	Insects, other than colonial forms, are main dietary staple. Includes other forms of invertebrate prey (worms, etc.). Other forms of nutrition may be ingested but at smaller proportions.
Diet: vertebrate prey	Vertebrates of all kinds are taken as main dietary staple. Includes species whose main prey item is fish. Other forms of nutrition may be ingested but in smaller proportions.
Diet: omnivore	Essentially equal amounts of animal and plant material are reported for diet.
Diet: ants	Ants and termites are main dietary staple. Obligate feeding on these colonial insects.
Body mass class (BMC) 1	0–200 g
BMC 2	200–400 g
BMC 3	400–800 g
BMC 4	800 g–1.6 kg
BMC 5	1.6–3.2 kg
BMC 6	3.2–6.4 kg
BMC 7	6.4–12.8 kg
BMC 8	12.8–25.6 kg
BMC 9	25.6–51.2 kg
BMC 10	51.2–102.4 kg
BMC 11	102.4–204.8 kg
BMC 12	204.8–409.6 kg

Table 3
Definition of Bridger and Uinta Formation faunal assemblage units.

Faunal assemblage unit (FAU)	Stratigraphic range	Formation member	Biochronological correlation[a]	Number of included localities
BFAU 1	68–79 m; middle Bridger C	Bridger Formation: Twin Buttes	Br3	8
BFAU 2	122–161 m; upper Bridger C	Bridger Formation: Twin Buttes	Br3	18
BFAU 3	200–207 m; lower Bridger D	Bridger Formation: Twin Buttes	Br3	12
BFAU 4	210–269 m; middle and upper Bridger D	Bridger Formation: Twin Buttes	Br3	11
BFAU 5	308 m; Bridger E	Bridger Formation: Turtle Bluff	Ui 1; Transitional Uintan	1
UFAU 1	0–87 m; Uinta B2	Uinta Formation: Wagonhound	Ui2	16
UFAU 2	96–128 m; Uinta C	Uinta Formation: Myton	Ui3	19
UFAU 3	134–366 m; Uinta C	Uinta Formation: Myton	Ui3	29

[a] Biochronological designations from Robinson et al. (2004) and Gunnell et al. (2009).

Collection practices and depositional environment were the only taphonomic factors that could be ascertained and evaluated for both formations. All of the fossils used in the present analysis were collected on the surface as they weathered out of the surrounding sediments. In comparing the element composition of the assemblages, much of the collection for both the Bridger and Uinta Formations include, in order of abundance, teeth, jaws, carpals and tarsals, damaged postcranial and cranial material suggesting that they are comparable samples (Rasmussen et al., 1999; Murphey et al., 2001; Townsend et al., 2006). Since the objective of this study is to evaluate regional habitat change within and across time units, the use of taxon presence rather than its abundance aids in eliminating taphonomic factors such as collections practices, predator removal, and other non-geological factors (Behrensmeyer et al., 2000; see Reed, 2008). Considering that each assemblage has experienced some degree of time-averaging that has obliterated any discrete communities or short-term variation. Thus, the habitat classifications for each of these middle Eocene faunal units will be considered as regional scale reconstructions, since multiple locality-level reconstructions for each stratigraphic interval could not be achieved.

Table 4
Middle Eocene faunal assemblage units: stratigraphic ranges and associated faunas.

BFAU1 fauna	BFAU 2 fauna	BFAU 3 fauna	BFAU 4 fauna	BFAU 5 fauna	UFAU1 fauna	UFAZ 2 fauna	UFAU 3 fauna
68–79 m	122–161 m	163–207 m	210–269 m	308 m	0–87 m	96–128 m	134–366 m
Antiacodon	*Antiacodon*	*Antiacodon*	*Antiacodon*	*Apatemys*	*Achaenodon*	*Amynodon*	*Auxontodon*
Apatemys	*Apatemys*	*Apatemys*	*Apatemys*	*Centetodon*	*Amynodon*	*Apataleurus*	*Colodon*
Centetodon	*Didelphodus*	*Centetodon*	*Helaletes*	*Entomolestes*	*Bunomeryx*	*Bunomeryx*	*Diplobunops*
Entomolestes	*Entomolestes*	*Entomolestes*	*Helohyus*	*Epihippus*	*Epihippus*	*Epihippus*	*Epihippus*
Gazinius	*Helaletes*	*Helaletes*	*Hyrachyus*	*Hemiacodon*	*Epitriplopus*	*Epitriplopus*	*Epitriplopus*
Helaletes	*Hemiacodon*	*Helohyus*	*Hemiacodon*	*Hyopsodus*	*Harpagolestes*	*Harpagolestes*	*Hyopsodus*
Helohyus	*Homacodon*	*Hemiacodon*	*Hyopsodus*	*Isectolophus*	*Hyopsodus*	*Hyopsodus*	*Pseudotomus*
Hemiacodon	*Hyopsodus*	*Hyopsodus*	*Mesonyx*	*Microsyops*	*Paramys*	*Pseudotomus*	*Isectolophus*
Homacodon	*Hyrachyus*	*Hyrachyus*	*Microsyops*	*Metanoiamys*	*Isectolophus*	*Isectolophus*	*Leptoreodon*
Hyopsodus	*Hyracotherium*	*Isectolophus*	*Notharctus*	*Notharctus*	*Leptoreodon*	*Uintaparamys*	*Uintaparamys*
Hyrachyus	*Ischyrotomus*	*Limnocyon*	*Nycthitherium*	*Nyctitherium*	*Uintaparamys*	*Leptotragulus*	*Leptotragulus*
Uintaparamys	*Uintaparamys*	*Metacheiromys*	*Omomys*	*Omomys*	*Leptotragulus*	*Limnocyon*	*Microparamys*
Mesonyx	*Microsus*	*Microparamys*	*Orohippus*	*Pantolestes*	*Mesomeryx*	*Mesomeryx*	*Mytonolagus*
Microparamys	*Notharctus*	*Microsus*	*Pantolestes*	*Paramys*	*Miacis*	*Miocyon*	*Mytonomys*
Mysops	*Omomys*	*Microsyops*	*Peratherium*	*Pauromys*	*Microparamys*	*Mytonolagus*	*Ourayia*
Notharctus	*Orohippus*	*Notharctus*	*Scenopagus*	*Pareumys*	*Natrona*	*Ourayia*	*Pareumys*
Nyctitherium	*Pantolestes*	*Nyctitherium*	*Thinocyon*	*Peradectes*	*Pareumys*	*Oxyaenodon*	*Pentacemylus*
Omomys	*Paramys*	*Omomys*	*Thisbemys*	*Peratherium*	*Peratherium*	*Pareumys*	*Protoreodon*
Oodectes	*Patriofelis*	*Oodectes*	*Viverravus*	*Pontifactor*	*Protoptychus*	*Peratherium*	*Protylopus*
Orohippus	*Pauromys*	*Orohippus*		*Protylopus*	*Protoreodon*	*Poebrodon*	*Proviverra*
Palaeosyops	*Peradectes*	*Pantolestes*		*Scenopagus*	*Protylopus*	*Protoptychus*	*Sciuravus*
Pantolestes	*Peratherium*	*Paramys*		*Sciuravus*	*Sciuravus*	*Protoreodon*	*Simidectes*
Paramys	*Pseudotomus*	*Peratherium*		*Taxymys*	*Stehlinella*	*Protylopus*	*Tapocyon*
Pauromys	*Scenopagus*	*Scenopagus*		*Tillomys*	*Tapocyon*	*Reithroparamys*	*Triplopus*
Peradectes	*Sciuravus*	*Sciuravus*		*Triplopus*	*Thisbemys*	*Sciuravus*	*Homacodontinae* sp. indet.
Peratherium	*Talpavus*	*Smilodectes*		*Trogolemur*	*Triplopus*	*Simidectes*	*Mesonychidae* sp. indet.
Pontifactor	*Thisbemys*	*Taxymys*		*Uintasorex*	*Zionodon*	*Spurimus*	*Brontotheriidae*
Scenopagus	*Uintatherium*	*Thisbemys*		*Notharctidae* sp. indet.	*Brontotheriidae*	*Tapocyon*	
Sciuravus	*Viverravus*	*Uintanius*		*Brontotheriidae*		*Thisbemys*	
Talpavus	*Washakius*	*Viverravus*		Sespedectine indet.		*Triplopus*	
Thisbemys	*Ischyromyidae* sp. indet.	*Ischyromyidae* sp. indet.		*Uintatheriidae*		*Trogolemur*	
Trogolemur	*Sciuavidae* sp. indet.	*Hyaenodontidae* sp. indet.				*Uintamys*	
Uintanius		*Leptictidae* sp.indet.				*Zionodon*	
Uintasorex						*Leptochoeridae*	
Uintatherium							
Viverravus							
Sicuravidae, sp. indet.							

Bridger Faunal Assemblage Zone = BFAZ. Uintan Faunal Assemblage Zone = UFAZ. All taxa are listed alphabetically. Bridger Formation meter levels begin in the Middle C interval, not at the base of the Bridger Formation (Murphey and Evanoff, 2007. Uinta Formation meter levels begin in the high Uinta B interval, not at the base of the Uinta Formation (Townsend et al., 2006).

Table 5
Analysis of variance testing of ecological variables among Neotropical macrohabitat localities.

ANOVA		Sum of squares	*df*	Mean square	*F*	Sig.
Frugivory	Between groups	0.200	3	0.067	4.633	0.016
	Within groups	0.230	16	0.014		
	Total	0.430	19			
Folivory	Between groups	0.298	3	0.099	51.709	0.000
	Within groups	0.031	16	0.002		
	Total	0.328	19			
Insectivory	Between groups	0.062	3	0.021	16.964	0.000
	Within groups	0.019	16	0.001		
	Total	0.081	19			
Omnivory	Between groups	0.005	3	0.002	2.534	0.094
	Within groups	0.010	16	0.001		
	Total	0.015	19			
Vertebrate Prey	Between groups	0.009	3	0.003	0.348	0.791
	Within groups	0.133	16	0.008		
	Total	0.142	19			
Ant/colonial insectivore	Between groups	0.006	3	0.002	2.465	0.100
	Within groups	0.012	16	0.001		
	Total	0.018	19			
0–200 g (BMC 1)	Between groups	0.041	3	0.014	0.681	0.576
	Within groups	0.321	16	0.020		
	Total	0.362	19			
201–400 g (BMC 2)	Between groups	0.007	3	0.002	0.867	0.479
	Within groups	0.045	16	0.003		
	Total	0.052	19			
401–800 g (BMC 3)	Between groups	0.015	3	0.005	2.246	0.122
	Within groups	0.035	16	0.002		
	Total	0.050	19			
801 g–1.6 kg (BMC 4)	Between groups	0.021	3	0.007	4.666	0.016
	Within groups	0.024	16	0.002		
	Total	0.046	19			
1.6–3.2 kg (BMC 5)	Between groups	0.005	3	0.002	1.212	0.338
	Within groups	0.020	16	0.001		
	Total	0.024	19			
3.2–6.4 kg (BMC 6)	Between groups	0.042	3	0.014	2.636	0.085
	Within groups	0.085	16	0.005		
	Total	0.127	19			
6.4–12.8 kg (BMC 7)	Between groups	0.036	3	0.012	8.380	0.001
	Within groups	0.023	16	0.001		
	Total	0.059	19			
12.8–25.6 kg (BMC 8)	Between groups	0.021	3	0.007	24.459	0.000
	Within groups	0.004	16	0.000		
	Total	0.025	19			
25.6–51.2 kg (BMC 9)	Between groups	0.008	3	0.003	1.579	0.233
	Within groups	0.027	16	0.002		
	Total	0.035	19			
51.2–102.4 kg (BMC 10)	Between groups	0.030	3	0.010	8.224	0.002
	Within groups	0.019	16	0.001		
	Total	0.049	19			
102.4–204.8 kg (BMC 11)	Between groups	0.044	3	0.015	4.797	0.014
	Within groups	0.049	16	0.003		
	Total	0.092	19			
204.8–409.6 kg (BMC 12)	Between groups	0.002	3	0.001	1.862	0.177
	Within groups	0.006	16	0.000		
	Total	0.007	19			
Arboreal mammals	Between groups	0.125	3	0.042	5.239	0.010
	Within groups	0.127	16	0.008		
	Total	0.251	19			
Terrestrial mammals	Between groups	0.068	3	0.023	4.194	0.023
	Within groups	0.087	16	0.005		
	Total	0.155	19			
Scansorial mammals	Between groups	0.041	3	0.014	3.423	0.043
	Within groups	0.065	16	0.004		
	Total	0.106	19			
Cursorial mammals	Between groups	0.072	3	0.024	4.197	0.023
	Within groups	0.092	16	0.006		
	Total	0.164	19			
Fossorial mammals	Between groups	0.029	3	0.010	3.268	0.049
	Within groups	0.047	16	0.003		
	Total	0.077	19			
Aquatic mammals	Between groups	0.017	3	0.006	1.818	0.184
	Within groups	0.049	16	0.003		
	Total	0.066	19			
All arboreal mammals	Between groups	0.292	3	0.097	16.962	0.000
	Within groups	0.092	16	0.006		
	Total	0.383	19			
All terrestrial mammals	Between groups	0.232	3	0.077	16.017	0.000
	Within groups	0.077	16	0.005		
	Total	0.309	19			

4.3. Univariate analysis—Neotropical localities

The percentages of extant genera exhibiting the 26 ecological adaptations at each of the Neotropical localities were compared by habitat category using a single factor ANOVA. The null hypothesis being that there were no differences in the mean proportion of the ecological adaptations between habitat categories. The Games–Howell post-hoc test was applied to evaluate the differences between pairs of habitats for each adaptation. The Games–Howell is used when variances are unequal and if the differences in those variances are large. Furthermore, it takes into account unequal sample sizes and performs better than the Tukey HSD when sample sizes are small (Seaman et al., 1991). Also, the sample sizes for each Neotropical locality were small, and the Games–Howell performs better than the Tukey HSD with small samples (Seaman et al., 1991).

4.4. Discriminant function analysis—Neotropical localities

Discriminant function analysis (DFA) was used to test the post-hoc classification success of the classification of each Neotropical locality into the four macrohabitat categories and to generate a model that could be used to reconstruct the habitats for the different fossil faunal assemblage units. A jackknifed classification method was used to evaluate the discriminant model. Twenty separate discriminant analyses were run where one modern locality was treated as an unknown and was then subsequently classified into a macrohabitat group by the model. The habitats of the Bridgerian and Uintan faunal assemblage units were classified using the DFA model by treating each as an unknown in the analysis.

4.5. Stratigraphic correlation

The Uinta Formation stratigraphic section (Townsend et al., 2006) was correlated to the GPTS based on correlation with Prothero's (1996) stratigraphic section. In constructing the stratigraphic section, Townsend et al. (2006) included marker beds reported by Prothero (1996) in order to correlate their localities with his Wagonhound Canyon section that is correlated to the GPTS.

5. Results

5.1. Univariate analyses—Neotropical habitats

Previously, Townsend (2004) evaluated the Neotropical habitat communities without using post-hoc analyses to test for Type I errors. Of the 26 adaptations used in this study, only 15 were significantly different between pairs of habitats based on the ANOVA results (Table 5). The Games–Howell test indicated that habitats with the most tree cover, forests and savanna woodlands, were not significantly different from one another for most adaptations, the exceptions being insectivory and animals in body mass class 7 (6.4–12.8 kg). Six adaptations were significantly different among at least two pairs of habitats: folivory, insectivory, body mass class 7, body mass class 8, arboreality, and total arboreality (Table 6). There is a significant difference

Table 6
Results of Games–Howell post-hoc testing[a].

Games–Howell							
Dependent variable	(I) Macrohabitat	(J) Macrohabitat	Mean difference (I–J)	Std. error	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Folivory	Sav-wood	Forest	0.07660000	0.03984420	0.359	−0.0962734	0.2494734
		Chaco	−0.02100000	0.03959377	0.947	−0.1968128	0.1548128
		Open	−0.24575000[a]	0.03955982	0.018	−0.4205602	−0.0709398
	Forest	Sav-wood	−0.07660000	0.03984420	0.359	−0.2494734	0.0962734
		Chaco	−0.09760000[a]	0.01550462	0.010	−0.1598316	−0.0353684
		Open	−0.32235000[a]	0.01541771	0.000	−0.3696517	−0.2750483
	Chaco	Sav-wood	0.02100000	0.03959377	0.947	−0.1548128	0.1968128
		Forest	0.09760000[a]	0.01550462	0.010	0.0353684	0.1598316
		Open	−0.22475000[a]	0.01475847	0.002	−0.2965917	−0.1529083
	5	Sav-wood	0.24575000[a]	0.03955982	0.018	0.0709398	0.4205602
		Forest	0.32235000[a]	0.01541771	0.000	0.2750483	0.3696517
		Chaco	0.22475000[a]	0.01475847	0.002	0.1529083	0.2965917
Insectivory	Sav-wood	Forest	0.10310000[a]	0.02246427	0.016	0.0246001	0.1815999
		Chaco	0.05600000	0.02704318	0.339	−0.0783345	0.1903345
		Open	0.17000000[a]	0.02023199	0.004	0.0873151	0.2526849
	Forest	Sav-wood	−0.10310000[a]	0.02246427	0.016	−0.1815999	−0.0246001
		Chaco	−0.04710000	0.02310433	0.401	−0.2132819	0.1190819
		Open	0.06690000[a]	0.01455369	0.003	0.0236700	0.1101300
	Chaco	Sav-wood	−0.05600000	0.02704318	0.339	−0.1903345	0.0783345
		Forest	0.04710000	0.02310433	0.401	−0.1190819	0.2132819
		Open	0.11400000	0.02094039	0.149	−0.1516490	0.3796490
	Open	Sav-wood	−0.17000000[a]	0.02023199	0.004	−0.2526849	−0.0873151
		Forest	−0.06690000[a]	0.01455369	0.003	−0.1101300	−0.0236700
		Chaco	−0.11400000	0.02094039	0.149	−0.3796490	0.1516490
6.4–12.8 kg (BMC 7)	Sav-wood	Forest	−0.063750[a]	0.018481	0.026	−0.12006	−0.00744
		Chaco	−0.001750	0.016036	0.999	−0.07289	0.06939
		Open	0.041500	0.021082	0.304	−0.03419	0.11719
	Forest	Sav-wood	0.063750[a]	0.018481	0.026	0.00744	0.12006
		Chaco	0.062000[a]	0.017461	0.049	0.00047	0.12353
		Open	0.105250[a]	0.022186	0.008	0.03231	0.17819
	Chaco	Sav-wood	0.001750	0.016036	0.999	−0.06939	0.07289
		Forest	−0.062000[a]	0.017461	0.049	−0.12353	−0.00047
		Open	0.043250	0.020194	0.281	−0.03905	0.12555
	Open	Sav-wood	−0.041500	0.021082	0.304	−0.11719	0.03419
		Forest	−0.105250[a]	0.022186	0.008	−0.17819	−0.03231
		Chaco	−0.043250	0.020194	0.281	−0.12555	0.03905
12.8–28.6 kg (BMC 8)	Sav-wood	Forest	0.027650	0.010599	0.133	−0.00847	0.06377
		Chaco	−0.067750[a]	0.012459	0.040	−0.12982	−0.00568
		Open	0.048250[a]	0.008616	0.034	0.00667	0.08983
	Forest	Sav-wood	−0.027650	0.010599	0.133	−0.06377	0.00847
		Chaco	−0.095400[a]	0.010914	0.028	−0.16671	−0.02409
		Open	0.020600[a]	0.006174	0.036	0.00133	0.03987
	Chaco	Sav-wood	0.067750[a]	0.012459	0.040	0.00568	0.12982
		Forest	0.095400[a]	0.010914	0.028	0.02409	0.16671
		Open	0.116000	0.009000	0.090	−0.09286	0.32486
	Open	Sav-wood	−0.048250[a]	0.008616	0.034	−0.08983	−0.00667
		Forest	−0.020600[a]	0.006174	0.036	−0.03987	−0.00133
		Chaco	−0.116000	0.009000	0.090	−0.32486	0.09286
All arboreal mammals	Sav-wood	Forest	−0.163300	0.066729	0.221	−0.44915	0.12255
		Chaco	0.037500	0.068865	0.943	−0.25072	0.32572
		Open	0.135750	0.066571	0.322	−0.15190	0.42340
	Forest	Sav-wood	0.163300	0.066729	0.221	−0.12255	0.44915
		Chaco	0.200800[a]	0.033388	0.044	0.01031	0.39129
		Open	0.299050[a]	0.028357	0.000	0.21098	0.38712
	Chaco	Sav-wood	−0.037500	0.068865	0.943	−0.32572	0.25072
		Forest	−0.200800[a]	0.033388	0.044	−0.39129	−0.01031
		Open	0.098250	0.033073	0.212	−0.10899	0.30549
	Open	Sav-wood	−0.135750	0.066571	0.322	−0.42340	0.15190
		Forest	−0.299050[a]	0.028357	0.000	−0.38712	−0.21098
		Chaco	−0.098250	0.033073	0.212	−0.30549	0.10899

[a] Only those variables that were found to be significant are included.

in the number of folivores between the forest habitats and both the Chaco ($p<0.01$) and open habitats ($p<0.0001$). The numbers of insect eating mammals differed significantly between forests and savanna woodlands ($p<0.05$) and forests and open habitats ($p<0.01$). With the medium sized mammals found in body mass class 7 (6.4–12.8 kg), significant differences are found between the forest and savanna woodland habitat ($p<0.05$), the forests and the Chaco habitats ($p<0.05$), and the forests and the open habitats ($p<0.01$). The subsequent larger body mass class 8 (12.8–25.6 kg), significant differences are seen between the forests and the Chaco habitat ($p<0.05$), the forests and the open habitats ($p<0.05$), and the savanna woodlands and Chaco habitats ($p<0.5$). The percentage of strictly arboreal mammals differs significantly between the forests and Chaco habitat ($p<0.01$) and between the forests and open habitat ($p<0.01$). Percentages of total arboreal mammals (arboreal and scansorial) also differ between the forests and Chaco habitat ($p<0.05$) and forests and open habitats ($p<0.0001$).

Four adaptations were significantly different among one pair of habitats: frugivory, terrestriality, scansoriality, and total terrestriality. A significant difference in the percentage of frugivores exists between forests and Chaco habitats ($p<0.0001$). The percentage of terrestrial mammals is significantly different between forests and open habitats ($p<0.05$) and the same pattern is present among scansorial mammals living in forests and open habitats ($p<0.05$). The percentage of total terrestrial mammals, those that do not enter the trees, also differs significantly between forests and open habitats ($p<0.0001$).

Based on these results, those adaptations that were found to be significantly different among more than one pair of habitats was used in the subsequent discriminant function analysis. The ANOVA results also indicated that other body mass classes (4 [801–600 g], 10 [51.2–102.4 kg], 11 [102.4–204.8 kg]) and the substrate use variables cursorial and fossorial were significantly different among habitats, but pair-wise post hoc testing did not support use of these variables.

5.2. Discriminant function analysis—Neotropical habitats

The five ecological variables identified by the ANOVA and Games–Howell post hoc test were used to generate the discriminate function model: folivory, insectivory, body mass class 7, body mass class 8 and total arboreality. The variable arboreality was not used in the analysis because it would have represented redundant information included in the total arboreality variable. The discriminant function analysis resulted in 100% post hoc classification success in placing the 20 Neotropical habitats into the correct category of forest, savanna woodland, Chaco, and open habitats. The discriminant model was based on two functions, both significant ($p<0.0001$; Wilks' Lambda DF 1 = 0.001, DF 2 = 0.042). Percentages of folivorous mammals loaded highest on the first function, followed by percentage of mammals in body mass class 8 (12.8–25.6 kg), and percentage of mammals exhibiting insectivory (Table 7). Folivory also loaded highest on the second function, followed by arboreality and body mass class 7 (6.4–12.8 kg) (Table 7).

Table 8
Results of jackknife classification testing.

Neotropical localities	Jackknife classification
Forests	
Manu	Forest
Sian Ka'an	Forest
Iguazu	Forest
Beni	Forest
La Selva	Forest
Yasuni	Forest
Rio Platano	Forest
La Amistad	Forest
Sierra Gorda	Forest
Maya Mountains	Forest
Savanna-woodlands	
Cerradão	Chaco
Caatinga	Savanna-woodlands
Panatanal	Savanna-woodlands
Bañados del Este	Savanna-woodlands
Chaco	
Estancia Toledo	Chaco
Estancia Zalazar	Chaco
Open habitat	
Ulla Ulla	Open
Laguna Pozuelos	Open
Lauca	Open
Huascaran	Open

A jackknife classification procedure classified the Neotropical localities correctly 95% of the time (Table 8), the misclassified habitat, the Cerradão, is categorized as a savanna woodland habitat but the model placed it in the Chaco category. The Cerradão is a habitat mosaic that is a mixture of both woodlands and open grasslands but with a xeromorphic vegetation (Eiten, 1974). It appears that the mammals of the Cerradão are similarly adapted as those from the more southern dry Chaco region (Townsend, 2004). Further discussion on the Neotropical ecological diversity analysis is provided in Townsend (2004).

Table 7
Structure matrix and casewise results for discriminant analysis.

Structure matrix

	Function		
	1	2	3
Folivory	−0.437	0.602[a]	0.017
All arboreal mammals	0.144	−0.455[a]	0.088
6.4–12.8 kg (BMC 7)	0.102	−0.316[a]	0.193
12.8–25.56 kg (BMC 8)	0.330	0.292	0.880[a]
Insectivory	0.303	0.108	−0.869[a]

Casewise statistics

	Formation assemblage units	Actual group	Highest group				
			Predicted group	P(D>d|G=g) *Prior probability*		P(G=g | D=d) *Posterior Probability*	Squared Mahalanobis distance to centroid
				p	*df*		
Original	BFAU 1	Ungrouped	Forest	0.000	3	0.830	24.250
	BFAU 2	Ungrouped	Forest	0.000	3	0.870	29.073
	BFAU 3	Ungrouped	Forest	0.036	3	1.000	8.549
	BFAU 4	Ungrouped	Forest	0.001	3	1.000	17.009
	BFAU 5	Ungrouped	Savanna-woodland	0.006	3	1.000	12.413
	UFAU 1	Ungrouped	Open	0.000	3	0.828	30.746
	UFAU 2	Ungrouped	Open	0.012	3	1.000	10.984
	UFAU 3	Ungrouped	Open	0.000	3	1.000	21.018

Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions.
Variables ordered by absolute size of correlation within function.

[a] Largest absolute correlation between each variable and any discriminant function.

5.3. H1—Ecological diversity of middle Eocene formation assemblage units

The complete results of the ecological diversity of all middle Eocene assemblage units are listed in Table 9, however, only those variables that were used in the discriminant model are detailed below. In the middle Eocene assemblages, the percentage of folivorous mammals ranges from 19.2 to 58.3 (Table 9; Fig. 2). This falls within the range of what is seen in Neotropical modern faunas, where the diversity of folivores ranges from as low as 5% in forests to as much as 42.9% in open habitats (Townsend, 2004). The number of middle Eocene insectivores ranges from zero to 38.5% of the adaptations exhibited by these faunas, which is a broader range than seen in Neotropical modern faunas, which range from 8% to 28% (Townsend, 2004). The first group of medium sized mammals belong to body mass class 7 (6.4–12.8 kg) comprises approximately 10% to just over 20% of the body masses seen in the middle Eocene formation assemblage units (Table 9). The modern Neotropical localities exhibit a slightly larger range for this body mass class at 5% to 19% (Townsend, 2004). There were fewer middle Eocene formation assemblage units that had taxa that fell into body mass class 8 (12.8–25.6 kg), only four assemblages (BFAU 2 and the three UFAU) had members in that class (Table 9) and these presented a very small range of percentages: 2.9–4.2. The modern Neotropical localities exhibited higher percentages of taxa that fell into body mass class 8 for those few localities that had this mass class (13 of the 20): 2% to 12.5% (Townsend, 2004). The variable, total arboreality, exhibits rather high proportions in each middle Eocene formation assemblage unit, ranging from 25% to 48.6%. This is similar to what is seen in the proportions of arboreal mammals from the Neotropics, which range from 20% to as high as 65% (Townsend, 2004). The general patterns exhibited by the eight middle Eocene formation assemblages for the five model variables all fall within the range of that observed in Neotropical modern mammal communities. These observations support Prediction 1.1, thus lending support to H1.

The discriminant model classified the eight middle Eocene faunal assemblage units into three habitat categories: forest, savanna woodlands, and open habitat with high posterior probabilities, or the chance that the case belongs to the predicted group (Table 7). The differences seen in the raw data between the middle Eocene formation assemblage units and the Neotropical habitat localities is no doubt reflected in the very low prior probabilities, the probability of the observed group score given membership in the predicted group. The largest posterior probability is used to classify the middle Eocene assemblage unit into the predicted group. The results of the discriminant function analysis also lend support to H1.

5.4. H2—Habitat reconstruction of middle Eocene formation assemblages

The model classified the first four BFAU as forest habitats. BFAU 5 was classified as a savanna woodland habitat. Table 9 lists the ecological diversity present at each formation assemblage unit. BFAU 1, the oldest unit in the analysis, has a high percentage of folivores (32.4%) and insectivores (27%) both larger proportions of the fauna than seen in modern Neotropical forests (5% to 12% for folivory and 8% to 20% for insectivory; Fig. 2; Townsend, 2004). But exhibit body mass percentages (body mass class 7 only) and proportion of arboreal mammals that is well within the range of mammal communities inhabiting Neotropical forests (body mass class 7 range: 10%–19%; arboreality range: 47%–65%; Townsend, 2004). BFAU 2, also classified as a forest shows a similar profile to that seen in BFAU 1 (Table 9), the only difference being that a few taxa existed in the body mass class 8 category (2.9%) and this proportion is similar to what has been reported for modern Neotropical forests (Townsend, 2004). BFAU 3 and 4 also have similar profiles, however, BFAU 3 has more arboreal mammals (51.7%) than BFAU 4, which at 36.8% is much lower than expected for a modern Neotropical forest locality (Fig. 2; Townsend, 2004). Both BFAU 3 and 4 have more folivores than seen in modern forests as well (24.1% and 31.6%, respectively). The youngest unit from the Green River Basin, BFAU 5 was classified by the discriminant model as savanna woodland and in fact, the discriminant score for this case falls very near the savanna woodland centroid (Fig. 3). BFAU 5 falls in the range of modern Neotropical savanna woodlands for both folivory and body mass class 7 and has the highest proportion of arboreal mammals of all of the middle Eocene formation assemblage units (65.4%; Table 9). This pattern is unlike what was observed with Neotropical modern savanna woodland localities where a typical

Table 9
Ecological diversity of middle Eocene Bridger and Uinta Formation assemblage units.

	BFAU1	BFAU 2	BFAU3	BFAU4	BFAU5	UFAU1	UFAU2	UFAU 3
Frugivore	32.4	29.4	37.7	26.4	38.5	34.5	34.4	33.3
Folivore	27	32.4	24.1	31.6	19.2	31.0	40.6	58.3
Insectivore	27	20.6	24.1	21.1	38.5	6.9	3.1	0
Omnivore	0	0	0	0	0	0	3.1	0
Vertebrate prey	10.8	8.8	13.8	21.1	3.8	17.2	18.8	8.3
Ants	0	0	0	0	0	0	0	0
BMC1	32.4	17.4	31.0	21.1	50.0	13.8	15.6	8.3
BMC2	5.4	5.9	3.4	5.3	7.5	3.4	3.1	4.2
BMC3	8.1	5.9	6.9	5.3	3.8	3.4	12.5	4.2
BMC4	10.8	14.7	10.3	10.5	11.55	10.3	6.3	8.3
BMC5	5.4	14.7	13.8	15.8	3.8	13.8	15.6	12.5
BMC6	10.8	11.8	6.9	10.5	7.5	6.9	12.5	20.8
BMC7	10.8	11.8	17.2	21.1	3.8	17.2	12.5	16.7
BMC8		2.9				3.4	3.1	4.2
BMC9	2.7		3.4	5.3	7.5	6.9	6.3	12.5
BMC10	2.7	2.9	3.4	5.3	0	3.4	3.1	4.2
BMC11	0	0	0	0	0	0	0	0
BMC12	5.4	2.9	0	0	0	0	3.1	0
Arboreal	48.6	41.2	51.7	36.8	65.4	31.0	37.3	25.0
Terrestrial	40.5	41.2	34.5	47.2	19.2	34.5	46.9	37.3
Scansorial	.	.	.	.		.	.	.
Cursorial	5.4	5.9	6.9	10.5	7.5	24.1	15.6	29.2
Fossorial	.	.	.	.	.	.	.	.
Aquatic	2.7	2.9	3.4	5.3	3.8	0		4.2
Total arboreality	48.6	41.2	51.7	36.8	65.4	31.0	37.3	25.0
Total terrestriality	48.6	50	44.8	63.2	30.7	58.6	62.5	70.9

Data are reported as percentages.

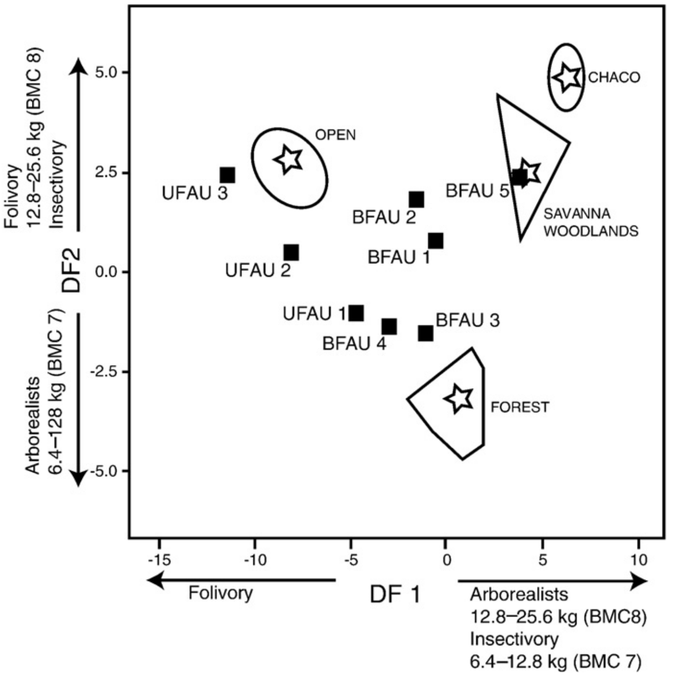

Fig. 3. Bivariate plot of the discriminant model generated by the ecological diversity analysis of 20 Neotropical modern mammal faunas. Results of an ecological diversity analysis on Neotropical faunas (legend), with North American Eocene faunas added (squares). A discriminant function analysis (DFA) including four macrohabitat categories as dependent variables and seven ecomorphological variables as independent variables showed over 99% confidence about allocation of the Neotropical habitats in 19 cases and over 90% confidence in one case. A jackknife resampling indicated that the discriminant function was highly accurate in classifying the Neotropical localities and produced a robust model. The loadings of each function are listed in order of significance. The star indicates the centroid for each macrohabitat and the dark squares indicate the positions of each middle Eocene formation assemblage unit.

range of arboreal mammals is 20% to 47% (Townsend, 2004). The observations for BFAU 1–4 support Prediction 2.1, but the classification of BFAU 5 as a woodland does not favor this prediction.

The discriminant model classified all three of the UFAU as open habitats (Table 7, Fig. 3). The major differences between the UFAU and BFAU profiles is that there are significantly fewer insectivorous mammals in the three UFAU than seen in the Bridgerian assemblages (Table 9). Significantly, there are fewer arboreal taxa as well, although 25% to 37.1% of the taxa do include arboreality as part of their lifestyle (Table 9; Fig. 2). Finally, the three UFAU all exhibit small proportions (3.1% to 4.2%) the larger class of medium sized mammals, body mass class 8 (12.8–25.6 kg) (Fig. 2). The raw data for UFAU 2 and 3 are reflective of the loadings for DF1 and DF2. Both have the largest proportions of folivores, which loaded highest on both functions and the smaller proportions of arborealists, which loaded high on the second function (Table 9; Fig. 3); these results do not support Prediction 2.2.

5.5. Stratigraphic correlation

Townsend et al. (2006) described a combined stratigraphic section measuring 366 m with detailed sections from Coyote Basin, Devil's Playground, Kennedy Wash, Red Wash, Glen Bench, Antelope Draw and Deadman's Bench, all well-demarcated regions within the Uinta Basin. Prothero (1996) published the magnetic stratigraphy of four sections within the Uinta Basin that spanned both the Uinta Formation and the overlying Duchesne River Formation and the underlying Green River Formation. The stratigraphic section of Townsend et al. (2006) in Coyote Basin followed Prothero's (1996) Wagonhound Canyon section, with their datum point 64 m below his 450-meter level mark, which is measured at the prominent bed called the *Amynodon* sandstone. The Townsend et al. (2006) section continues to the Uinta/Duchesne River Formation contact above Devil's Playground with only a 0.4-meter measurement difference between this section and that of Prothero (1996). The Townsend et al. (2006) section and related UFAUs were correlated to the GPTS based on the magnetostratigraphic calibration of Prothero's (1996) Wagonhound section. As illustrated in Fig. 4, UFAU 1 correlates with Chrons 20r and 20n, UFAU 2 spans the boundary of Chrons 20N and 19R, and UFAU 3 correlates with the middle of Chron 19R.

6. Discussion

6.1. Middle Eocene habitat reconstruction

6.1.1. Bridger Formation assemblage unit habitat reconstruction

BFAU 1 corresponds to the middle Bridger C unit of the Twin Buttes Member of the Bridger Formation and consists mainly of green and brown sandstone and mudstone beds. The fossils occur mostly in the limestone and marlstone beds (Murphey and Evanoff, 2007). Large logs, silicified wood, and plant debris are found in local pockets in this interval. The fauna indicates that the habitat was forested based on the position of the BFAU 1 to the Neotropical forest communities. The depositional environment of this unit begins with a lacustrine phase (Soap Holes limestone) followed by carbonaceous deposits (Murphey and Evanoff, 2007). A smaller, less extensive lacustrine interval (Hickey Mountain limestone) is overlain by a thin calcareous mudstone that has numerous vertebrate and plant fossils. The fauna of BFAU 1 comes from both of these layers. The Henry's Fork tuff, which directly overlies the middle C unit, has a radiometric age of 46.92 ± 0.17 Ma, indicating that the fauna from middle C are slightly older than this (Murphey and Evanoff, 2007). The adaptations of the fossil mammals from BFAU 1 indicate a forest fauna.

The BFAU 2 fauna corresponds to the upper C unit of the Twin Buttes Member of the Bridger Formation, which is comprised of lacustrine limestones (Henry's Fork and numerous smaller unnamed limestones), calcareous mudstones, and channel sand deposits (Murphey and Evanoff, 2007). The fossils of this unit are primarily found in the Henry's Fork limestone and the mudstone overlying the Henry's Fork tuff (Murphey and Evanoff, 2007). The mammalian adaptations indicate that the habitat of BFAU 2 was forested. The base of the upper C unit is the Henry's Fork tuff, indicating that it is younger than 46.92 Ma (Murphey and Evanoff, 2007).

BFAU 3 is equivalent to the lower D unit of the Twin Buttes Member and is characterized lithologically by sandstones, mudstones, and claystones. The boundary of this unit is formed by two limestones: the lower Lonetree and upper Hickey Reservoir (Murphey and Evanoff, 2007). Vertebrate fossils are found in the overlying sandstones, mudstones, and claystones. The adaptations of the fossil mammals of BFAU 3 indicate that the habitat of this interval is forested.

BFAU 4 is a combination of the assemblages from both the middle and upper D units of the Twin Buttes Member. This integrated assemblage was yielded from sediments that range from pumice bearing sandstone beads (in the middle D) and brown and tan mudstones and claystones (upper D). The fossils from the middle D are only found locally in the blue sheet sandstone (Murphey and Evanoff, 2007). Locally abundant plant fragments are found in the upper D portions of this interval (Murphey and Evanoff, 2007). Terrestrial vertebrates are abundant in the dark brown mudstones overlying the Upper White limestone and fossils are found within unnamed limestones scattered throughout the upper D. The faunal reconstruction for BFAU 4 is forested.

The Bridger Formation BFAU 1–4 are taxonomically similar, all with high percentages of arboreal and insectivorous forms, which clearly drives the classification of each of these assemblages with the Neotropical forest localities. For BFAU 1 and 2, 54% of the fauna is

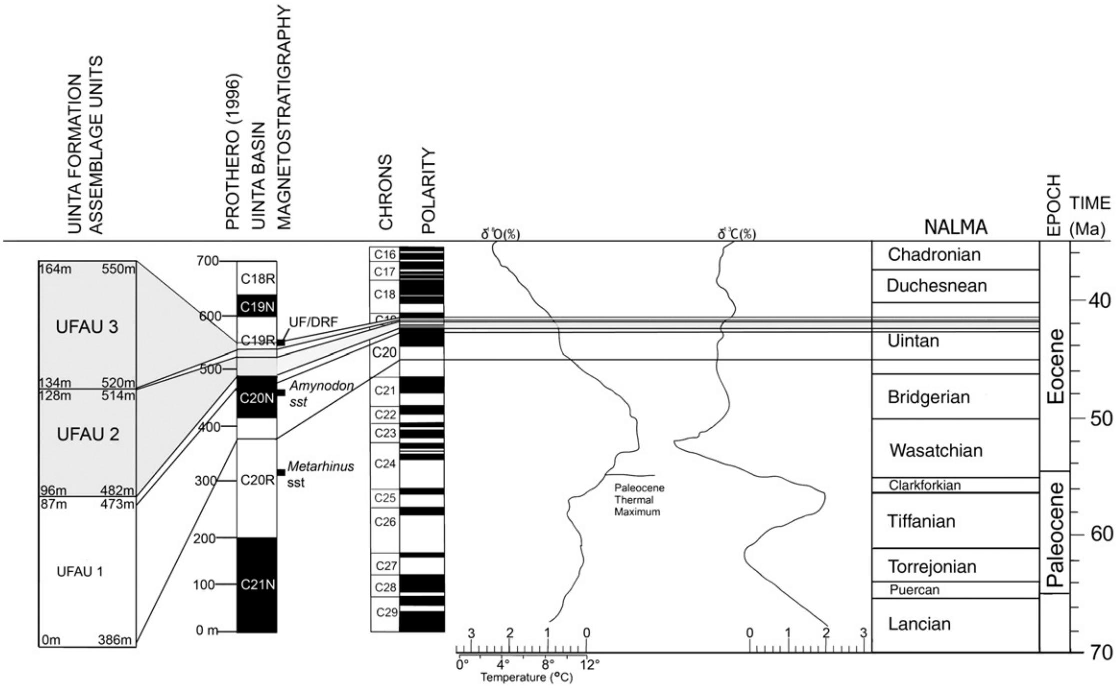

Fig. 4. Stratigraphic, temporal, and climatic correlation of the three Uinta Formation assemblage units. Stratigraphically constrained faunal zones of the Uinta Formation correlated to Prothero's (1996) magnetostratigraphic column allows for a direct correlation with the GPTS, deep sea oxygen isotope records, carbon isotope records, and North American Land Mammal Ages. After Zachos et al. (2001) and Woodburne (2004). Uinta Formation stratigraphic section, local aggregate thickness in the eastern basin is 164 m for this interval, showing correlations with Prothero's section.

comprised of primates, rodents, and insectivores: all either committed arborealists, or exhibiting dentitions suggestive of insectivory, or both (Table 9; Townsend, 2004; Gunnell, 1997). High percentages of primates and rodents are also found in BFAU 3 and 4. Other faunal elements also are driving the forest classification, marsupials and smaller apatemyids (e.g., *Apatemys*), but are not dominant components of each assemblage (Table 4).

BFAU 5 encompasses the Bridger E interval, which is also known as the Turtle Bluff Member of the Bridger Formation. Murphey and Evanoff (2007) consider this member to be transitional between the Bridgerian and Uintan NALMAs, and identify it as "Transitional Uintan". Lithologically, this unit is comprised of reddish-brown and gray gypsum-bearing claystones with a basal limestone (Basal E limestone) and capped by the Behunin Reservoir gypsum bed. Directly below the Basal E limestone is the Bridger E tuff, which has been aged at 46.16 ± 0.44 Ma indicating that the fauna from the overlying interval is at least this age or younger (Murphey and Evanoff, 2007). The fauna from this unit are correlated with the savanna woodland mammals, suggesting less tree cover during this interval for this region of the and it is interesting that this Transitional Uintan fauna would also represent a habitat that is transitional between forests and more open areas.

BFAU 5, the only Bridger Formation assemblage that was classified as savanna woodlands and discriminant function plot shows it as closer to the savanna woodland centroid than any of the modern faunas (Fig. 3). BFAU 5 has an extremely depauperate fauna with only seven mammalian orders represented, clearly the result of taphonomic bias (Table 4). Currently, the localities in the Bridger E are being meticulously screenwashed and more taxa will certainly emerge from these efforts (Murphey pers. comm.). Despite this clear taphonomic influence, the mammals represented in BFAU 5 do show similar proportions to what was seen in the older BFAU assemblages: the dominant taxa being rodents and primates, typical of more forested habitats. With more fossils being collected from this Bridger Formation interval, it can be predicted that the habitat classification for BFAU 5 would be pulled towards the forest centroid.

6.1.2. Uinta Formation assemblage unit habitat reconstruction

Unfortunately, comprehensive facies data cannot be added to these habitat reconstructions of the Uinta Formation since the depositional environments and local facies throughout this formation have not been studied in detail. The UFAU 1 assemblage is comprised of fossils from localities that span the 0–87-meter levels of the Uinta Formation. The primary depositional environments in this interval include mudstone overbank deposits, large sheet sandstones, and smaller channel sandstones (Osborn, 1895; Riggs, 1912; Stagner, 1941; Townsend et al., 2006). The UFAU 2 assemblage is comprised of localities from the 96 and 128 levels, the depositional environment does not differ greatly from that observed in UFAU 1, as it is also dominated by overbank deposits comprised of mudstones, however, the larger sheet sandstones are not present in this interval (Townsend et al., 2006). The UFAU 3 assemblage spans the 134–366-meter levels. Two types of depositional regimes are prevalent in this interval: numerous high-energy stream channels and well-developed paleosols (Rasmussen et al., 1999; Townsend et al., 2006). The faunas of all three UFAU are classified with the Neotropical high-altitude open country mammals, whose assemblages are dominated by cavioid and murid rodents and cetartiodactyls (camelids) both exhibiting terrestrial and folivorous adaptations and who fall into the medium body-size categories (Townsend, 2004). UFAU 1 has a function that is farthest from the open habitat centroid, likely due to the presence of insectivorous mammals (7% of fauna, Table 9). The raw ecological diversity data (Table 9) indicate that UFAU 3 has the lowest percentage of arboreal taxa, no insectivores, and the highest percentage of folivorous taxa, thus having the strongest "open habitat" signal of the three UFAU. Although not a variable used in these statistical analyses, 71% of the mammals in UFAU are terrestrial, lending further support to the open habitat reconstruction.

Hamblin (1987) published the only detailed sedimentary study of outcrops in the Uinta Formation with a goal to reconstruct local paleoecology. Hamblin's (1987) study of channels of the Myton Pocket region indicated that numerous streams were present at that time and they were flowing eastward into the remnant of Lake Uinta.

Based on comparisons with the earlier occurring Green River flora, presence of *Lepisosteus* (gar) and *Amia*, he suggested a warmer, tropical, savanna environment with streamside forests (Hamblin, 1987). Recent studies of late Uintan plant localities from the western Uinta Formation (unfortunately outside of the stratigraphic study area used in this report) point to a lower mean annual rainfall than seen during the earlier Eocene and a trend towards drying during the Uintan NALMA (Sandau, 2005). Woodburne et al. (2009) also suggest, that based on immigration and extinction patterns associated with each Uintan biochron (Ui1–3), could suggest a habitat change to more open habitats subsequent to the EECO.

UFAU 2 and 3 are both late Uintan assemblages and they reflect that there was less tree cover during this interval than during the Bridgerian in this region of the Western Interior. While both assemblages are classified with open country modern faunas, perhaps indicative of a savanna, it is well-known that large grass-dominant biomes were not typical vegetation formations until the Miocene (Graham, 1999; Woodburne, 2004). The floral study of Sandau (2005) and the larger-scale studies of Woodburne et al. (2009) indicated that the forested habitats typical of the early Eocene were no longer the predominant vegetation formation during the Uintan. This study confirms that open habitats with fewer trees were the common vegetation formation for the later Uintan. Additionally, the high percentages of arboreal and insectivorous mammals from BFAU 5, a Uintan NALMA assemblage, could be indicative of the maintenance of forest habitats during the early Uintan. UFAU 1 is comprised of the stratigraphically youngest early Uintan mammals from the Uinta Formation. With the largest squared Mahalanobis distance from the open habitat centroid (Table 7) UFAU 1, it is not possible to strongly assert at this time that this assemblage is more or less forested than preceding Bridgeian assemblages or the later UFAU.

6.2. Timing of habitat shift and relationship to global climate change

Numerous authors have indicated that the shift in taxonomic composition seen at the Bridgerian–Uintan boundary is another example of the response of mammalian communities to climatic change from the warmer greenhouse environment of the early Eocene to the icehouse of the later Paleogene (Gazin, 1955; Gingerich, 1979; Lillegraven, 1979, 1980; Stucky, 1990, 1992; Woodburne, 2004; Gunnell et al., 2009; Woodburne et al., 2009). This study is the first to report habitat change based on local fossil assemblages for this transitional period for two adjacent regions. As predicted, the mammals from Bridgerian and the Uintan assemblages appear to represent two different habitat types based on the DFA: a forest mammal assemblage and an open habitat mammal assemblage, respectively. However, the unexpected statistical results of this study indicate that all three of the UFAU assemblages are quite far from the open habitat centroid likely due to the high proportions of arboreal mammals preserved in these Uintan sediments (i.e., committed arborealists like primates). The likely reason these Uintan assemblages did not classify with either the savanna-woodland or Chaco mammals is due to the low frequencies of insectivorous taxa known from the three UFAU, clearly an artifact of taphonomic bias since insectivorous mammals are known from other Uintan NALMA deposits (e.g., see Black and Dawson, 1966; Walsh, 1996). The four modern Andean localities have less than 10% insectivorous taxa, similar to the UFAU assemblages. Clearly the presence of arboreal primates and rodents indicate that the local habitats that existed in the Uinta Formation were not free of trees, like that seen in the high altitude Andean sites. As indicated by the mammalian fauna of the Uinta Formation, the degree of tree cover in this region of northeastern Utah, during the Uintan NALMA was much less than what is indicated by the earlier fossil mammals of the more northern Bridger Formation.

Since the UFAU are stratigraphically linked to the GPTS via the Prothero (1996) Wagonhound Canyon section, a time can be suggested for the transition from the more forested habitats of the Bridgerian to the less forested, more open habitats of the Uintan (Fig. 4). UFAU 1 is comprised of the stratigraphically youngest early Uintan mammals of the Uinta Formation. UFAU 1 spans the largest stratigraphic interval, 87 m, and correlates temporally to the earlier Uintan NALMA (approximately 45 Ma; Fig. 4). With the largest squared Mahalanobis distance from the open habitat centroid (Table 7) UFAU 1 and with the base of this unit correlating with the period of oxygen isotope stasis (and thus temperature stasis) after the initial drop in cooling (Fig. 4) it is likely that the more drastic habitat change did not appear during UFAU 1. Multiple lines of evidence point to UFAU 2 and 3 having the criteria for less forested habitats: UFAU 2 is closest to the open habitat centroid and UFAU 3 has the fewest arboreal taxa, no insectivorous taxa, highest frequency of terrestrial taxa and exhibits numerous stream channels and fine-grained paleosols, indicative of the savannas with forested streams suggested by Hamblin (1987) and is stratigraphically associated with later Uintan plants that indicate less rainfall for the region (Sandau, 2005). Furthermore, UFAU 2 and 3 correlate with a global cooling trend recorded in the Cenozoic deep sea oxygen and carbon isotope records that was renewed after a very brief period of stasis during the post-EECO decline in global warmth (Fig. 4; Zachos et al., 2001; Woodburne, 2004). The base of UFAU 2 correlates near the top of Chron 20N, putting this shift to less forested environments in the Uinta Formation at approximately 42 Ma (Fig. 4).

6.3. Ecological diversity of other Uintan mammalian faunas

The late middle Eocene Uintan NALMA has been characterized as a time when increased endemism and corresponding provinciality become apparent in the mammalian fossil record (Lillegraven, 1979; Golz and Lillegraven, 1977; Lillegraven, 1980; Storer, 1984, 1996; Walsh, 1996). Uintan assemblages are well-known from deposits in the Rocky Mountain intermontane basins, Saskatchewan, southern Texas, and southern California. Each of these regions have been characterized as being representative of a unique faunal province (Lillegraven, 1979; Golz and Lillegraven, 1977; Lillegraven, 1980; Storer, 1984, 1996). As global climates shifted during the Cenozoic and local habitats changed, faunal provinces (even refugia) with highly endemic taxa seemingly were the prevailing pattern in North America and this ecogeographic pattern continues today (Van Valkenburgh and Janis, 1993). Globally, endemism is the norm for modern mammalian faunas as the majority of genera (64%) are endemic and occupy only one zoogeographic region (Nowak, 1999; Danell and Aava-Olsson, 2002; Wilson and Reeder, 2005).

Endemism and corresponding provinciality reflects some kind of isolation generally due to a geographic barrier. Apparently during the early Eocene and into the early intervals of the middle Eocene Uintan NALMA, such barriers did not exist or were ephemeral within North America. Lillegraven (1979) made initial paleobiogeographic comparisons between the fossil rich southern California Uintan assemblages and those of the Rocky Mountains. Lillegraven (1979) noted that faunas from the early Uintan of southern California had few endemics and was overall taxonomically similar to the latest Bridgerian–earliest Uintan mammals of the Western Interior. He reported that during the later Uintan and Duchesnean intervals, exchange was limited (Lillegraven, 1979). Both Golz and Lillegraven (1977) and Storer (1984, 1996) reported endemism in late Uintan faunas from California and Saskatchewan, respectively. Walsh (1996) published a more complete comparison of North American regions with updated faunal lists where he used Simpson Coefficients to evaluate faunal similarity. Walsh (1996) found that there was some degree of endemism among both early and late Uintan faunas in the regions where these assemblages were found. Unlike previous authors, however, he did not speculate upon the paleobiogeographic implications of these findings among North American regional faunas (Walsh, 1996).

Recently, Townsend and Gunnell (2009 and unpublished data) evaluated both the taxonomic and ecological diversity of both early (Ui2) and late Uintan (Ui3) mammalian faunas from each of these major North American regions to discern if unique paleoecological patterns existed. In modern mammalian faunas, the highest proportions of genera are endemic, so it is reasonable to presume that those taxa unique to each region would preserve a more distinctive ecological pattern (Danell and Aava-Olsson, 2002). The results of the Townsend and Gunnell (2009) study indicated that at a regional level, ecological patterns did not differ greatly between Ui2 and Ui3 faunas. It appears that the taxonomic provinciality, at the regional level, does not translate to ecological provinciality. Hence, the taxonomic provinciality evident during the Uintan NALMA does not affect the results of this study, particularly since the data for this study were evaluated at a local level via high-resolution stratigraphic data in Wyoming and Utah.

7. Conclusions

The goal of this study was to ecologically characterize the stratigraphically organized mammal communities of both the Bridger and Uinta Formations in order to reconstruct and evaluate habitat change for each local area through time. The habitats of the middle Eocene of the Western Interior have been difficult to characterize at a regional level due to only a few well-known mammal faunas for both the late Bridgerian and entire Uintan, and a lack of temporally or geologically co-occurring (with mammals) floral assemblages for these NALMAs (Townsend and Gunnell, 2009). From the Bridger Formation of southwestern Wyoming, BFAU 1–4, were reconstructed as forested habitats, due to the high frequencies of forest adapted mammals found in each assemblage. This reconstruction is not unlike what has been predicted by some authors for other earlier Bridgerian sites (Gunnell, 1997). Habitats of the Uinta Formation proved to be more challenging to reconstruct since there are clearly components of forest adapted mammals combined with higher frequencies of potentially open country adapted mammals, such as cetartiodactyls. The discriminant analyses suggest that the fauna of the Uinta Formation is dominated by open habitat mammals. However, a closer look at each UFAU (Table 9) indicates, that while they certainly differ ecologically from the earlier occurring Bridgerian assemblages, they are not completely lacking in arboreal and frugivorous mammals normally found in forested habitats.

Based on a decrease in the frequency of arboreal, frugivorous, and insectivorous mammals, this study suggests that by approximately 42 Ma, during the later Uintan NALMA, closed canopy forests were likely not present in the area of northeastern Utah. The discriminant function analysis shows that the ecological differences between the Bridgerian and Uintan communities is apparent, and that perhaps that the differences in body size, dietary and substrate use adaptations, were more subtle than previously thought. The fauna from BFAU 5 could be indicative of a forest habitat, suggesting that regional habitats during the early Uintan had not transitioned to more open savanna, with woodlands more likely found around water sources such as ponds and streams.

The climate deterioration during UFAU 2 and 3 was a likely source of the more open habitats, but the presence of arboreal and fruit-eating mammals indicates that the habitat transition from the Bridgerian to the Uintan was not extreme in the Western Interior. With more fossils coming from early Uintan deposits from the Rocky Mountain region, it will be possible to evaluate if or how taxa specific to the Uintan enriched or triggered changes in the later Bridgerian faunas and the ecological scale at which these interactions occurred. Although the studies of Townsend and Gunnell (2009) and numerous other scholars have indicated that while taxonomic diversity increased at a regional level during the Uintan NALMA due to provinciality, ecological diversity, however, did not shift that much between the early and late faunas. The results of the present study have shown that such regional patterns are not apparent at the local level, once again, proving that both regional and local processes must be integrated in order to fully understand the evolution of both communities and their different components of diversity (Ricklefs and Schluter, 1993; Van Valkenburgh and Janis, 1993).

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