DIVERSITY OF EOCENE COLEOPTERA IN COLORADO

DURING A GLOBAL COOLING EVENT

by

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A thesis submitted to the Faculty of the Graduate School of the University of Colorado in partial fulfillment of the requirement for the degree of Master of Science Department of Museum and Field Studies 2015 This thesis entitled: Diversity of Eocene Coleoptera in Colorado during a global cooling event written by Lindsay J. Walker has been approved for the Department of Museum & Field Studies.

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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline.

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The fossil record provides an excellent study system for understanding how organisms respond to climate change free from human interference. In this study I test the hypothesis that global cooling altered the diversity of Coleoptera (beetles) in the Western Interior of North America during the middle Eocene. This hypothesis was addressed by comparing two fossil beetle assemblages from the Green River Formation of Colorado. These assemblages bracket a ~2.5 million year (m.y.) cooling interval that followed a period of maximum warming (~52-50 Ma) in the Cenozoic. Based on modern biogeographic patterns of insect diversity, I predicted overall community richness decreased and evenness increased over time, and that taxon-specific feeding strategies drove differential responses to cooling, with non-herbivores showing a greater decrease in richness and abundance than herbivores. Compositional turnover was also anticipated with time and cooling.

In total, 580 specimens were sorted into morphospecies within the Carabidae, Staphylinidae, or Curculionoidea (weevils). By using individual-based rarefaction and rank abundance distributions, I found that total community richness and evenness did not significantly change with time/cooling. This pattern also held when beetle data were parsed by feeding guild and taxon. Non-herbivores became more abundant, and there is growing evidence that compositional turnover also occurred with time. One factor complicating comparisons of raw abundances and compositional change was undersampling, which was estimated to be more than double the observed richness for both beetle collections.

This study shows that the response of beetle communities to climate change is complex, and that resultant diversity patterns are sensitive to both ecologic and taxonomic resolution. Moreover, if the beetles assessed here are taken as a representative subset of the entire Green River insect fauna, the environment surrounding ancient Lake Uinta likely accommodated an exceptionally speciose insect community during the middle Eocene. By comparing the diversity and composition of this fossil beetle community to others known from the Western Interior, a more holistic interpretation of how insects respond to the different rates and magnitudes of global climate change should crystallize.

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CHAPTER 1:

Introduction

1.1 Overview

The recent rise in global temperatures has affected life across all latitudes, continents, and oceans (e.g. Dunn & Winkler, 1999; Gottfried et al., 2012; Hoegh-Guldberg, et al., 2007; Parmesan, 2006; Parmesan & Yohe, 2003; Root et al., 2003; Smol et al., 2005; Wassman et al., 2011). As ectothermic organisms, it is unsurprising that insects have been directly impacted by global warming. Seemingly negligible temperature changes (<2°C) have been shown to alter insect population distributions (Parmesan, 1996; Parmesan et al., 1999), reproductive cycles (Strathdee et al., 1995), ecology and evolution (Thomas et al., 2001), and phenology (Nufio et al., 2010). On a global scale, the rate of warming is expected to drive extinctions (Cahill et al., 2013), and that the loss of species will accelerate as the magnitude of this temperature change increases through the 21st century and beyond (Urban, 2015).

The fossil record presents opportunities to test patterns of community-level diversity and compositional change during past episodes of global warming and cooling. Unlike in neoecological investigations, these study systems are free from human disturbance and can be traced along macroecological and evolutionary time scales. For example, the Paleocene-Eocene Thermal Maximum (PETM) (~55 Ma) is thought to represent a global warming event of similar rate and magnitude to present-day climate change (Zachos et al., 2001, 2008). In North America, this event may have directly affected mammal diversity by stimulating immigration on a continental scale (Woodburne et al., 2009) and causing extinctions more locally (Burger, 2009). Sustained warming following the PETM during the Early Eocene Climatic Optimum (EECO)

(~52-50 Ma) does not appear to have altered the generic richness of mammals on either spatial scale, but subsequent cooling may have driven both extinctions and extirpations (Dutchak, 2010; Woodburne et al., 2009).

Cenozoic climate has also been correlated with patterns of diversity and compositional turnover in plant (Wilf, 2000; Wing et al., 2005), vertebrate (Hutchison, 1982; Woodburne et al., 2009), and marine invertebrate communities (Ivany et al., 2003; Smith & Jeffery, 2004). However, these communities have not uniformly responded to past global climate change with respect to their diversity, composition, or response timing (Ivany et al., 2003; Wing et al., 1995; Zanazzi et al., 2007). In this study, past diversity patterns are examined in the context of global cooling using fossil beetle communities from the middle Eocene of western North America.

The predicted responses of these beetle communities to post-EECO cooling follow from modern biogeographic patterns. In the present-day, global-scale biological phenomena with climatic correlations exist in nature. The latitudinal biodiversity gradient offers one example, and refers to the general increase in species richness that occurs toward the tropics (Rosenzweig, 1995). Although the causal mechanisms of this gradient are not fully understood, climate is frequently cited as an important driver (e.g. Erwin, 2009; Hawkins et al., 2003; Mannion et al., 2014, Wright et al., 1993). Global insect diversity broadly conforms to this gradient as the total number of insect species increases toward lower latitudes (Gullan & Cranston, 2010). Estimates of tropical insect and arthropod richness are thus orders of magnitude greater than those found for higher latitude environments (Basset et al., 2012; Danks, 1981, 1988; Erwin, 1982; Sømme & Block, 1991). Additionally, insect richness patterns have been shown to persist from global to local scales at the family level (Finlay et al., 2006).

In combination with richness, biological diversity is also described through abundance, or "evenness". Specifically, when most species in a given community are similarly abundant, evenness is considered "high"; and, were the same community compositionally dominated by relatively few species, evenness would then be "low" (Magurran, 2004). Evenness patterns may warrant closer attention in the context of climate change considering many species abundances will shift as populations migrate in response to temperature, possibly through the formation of non-analogue communities (Walther, 2010; Williams & Jackson, 2007). Yet, compared to richness, the relationship between evenness and climate are poorly understood (Magurran & Henderson, 2011; Soininen et al., 2012; Stirling & Wilsey, 2001). Understanding abundance distributions in fossil communities is further complicated by taphonomic processes that prevent some species from being preserved (E. P. Anderson & D. M. Smith, unpublished data). Keeping these potential limitations in mind, meaningful evenness patterns can still be interpreted from the fossil record (Kidwell & Flessa, 1996).

On a global scale, it has been speculated that species evenness should generally decrease as richness increases with latitude, but exceptions have been observed (Willig et al., 2003). Inverse patterns of richness and evenness are also expected for tropical and subtropical communities, whereby richness increases and evenness decreases toward the tropics (Stevens & Willig, 2002). This pattern may be partially driven by the general preponderance of "rarity" in tropical ecosystems, as exemplified by high proportions of singleton species uncovered by tropical insect surveys (e.g. Basset et al., 2012; Novotný & Basset, 2000). This addition of rare species increases richness in tropical communities, and, in turn, decreases evenness (Stevens & Willig, 2002).

Ecological information can provide complimentary insight into why species richness and evenness may (or may not) have changed in a given insect community. Therefore, some neoecological studies of insect diversity have emphasized functional feeding groups (e.g. Andrew & Hughes, 2005a; Basset et al., 2012; Lassau et al., 2005; Novotný & Basset, 2000). Paleoentomology has also shown that richness patterns must be interpreted cautiously and with consideration for factors such as host-herbivore relationships (Ponel et al., 2003). For these reasons, when Quaternary insects are used as paleoclimatic indicators, as in the Mutual Climate Range (MCR) method (Atkinson et al., 1986, 1987), generalist (predaceous, scavenging) and specialist (herbivorous) feeding guilds are treated separately. Beetles with generalist feeding strategies are presented as more appropriate indicators of climate change as their ranges are less likely to be restricted by their host plant populations, allowing them to respond more rapidly to the direct effects of temperature (Bale et al., 2002; Elias, 2010). Herbivorous insects, on the other hand, are often omitted from MCR temperature reconstructions (e.g. Elias & Mathews, 2002). Although the MCR approach was first developed for Quaternary paleoclimate research (Atkinson et al., 1986), this method has yielded promising results when applied to latest Eocene Diptera (Moe & Smith, 2005). However, because the pre-Quaternary fossil record does not typically yield a temporal resolution as fine as that of the last ~ 1.6 m.y. some underlying assumptions of the MRC method may not hold over longer time intervals (>100,000 years), which may be important to understanding how ecological patterns operate on different time scales.

1.2 Hypothesis & Predictions

In this study I tested the hypothesis that global cooling altered the diversity of Coleoptera (beetles) during the middle Eocene. Two fossil beetle assemblages that were deposited in the same lake environment, but at different times, were used to address this hypothesis. First, I predicted that the overall species richness of this ancient beetle community decreased as global climate cooled. Second, I predicted that changes occurring in the diversity of this community reflected taxon-specific ecology, such that different feeding guilds responded differentially to global climate change. Finally, I expected that the overall composition of the beetle community changed as cooling progressed.

1.3 Geologic & Paleoclimatic Setting

The Eocene Green River Formation was produced by an extensive lake system overlapping the present-day boundaries of Colorado, Wyoming, and Utah (Smith et al., 2008) (Fig. 1). Numerous fossil insect deposits are known throughout the formation in the Piceance Creek Basin of western Colorado (Pribyl et al. 1996; Duncan, 1997), and the two localities included in this study represent end-member assemblages with respect to all fossil insect collections from the Green River Formation reposited at the University of Colorado (UCM) (D. Kohls, pers. comm.). All specimens included in this work were collected at the "Denson" and "Claudia's Place" field sites (UCM localities 2007238 and 2009063), herein referred to as the "lower" and "upper" localities, respectively (Fig. 2).

The lower locality is collectively comprised of four fossiliferous deposits (~8 lateral meters each) along a ~2 meter-thick horizon within the Parachute Creek Member of the Green River Formation (D. Kohls, pers. comm; Duncan, 1997). Duncan (1997) illustrates this layer as

occurring in the lowermost section of the "B Groove" lean oil shale zone designated for hydrocarbon exploration (see also Donnell, 2010; O'Sullivan & Hail, 1987). The lower locality is also ~25 m below the "Curly" tuff marker bed dated at 49.02 ± 0.30 Ma (Smith et al., 2008). The upper locality is not within the Parachute Creek Member, but is part of an overlying unit of the Green River Formation, informally known as the "Marlstone at Jackrabbit Ridge", between Units C and D of the Uinta Formation (O'Sullivan & Hail, 1987). Fossils from this locality were collected over an area of ~60 lateral meters within a series of recumbent marlstone folds (Fig. 3) (D. Kolhs, pers. comm.). Sandstone tongues of the Uinta Formation above and below this locality demarcate the onset of basin infilling during the lake's closing phase (Donnell, 2010).

Radiometric dating of volcaniclastic deposits in the Piceance Creek Basin has been hindered by a lack of suitable unaltered material (Griggs, 1968; P. Robinson, pers. comm.); however, the lateral continuity of several marker beds across the Uinta and Piceance Creek Basins (Cashion & Donnell, 1972) allows the age model established by Smith et al. (2008) to be applied to the stratigraphy used in this work. The Curly Tuff, noted above, is one of these maker beds (Cashion & Donnell, 1972). A second reference horizon, the oil-rich Mahogany Bed, is stratigraphically intermediate to the lower and upper localities and has been approximated to ~48.7 Ma by Smith et al. (2008). The Mahogany Bed lies ~50 vertical meters above the lower locality (Duncan, 1997) and ~200 m below the upper locality (approximated from O'Sullivan & Hail, 1987). Assuming the ancient lake sustained relatively slow and constant sedimentation rates through time, as supported by the dominance of finely laminated marlstones throughout the stratigraphic section, it is reasonable to believe the lower and upper fossil beetle assemblages were deposited after EECO warming (~52-50 Ma) and during the onset of global cooling (Zachos et al., 2001) (Fig. 4). To estimate the interval of time occurring between the deposition of the two fossil localities, sedimentation rates suggested by the 40 Ar/ 39 Ar ages (Smith et al., 2008) for the Wavy and Curly tuff marker beds were extrapolated to encompass the complete sedimentary thickness separating the lower and upper localities in space and time (Fig. 2). By using these mean ages and their corresponding maximum errors, the amount of time intervening between the deposition of the lower and upper fossil beetle assemblages may have ranged from ~460,000 to ~4,500,000 years with a mean interval of ~2.5 m.y. The mean estimate will be herein referenced for simplicity, although it must be acknowledged that this amount of time is an approximation, as neither locality has been precisely dated using radiometric or biostratigraphic methods.

Following the EECO, from ~50-44 Ma, deep sea temperatures may have decreased by ~4°C, as suggested by the stable isotopic compositions of benthic marine foraminifera (Fig. 4) (Zachos et al., 2001). Although an equivalent terrestrial record has not been developed for the Western Interior, stable isotope excursions spanning the PETM (Burger, 2009) and EECO (Dutchak, 2010) from the Piceance Creek Basin correlate with the marine isotope record, as does the ontogeny of ancient Lake Uinta (Tänavsuu-Milkeviciene & Sarg, 2012). This overall cooling pattern is corroborated by fossil floras, which collectively indicate that mean annual temperatures (MAT) in western North America concomitantly declined alongside cold month mean temperatures (CMMT) through the remainder of the Eocene (Wolfe, 1994). With respect to the early middle Eocene, MacGinitie (1969) described the paleoclimate in the midcontinent as being subtropical ("Orizaban") and characterized by little to no frost occurring throughout the year (CMMT>13°C; MAT 16-21°C).

Despite similarities in patterns inferred from paleoclimate proxies, uncertainty remains regarding the response rates of marine and terrestrial organisms to global temperature change.

For instance, Eocene-Oligocene cooling (Zachos et al., 2001) did not synchronously affect marine and terrestrial communities, as demonstrated by turnover in marine invertebrates (Ivany et al., 2003), North American mammals (Zanazzi et al., 2007), and plants (Wolfe, 1994). The magnitude of this climate change event may have also differed across the terrestrial and marine realms, with MAT cooling being more pronounced on land (Zanazzi et al., 2007). However, because beetles are thought to respond relatively quickly to temperature due to their ectothermic metabolisms, short generation times, and rapid dispersal potential (e.g. Ashworth, 1996; Butterfield, 1996; Elias et al., 2006; Ponel et al., 2003), climatically-induced changes in beetle communities may precede those of more sessile or slower developing terrestrial organisms. Following this premise, one might expect Eocene beetle communities to have changed if continental climates were cooling in phase with marine temperatures, although the direct effects of this forcing mechanism may have been moderated or accelerated by more localized conditions in the continental interior.



Figure 1. Location map. Shaded areas represent the extent of oil shale beds in three basins containing the Green River Formation. The fossil localities included in this study stratigraphically bracket the richest oil shale beds ("Mahogany Zone") in the Piceance Creek Basin. A smaller fourth basin (not pictured) lies immediately west of Kemmerer, WY and is known for the Early Eocene Green River lagerstätten of Fossil Butte National Monument (Grande, 2013). Map modified from Johnson (2014).



Figure 2. Stratigraphy. Fossil beetles included in this study were collected from two localities. The lower locality corresponds to the base of the B-Groove lean oil shale and the top of the R-6 rich oil shale zone; the upper locality is located within the uppermost unit of the Green River Formation, which intertongues with massive sandstone beds of the overlying Uinta Formation.



Figure 3. Annotated lithology of upper locality. The upper locality is comprised of marlstone interbedded with thin (~2 cm) sandstone layers within a recumbent fold (dipping <5° N-S). This site lies within the uppermost unit of the Green River Formation, informally known as the Marlstone at Jackrabbit Ridge (O'Sullivan & Hail, 1987; Donnell, 2010). Specimens from the lower locality were also collected from similarly laminated marlstone deposits (D. Kohls, pers. comm.)



Figure 4. Paleoclimatic context. The fossil beetles included in this study were deposited in Lake Uinta during the onset of global cooling following the Early Eocene Climatic Optimum (EECO) (52-50 Ma) (Zachos et al., 2001). The age range covered by these assemblages are derived from Smith et al. (2008). Figure modified from Zachos et al. (2001).

CHAPTER 2:

Materials & Methods

2.1. Field Collection

The fossil beetles included in this study were acquired over six field seasons (2006-2010) from the lower and upper fossil insect localities of the Green River Formation. These collections represent a sampling effort of 90 days by one individual, Mr. David Kohls, and all specimens are cataloged and reposited at The University of Colorado Museum of Natural History (UCM localities 2007238 and 2009063). Mr. Kohls consistently collected every specimen rather than high-grade a selection of the most aesthetically pleasing or "interesting" individuals. As a result, the collections he amassed are suitable for robust paleoecological analyses (Smith, 2011). The two fossil localities included in this work were chosen for several reasons. First, insects collected at these localities were preserved under isotaphonomic conditions, as all compression fossils from these sites were obtained from lithologically equivalent marlstones deposited in the same lake environment (E. P. Anderson & D. M. Smith, unpublished data). Second, fossils from these localities could be confidently considered temporally distinct assemblages sequentially derived from the same insect community following EECO warming.

2.2 Specimen Imaging & Identification

All Coleoptera from 90 collecting days were examined. From these specimens, all individuals identified as Carabidae, Staphylinidae, and Curculionoidea (weevils) following Arnett and Thomas (2000) and Arnett et al. (2002) were imaged using a Canon EOS 5D Mark II and Canon MP-E65mm f/2.8 1-5x macro lens with a Tamron SP 1.4x Pro teleconverter.

Uncompressed, unaltered image files were imported through Adobe Lightroom CS6 and stacked using Helicon Focus software. Scales were inserted into unaltered uncompressed images through Adobe Photoshop CS6 and then down-sampled to JPG format to reduce file sizes.

Carabids, staphylinids, and weevils were targeted groups, as all three represent beetle taxa with similarly high levels of diversity and ecologically distinct feeding strategies (Arnett & Thomas, 2000; Arnett et al., 2002). In combination, these qualities enable the testing of predictions related to the richness, evenness, and ecology within beetle communities. These beetles are present in relatively high abundances and show high quality preservation within the Green River Formation (Duncan, 1997; E. P. Anderson & D. M. Smith, unpublished data).

As habitus views of beetle compression fossils rarely reveal diagnostic characters necessary for identification using traditional keys, a conservative approach was taken to generating taxon counts, and new species were only differentiated when unambiguous differences could be distinguished between individuals (e.g. distinct setation, punctation, elytra, rostra, or antennae). Specimens were categorized by "morphospecies" and further advice was sought from specialist workers to increase confidence in taxon differentiation and, where possible, taxonomic assignment. Each morphospecies belongs to a distinct species, but has yet to be identified as a previously established species or assigned a new species name. Morphospecies are hereafter referred to as "species". Identifying specimens below the familial taxon level using the most current descriptions of Green River beetles was difficult because these original works often diagnose new species using isolated elytra or obscured habitus views (e.g. Scudder, 1890, 1893, 1900). It was therefore necessary to approach this component of the project with input from experts on modern Coleoptera.

2.3 Assessment of Sampling Effort: Sample-Based Rarefaction

All species accumulation curves and diversity estimations were obtained using EstimateS 9.1.0 software (100 randomizations without replacement) (Colwell, 2013a). To assess sampling adequacy, all taxon counts were pooled by locality with each unit of sampling effort equating to one of Mr. Kohl's collecting days. Sample-based rarefaction was performed for each fossil locality. These curves were also extrapolated by a factor of three to estimate the amount of additional sampling effort necessary to recover the difference between estimated and observed species richness (Colwell et al., 2012).

2.4 Total Species Richness: Non-parametric Extrapolation

Total species richness was extrapolated from observed abundance data using nonparametric estimators simultaneously output with sample-based rarefaction data. As Chao 1 (classic) and ACE (Abundance-based Coverage Estimator) estimators were developed for use with abundance-based data, the outputs of these formulae (Table 1) were prioritized (Colwell & Coddington, 1994). EstimateS software prompts users to report the greater richness estimate produced by either Chao 1 or ACE for abundance-based datasets, although both values are noted herein. Chao 2 (classic) was also considered, as this incidence-based estimator may become more relevant to the paleontological literature as non-parametric estimators become more established in paleoecology (Hammer & Harper, 2006). All three estimators have fared well in performance comparisons (e.g. Hortal et al., 2006) and the Chao estimators in particular are widely used in modern insect ecology (e.g. Andrew & Hughes, 2004; Basset et al., 2012; Maveety et al., 2011). Singletons are defined as single occurrences (n=1), whereas doubletons include species with exactly two occurrences. Non-parametric formulae are somewhat dependent on the recurrence of singleton species (Table 1), which intuitively decrease with increased sampling effort. Therefore, by this method, estimated and observed species richness values should align when no singleton species remain (Colwell & Coddington, 1994).

2.5 Richness Comparisons: Individual-Based Rarefaction

Individual-based rarefaction was performed to facilitate direct comparison of species richness between fossil beetle collections. This method holds sampling protocols constant between collections (Gotelli & Colwell, 2001), and is thus particularly useful to paleo- and neoecologists when this information in unavailable for historic/museum collections. However, in this case, sampling was rigorously standardized, and comparisons drawn from individual-rarefaction analyses reported herein can be considered reasonably robust and depicting biologically meaningful patterns. This analysis was performed several times to make comparisons between species richness and evenness by pooling all beetle data by locality (and repeating this analysis with singleton species removed), as well as by separating beetles by feeding guild and taxon. Output curves were directly compared only after they were rarified to lowest sampling effort.

2.6 Evenness Comparisons: Rank Abundance & Individual-Based Rarefaction

Changes in evenness were assessed in two ways. First, rank abundance distributions were compared for all beetle data pooled by locality and, again, with singleton species removed. These distributions were compared using a Kolmogorov-Smirnov two-sample test (Hammer & Harper, 2006; Magurran, 2004). Second, in addition to facilitating richness comparisons, individualbased rarefaction data reflect species accumulation rates, thereby allowing one to infer community evenness from the slopes of these curves (e.g. increasing evenness accelerates the rate of species accumulation, in turn causing the slope of the rarefaction curve to increase/steepen) (Gotelli & Cowell, 2001). Both rank abundance and rarefaction methods are additionally useful for making diversity comparisons between communities with unknown taxonomic overlap (McGill et al., 2007).

2.7 Feeding Guild Abundances

Following the precedent of ecological work using functional feeding groups (e.g. Andrew & Hughes, 2005a; Basset et al., 2012; Lassau et al., 2005), beetle feeding preferences were assigned by family and, in the case of weevils, superfamily. All weevils were treated as herbivores. With the exception of "broad-nosed" weevils (Curculionidae: Entiminae), most weevils are typically considered specialist herbivores, with host associations being restricted to a narrow range of plant species for adults and larvae (Arnett et al., 2002; Oberprieler et al., 2007). Carabids and staphylinids were grouped as "non-herbivores" because members of these families are predominantly predators or scavengers (Arnett & Thomas, 2000; Larochelle, 1990; Thayer, 2005). Observed abundances of each beetle taxon were pooled by feeding group and compared between localities using contingency table (chi-square) analysis.

Table 1		
Estimator	Formula	Variables
Chao 1	$S_{est} = S_{obs} + \frac{n-1}{n} \left(\frac{F_1^2}{2F_2}\right)$	S_{est} = estimated richness S_{obs} = total observed richness n = total # samples F_1 = singleton frequency F_2 = doubleton frequency
Chao 2	$S_{est} = S_{obs} + \frac{m-1}{m} \left(\frac{Q_1^2}{2Q_2} \right)$	m = total # samples Q ₁ = uniques frequency Q ₂ = duplicate frequency
ACE	$S_{est} = S_{abund} + \frac{S_{rare}}{C_{ACE}} + \frac{F_1}{C_{ACE}} \gamma_{ACE}^2$	$S_{obs} = S_{rare} + S_{abund}$ $C_{ACE} = 1 - (F_1/N_{rare})$ (where $N_{rare} = \sum_{i=1}^{10} iF_1$)

Table 1. Formulae of non-parametric estimators used to extrapolate total species richness from observed species richness and abundances (formulae used by EstimateS 9.1.0; Colwell, 2013b).

CHAPTER 3:

Results

3.1 Overview: Raw Abundances & Observed Richness

All cataloged Coleoptera (2802 unique individuals) from 90 samples (collecting days) were examined in this study (Table 2a). Of the 972 cataloged specimens identified as Carabidae, Staphylinidae, or Curculionoidea (weevils), 580 individuals could be differentiated into distinct species within Carabidae, Staphylinidae, and Curculionoidea. Any individuals that were too incomplete to be designated as new or existing species were removed from all further analyses (Table 2a). At the lower locality, 39 collecting days produced 389 individuals and 80 species; at the upper locality, 51 collecting days produced 191 individuals and 59 species (Table 2a).

These data were further differentiated by feeding guild and taxon for each locality. From the same 580 individuals, at the lower locality, 389 specimens were differentiated into 24 carabid, 22 staphylinid, and 34 weevil species; at the upper locality, 191 individuals were differentiated into 16 carabid, 16 staphylinid, and 27 weevil species (Table 2b). Although statistical comparison of species overlap between the two localities was not possible (see identification results reported and discussed below), the lower and upper beetle assemblages could be compared in terms of richness, evenness, and relative abundance.

3.2 Assessment of Sampling Effort: Sample-Based Rarefaction

Neither sample-based rarefaction curve achieved asymptotic saturation for all beetles combined by locality (Fig. 5a-b). This includes the extrapolated portions of these curves that triple observed sampling effort. Even lower-bound 95% confidence intervals were still increasing at 117 and 153 samples for the lower and upper localities, respectively (Fig. 5a-b). Together, these results suggest that, at minimum, sampling intensity for both sites must be quadrupled before true species richness would be captured. That both localities were undersampled requires true species richness to be extrapolated from observed data using non-parametric richness estimators; doing so also allows sampling adequacy to be further quantified as the ratio of observed (S_{obs}) to total estimated richness (S_{est}), as discussed in the following section.

3.3 Species Richness Estimates: Non-Parametric Extrapolation

Non-parametric species richness extrapolations ranged from 143 (ACE) to 184 ± 50 (Chao 1) species for the lower locality, and 105 (ACE) to 154 ± 55 (Chao 1) species at the upper locality. Chao 2 estimates were intermediate to Chao 1 and ACE, although the Chao 2 estimate for the lower locality (182 ± 49) was more closely aligned with Chao 1 than Chao 2 for the upper locality (126 ± 36) (Fig. 5a-b). All non-parametric estimators produced lower estimated species richness for the upper locality, but these results do not differ significantly from the lower locality (Table 3). Although there was broad variation around the mean for all estimators, all of these curves trend towards increasing (non-asymptotic) richness at maximum sampling effort for both localities. This pattern is further reflected in the gradual increase in singletons sampled from both assemblages, as non-parametric estimators reach saturation when n>1 for all species (Fig. 5a-b).

Sampling adequacy at each locality was further approximated as the ratio of observed to extrapolated (Chao 1) species richness (S_{obs}/S_{est}). These results suggest that less than half of the total species richness was observed at each site, with 46% sampling completeness at the lower locality and 38% at the upper locality. These results broadly agree with the under-sampling indicated by sample-based rarefaction curves (Fig. 5a-b).

3.4: Richness Comparisons: Individual-Based Rarefaction

Individual-based rarefaction was performed on all beetle abundances combined by locality (Fig. 6a, Table 4a), separated by feeding guild (Fig. 7, Table 5), and separated by taxon (Fig. 8, Table 6). This analysis was repeated on the pooled datasets, but with singletons removed (Fig. 6b, Table 4b). In all cases, species richness did not significantly change with time (Fig. 6a, 7-8), except when singleton species were removed, which caused estimated richness to be significantly lower at the upper locality with both curves reaching asymptotic saturation (Fig. 6b)

3.5 Evenness Comparisons: Rank Abundance & Individual-Based Rarefaction

Rank abundance distributions of observed beetle species produced similar patterns for all beetle abundances combined by locality (Fig. 10a) and when singleton species were removed (Fig. 10b). A Kolmogorov-Smirnov two-sample test did not find these distributions to be significantly different between localities (P > 0.05). Approximately half of observed species were singletons at both the lower (51%) and upper locality (47%) (Appendix A). Corresponding individual-based rarefaction curves also follow near-identical rates of species accumulation, both with (Fig. 6a) and without (Fig. 6b) singleton species. Collectively, these results indicate community evenness did not change through time.

3.6 Feeding Guilds: Observed Abundances

Relative abundances of observed herbivores (weevils) and non-herbivores (carabids and staphylinids) significantly differed between localities (Yates $x^2=9.34$, df = 1, P = 0.0022) (Fig. 9). Individual-based rarefaction was also performed to make richness comparisons between feeding groups. While none of these curves significantly differed within 95% confidence (Table

5), there was a slight decrease in the richness and evenness of non-herbivores, and slight increase in the richness and evenness of herbivores between localities (Fig. 7).

3.7 Assemblage Compositions

Forty-seven percent of the study specimens could be identified to subfamily, tribe, or genus (Appendix A, arranged in order of descending abundance at the lower locality). Eighty and fiftynine beetle species were observed for the lower and upper localities, respectively (Table 4a). Overall, weevils were the most abundant beetle group, with well over twice the number of morphotyped specimens occurring at the lower (229 individuals) versus the upper locality (86 individuals). No morphospecies within the weevil subfamily Entiminae (Curculionidae) occurred at both localities, but some specimens from the families Nemonychidae and Brentidae, as well as several others from the subfamilies Baridinae, Ceutorhychinae, Molytinae, and Mesoptilinae (all Curculionidae), occur at both localities. The genus *Bembidion* dominated the lower and upper locality carabid assemblages (39% and 42% *Bembidion*, respectively). The subfamily Paederinae (47%) dominated the lower locality staphylinid assemblage, whereas the upper locality assemblage contained proportionally more *Stenus* (Steninae) (30%).



Figure 5. Results of sample-based rarefaction analyses of all beetle abundance data combined for the A) upper and B) lower locality. Sample-based rarefaction curves (S_{est}) and 95% confidence intervals are shown with non-parametric richness estimates (Chao 1, Chao 2, ACE) (Table 3) and singleton and doubleton curves. Sample-based rarefaction curves were extrapolated to three times observed sampling effort for each locality (S_{est}).

100

10

Samples

1

Α

В



Figure 6. Individual-based rarefaction of all beetle species A) combined by locality and B) combined by locality with singleton species removed. A) Rarefaction curves do not significantly differ as both 95% confidence intervals overlap (Table 4a) (P > 0.05). B) When singleton species were removed, both curves reached asymptotic saturation. The thin black lines depict 95% confidence intervals, which show that these curves significantly differ when rarified to the lowest sampling effort (160 individuals) (Table 4b).



Figure 7. Individual-based rarefaction of herbivores (weevils) and non-herbivores (carabids, staphylinids) by locality. These curves do not significantly differ as all 95% confidence intervals overlap (95% confidence intervals not shown, see Table 5; P > 0.05).



Figure 8. Individual-based rarefaction of beetles compared by taxon. These curves do not significantly differ as all 95% confidence intervals overlap (95% confidence intervals not shown, see Table 6; P > 0.05).



Figure 9. Observed abundances of herbivores (weevils) and non-herbivores (carabids, staphylinids) by locality. Feeding guild abundances significantly differ between localities (Yates $x^2=9.34$, df = 1, P = 0.0022).



Figure 10. Rank abundance distributions of A) all beetle species combined by locality (P > 0.05) and B) with all singleton species removed (P > 0.05).

Α

В

Table 2. Sampling summary tables. A) Table 2a summarizes: total sampling effort; total cataloged Coleoptera; total cataloged Carabidae, Staphylinidae, and Curculionoidea (Focal Taxa); and total individuals (n) differentiated to species used in analyses. B) Table 2b summarizes: total specimens used in analyses (n); total indeterminate specimens omitted from analyses (Indet); and observed species richness (S_{obs}) per focal taxon.

Table 2A									
Locality		Samples		Coleop	tera	Focal T	`axa	n	
Upper		51		1023 372			191	l	
Lower		39		1779 603		389)		
Total		90		2802 972		580			
Table 2B									
		Carabid	5	St	taphylin	ids		Weevils	
Locality	n	Indet	\mathbf{S}_{obs}	n	Indet	\mathbf{S}_{obs}	n	Indet	\mathbf{S}_{obs}
Upper	57	47	16	48	55	16	86	79	27
Lower	64	23	24	96	17	22	229	174	34

Table 3. Estimated species richness (S_{est}) produced by non-parametric estimators. Standard deviations (SD) and 95% confidence intervals (CI) for all mean values (unrarified) are reported for estimators that output these values. For all non-parametric richness estimates, there is no significant difference between localities (P > 0.05).

Table 3								
Locality		Chao	01		Cha	o 2	AC	E
Locanty	Sest	SD	95% CI	Sest	SD	95% CI	Sest	SD
Upper	154.6	55.7	92.13-334.8	126.3	36.04	84.15-239.1	105.8	-
Lower	184.79	50.49	122.8-336.6	182.4	49.34	121.8-330.7	143.8	-

Table 4. Results of individual-based rarefaction analysis performed on A) all beetle abundance data and B) again on the same datasets, but with singleton species removed. Results of observed (S_{obs}) and interpolated (S_{est}) richness estimates are reported with standard deviations (SD) and 95% confidence intervals (CI). Reported S_{est} values are rarifed to the lowest sampling effort (*n* individuals). Where $S_{obs} = S_{est}$, S_{est} is reported as (-). Rarified richness estimates (S_{est}) do not significantly differ for any taxa between localities (P > 0.05).

Table 4			Α	В				
Locality		All	Coleopter <i>n</i> =191	°a	Singletons Removed n=160			
-	Sobs	Sest	SD	95% CI	Sobs	Sest	SD	95% CI
Upper	59	_	6.04	47.16-70.84	28	-	0.91	26.22-29.78
Lower	80	55.93	5.12	45.9-65.96	39	35.25	0.5	34.27-36.23

Table 5. Individual-based rarefaction values by feeding guild. Results of observed (S_{obs}) and interpolated (S_{est}) richness estimates are reported with standard deviations (SD) and 95% confidence intervals (CI). Reported S_{est} values are rarifed to the lowest sampling effort (86 individuals). Where $S_{obs} = S_{est}$, S_{est} is reported as (-). Rarified richness estimates (S_{est}) do not significantly differ for any taxa between localities (P > 0.05). Note that because all herbivores are also weevils, these values are duplicated in Table 6, and that S_{obs} for non-herbivores equates to observed species richness of carabids combined with staphylinids (separated in Table 6).

Table 5								
Locality		Н	erbivore	8		Non-F	Ierbivoi	res
Locality	Sobs	S _{est}	SD	95% CI	Sobs	S _{est}	SD	95% CI
Upper	27	-	3.43	20.27-33.73	32	28.69	4.66	19.56-37.82
Lower	34	22.6	3.12	16.48-28.72	46	32.19	3.96	24.44-39.95

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Table 6. Individual-based rarefaction values by taxon. Results of observed (S_{obs}) and interpolated (S_{est}) richness estimates are reported with standard deviations (SD) and 95% confidence intervals (CI). Reported S_{est} values are rarifed to the lowest sampling effort (*n* individuals). $S_{obs} = S_{est}$ for categories representing lowest sampling effort (i.e. where S_{est} is reported as -). Rarified richness estimates (S_{est}) do not significantly differ for any taxa between localities (P > 0.05).

Table 6												
Locality	Carabids ity					Staphylinids n=48				Weevils n=86		
	Sobs	Sest	SD	95% CI	Sobs	Sest	SD	95% CI	Sobs	Sest	SD	95% CI
Upper	16	-	3.43	8.34- 20.5	16	-	3.25	9.62- 22.38	27	-	3.43	20.27- 33.73
Lower	24	22.14	4.17	13.97- 30.31	22	15.63	2.1	11.51- 19.74	34	22.6	3.12	16.48- 28.72

CHAPTER 4:

Discussion

The height of Cenozoic global warmth (~52-50 Ma) was followed by an interval of protracted cooling that lasted for ~16 million years (Zachos et al., 2001, 2008). After cooling began, fossil beetles were sequentially deposited in ancient Lake Uinta over ~2.5 million years (Smith et al., 2008) (Fig. 4). I hypothesized that globally decreasing temperatures altered the diversity, feeding guilds, and composition of this beetle community as cooling progressed. Contrary to expectations, community richness and evenness did not change, nor did the richness of herbivores or non-herbivores, although non-herbivores may have become more abundant with time. Evidence for compositional turnover was found, and research in this area is continuing.

Sample-based rarefaction and non-parametric diversity estimators indicate the true total beetle richness was substantially undersampled in both the lower and upper fossil assemblages (Fig. 5, Table 3). However, because individual-based rarefaction methods control for sampling effort (Gotelli & Colwell, 2001), there is no reason to believe the patterns observed for either locality do not accurately reflect the ancient communities they represent (Fig. 6-8), even if reported values are somewhat imprecise (Willig, 2003). Additional confidence comes from the unique preservational qualities of the two fossil localities, which permit taphonomy to be considered constant with time, in addition to collector and identification biases.

4.1 Richness: Patterns & Estimates

I anticipated total species richness would decrease with time and cooling. This prediction was drawn from the present-day latitudinal pattern of increasing species richness observed toward the tropics (Gullan & Cranston, 2010; Rosenzweig, 1995). However, no significant directional change occurred with time for individual-based rarefaction analysis of all beetle abundances combined (Fig. 6a). These findings are only somewhat surprising considering observed changes occurring in the context of global warming (Parmesan, 2006). Much of the literature on insect response to current climate change has also examined shifting population distributions rather than species richness (Andrew et al., 2013), and current climate change is projected to increase species extinctions (Urban, 2015) even if some species successfully redistribute to higher latitudes and/or elevations. The results of this work are also in contrast to those of late Neogene and Quaternary beetle communities, which demonstrated overall decreased diversity with cooling (Elias et al., 2006), as well as a positive relationship between species richness and warming (Ponel et al., 2003), but over shorter time scales (<100 kyr - <1 myr).

Rarefaction, as applied here, controls for sampling effort when comparing communities across time and space (Gotelli & Colwell, 2001, 2011), and the richness patterns presented here (Fig. 6a-b) are consistent with the results of studies that have employed similar methods. In these investigations (Andrew & Hughes, 2004, 2005a, 2005b, 2005c), arthropod communities were sampled along a tropical-temperate latitudinal gradient representing a 4.3°C change in mean annual temperature (MAT). Temperature seasonality and precipitation could be considered constant between latitudes, and MAT was anticipated to affect various components of arthropod community structure. In many cases, this was not shown to be true, or only weakly so (Andrew & Hughes, 2005b, 2005c). For example, no relationship was found between

latitude and herbivory or the richness of herbivorous Hemiptera, which were both predicted to increase toward the tropics (Andrew & Hughes, 2005b, 2005c). In contrast, the richness of herbivorous beetles did increase, but only after rare species were removed from datasets pooled by latitude (Andrew & Hughes, 2004), which was also true for Green River beetles (Fig. 6b).

True species richness was estimated to be much higher than observed richness ($\sim 2x$) at both localities, and asymptotes were not achieved for any sample-based rarefaction curves or non-parametric estimators (Fig. 5a-b, Table 2). The former data are also likely to be conservative underestimates of extrapolated species richness because the Chao formulae are regarded as lower-bound predictors of total richness when rarefaction curves do not achieve asymptotic saturation (Colwell, 2013b; Gotelli & Cowell, 2001). Total estimated richness is further reduced by taphonomic biases, which inevitably contributed to the systematic omission of certain species from the fossil record due to their life habits, habitats, and body sizes, acting in combination with the physical and chemical conditions of the original depositional environment (Smith, 2000; Smith et al., 2006; Wilson, 1988). Even working within these constraints, and in addition to limiting analyses to three specific beetle groups, total estimated richness was high (Table 3). These results are consistent with extrapolated richness estimates (Chao 1) for lower latitude phytophagous beetles (26° 7' S) (Andrew & Hughes, 2004). Previous studies of Western Interior fossil floras also support an interpretation of humid subtropical to tropical (frost-free) conditions in the ancient Green River environment (MacGinitie, 1969; Wilf, 2000), and similarly high insect diversity has been found for beetles, among other insects, during the early to middle Eocene of western North America (Archibald et al., 2010, 2013).

4.2 Evenness: Patterns & Influences

Evenness was expected to increase with time and cooling, but individual-based rarefaction (Fig. 6a) and rank abundance distributions (Fig. 10a) demonstrate similar patterns of evenness for all beetle data combined. The expectation of increasing evenness with time was based on the inverse patterns of richness and evenness associated with tropical and subtropical communities, such that subtropical (cooler climate) communities have lower richness and higher evenness than tropical communities (Stevens & Willig, 2002). But, taken as a whole, variation in species evenness along broad environmental gradients is not well understood relative to species richness, which shows a clearer relationship with latitude and temperature (Soininen et al., 2012; Willig et al., 2003). For example, the richness of globally distributed bat communities have shown a strong relationship with latitude, but not for evenness, which may be more indirectly affected by latitude via the presence (or absence) of rare species (Stevens & Willig, 2002).

Not only do rare species indirectly affect community evenness, but they also prevent rarefaction curves generated for tropical communities from achieving asymptotic saturation (Basset et al., 2012; Magurran & Henderson, 2011; Novotný & Basset, 2000). In this study, rarity was synonymized with singleton species (*n*=1). By this measure, nearly half of all species observed at both fossil beetle localities were "rare" (e.g. Maveety et al., 2011), as clearly shown by rank abundance distributions of all beetles combined by locality (Fig. 10a). Because removal of rare species can impart significant differences to patterns of diversity along climatic gradients (Andrew & Hughes, 2004), individual-based rarefaction of pooled beetle data were re-performed with all singleton species removed. Doing so not only produced a significant pattern of decreased richness with time and cooling, but asymptotes were also achieved for curves representing both the lower and upper fossil beetle assemblages (Fig. 6b). Interestingly, omission of singleton

species did not affect evenness patterns shown by the slopes of individual-based rarefaction curves (Fig. 6b), nor did it drive any significant differences between rank abundance curves (Fig. 10b). These observations support prior interpretations that measures of evenness are less sensitive to sampling effort than measures of richness, and that richness and evenness may be independently affected by environmental change (Steven & Willig, 2002; Willig, 2003). These results also support previous interpretations that rare species can significantly contribute to the total diversity and compositions of beetle communities (Andrew & Hughes, 2004).

4.3 Feeding Guilds: Richness & Abundance

Individual-based rarefaction of abundance data pooled by feeding guild did not reveal any significant change in the richness of herbivores or non-herbivores with time (Fig. 7, Table 5); however, the relative proportion of non-herbivores did increase (Fig. 9). Non-herbivores were anticipated to show more change in richness and abundance than herbivores because plantfeeding insects are thought to respond relatively slowly to climate change. This potential "lag" in herbivore response is attributed to the slower dispersal and development of their host plants, which in turn limits the migration rates of their insect herbivores (Elias, 2010), as many are restricted to feeding on one or a few plant species (Bernays & Chapman, 1994). However, it may be that this assumption holds true for finer-resolution fossil insect deposits, such as those that can be recovered from the Quaternary record (<100,000 years), but not over longer time intervals. Considering the amount of time occurring between the deposition of the lower and upper fossil beetle localities was a minimum of ~460,000 years, this may explain why the beetle feeding guilds did not change as predicted. That non-herbivores show an overall pattern toward slightly decreased richness with time and cooling is consistent with prior assertions that non-herbivorous beetles are particularly sensitive to temperature change (Elias, 2010). On the other hand, the weak increase in herbivore richness with time was unexpected, and, as such, there may be reason to consider alternative primary forcing mechanisms. Specifically, had global cooling affected plant communities, one would expect herbivore richness to concomitantly decrease with host plant richness; or, if plant communities were very slow to respond to climate change, herbivore richness may appear constant during this interval. Statistically speaking, herbivore richness did not change, which may be a consequence of little to no change in the richness of the surrounding plant community. Alternatively, as previously mentioned, some ecological patterns demonstrated by Quaternary insects may not apply at longer macroecological time scales. As of yet, plants collected alongside these beetles have not been studied, and applying individual-based rarefaction to these floras (and/or their feeding damage) may provide additional insight into richness patterns of their insect herbivores.

While neither herbivore nor non-herbivore richness showed significant change, their relative abundances did, with non-herbivore abundances increasing through time (Fig. 9). Taken at face value, this pattern may point to an interpretation that non-herbivores were more resilient to climate change than herbivores due to their feeding habits. However, these results do not agree with the findings of Andrew & Hughes (2005a), who found carnivorous (predators, parasites) and herbivorous (leaf chewers, sapsuckers) arthropods to be present in nearly equal proportions (~1:1) along a 1150 km latitudinal gradient. It may be that true feeding guild proportions have been obscured by undersampling of total beetle diversity, as conclusions drawn from direct

comparisons of raw abundances should be considered tenuous before true species richness is fully captured (Gotelli & Colwell, 2001).

4.4 Diversity: Taxonomic Nuances

Although taxon-specific predictions regarding richness and evenness were not made for carabids, staphylinids, and weevils, their respective responses ultimately underlie individualbased rarefaction patterns showing an overall net effect of "no change" for all beetles pooled by locality (Fig. 6a, 10a). The same can be said for the preceding comparison of herbivore versus non-herbivore richness, which is essentially a comparison of weevils to carabids and staphylinids combined (Fig. 7). When beetle data were parsed and re-analyzed by taxon, patterns of richness and evenness emerged with some directionality (Fig. 8, Table 6). Specifically, with time, carabids showed decreased richness and evenness; weevils showed increased richness and evenness; and staphylinids showed no change in richness or evenness.

That weevil and carabid richness responded with opposite directionality is not surprising because these groups markedly differ in their feeding strategies. But, by this logic, one might also anticipate carabids and staphylinids to respond with similar directionality due to their broadly equivalent feeding strategies as predators and scavengers (Arnett & Thomas, 2000; Thayer, 2005). This was not the case, as illustrated by individual-based rarefaction curves, which show unchanged richness and evenness for staphylinids (Fig. 8). This pattern appears to have been obscured when carabids and staphylinids were lumped as non-herbivores (Fig. 7). Similarly, the opposite directionality of richness and evenness in weevils and carabids may have negated one another, producing the output pattern of no change when all beetle data were pooled by locality (Fig. 6a).

These results support an interpretation that, within feeding guilds, not all guild members are necessarily "equal", as the effects of other preferences (such as climatic tolerances) may be superimposed on the directionality of diversity change driven by feeding habits. This scenario has been predicted for herbivorous beetles and Hemiptera, which do not show equal potential for resilience to global warming (Andrew & Hughes, 2004, 2005b). Additionally, much of the literature employing insects as paleoclimate proxies has relied on the assumption that beetle ecology and physiology have been relatively stable since the late Neogene (Elias, 2010). It may be that this assumption is less applicable to Eocene beetles due to the potential for evolutionary change over the past ~50 Ma.

4.5 Compositional Change & Future Directions, Pt. I

Although obtaining identifications for all beetle taxa in the assemblages is ongoing, it is clear that many species differ between the two Green River localities (Appendix A) and likely reflect subtle compositional change. Some preliminary interpretations can be made related to differential change in diversity and turnover within feeding guilds. Weevils most clearly illustrate this possibility, as host plant specialization varies considerably within and between families (Arnett et al., 2002). For example, the Entiminae (Curculionidae), a subfamily of non-specialist root and foliage feeding weevils (Oberprieler et al., 2007), are not tethered to one or a few plant species, and therefore may be fairly responsive to temperature change. Interestingly, while no significant change was detected in the richness or evenness of weevils with time, no Entimine species found at the lower locality could be matched to Entimines found at the upper locality. Individuals from this subfamily were also more abundant at the lower locality, with many additional individuals being omitted from rarefaction analyses due to low quality

preservation (Table 2a). On the other hand, at least one species of Nemonychidae, a pollenfeeding family specializing on *Pinus*, did persist through time, which may be a consequence of host plant distribution as these primitive weevils are associated with montane and boreal forests in North America today (Arnett et al., 2002; Oberprieler et al., 2007). Continued investigation of host specificity and turnover among Green River weevils would be useful in drawing more conclusive support for climatically-driven changes among herbivores.

Some carabids and staphylinids also overlapped between the two localities, as shown by the persistence of *Bembidion* spp. (Carabidae), *Lebia* spp. (Carabidae), *Dyschirius* (Carabidae), *Platydracus* sp. (Staphylinidae), and *Stenus* spp. (Staphylinidae), while others disappeared (*Pinophilus*?) or appeared (*Carpelimus*) with time. Like the weevils, some of these species can be tentatively associated with the ecological preferences of their nearest extant relatives. For instance, the staphylinids *Platydracus* sp. and *Stenus* spp. were recovered from both localities and are cosmopolitan in distribution, with the latter genus collectively preying on Collembola (Arnett & Thomas, 2000; Thayer, 2005). The carabids *Lebia* spp., *Bembidion* spp., and *Dyschirius* sp. are also widely distributed (Arnett & Thomas, 2000), with the larvae of *Lebia* spp. being parasitic on Chrysomelidae (Coleoptera) (Larochelle, 1990). Conversely, the staphylinids Procirrina sp. and *Pinophilus* sp. were only found at the lower locality, and whose nearest living relatives belong to the primarily tropical-subtropical tribe Pinophilini (Arnett & Thomas, 2000). These preliminary findings suggest that geographically cosmopolitan predators and scavengers were less affected by environmental change than species with more restricted climatic affinities.

4.6 Comparison to Other Eocene Communities & Future Directions, Pt. II

Although the overall richness and evenness of Green River beetles did not change during the ~ 2.5 million year interval following the initiation of global cooling, a shifting community composition is consistent with changes seen in other Western Interior plants and vertebrates from the early to middle Eocene. During EECO global warming (52-50 Ma), Western Interior macrofloras experienced two episodes of significant change, with >80% species turnover at ~52.5 Ma and again at ~50 Ma (Wilf, 2000). However, unlike beetles, high compositional turnover resulted in increased species richness within these plant communities (Wilf, 2000), accompanied by approximately synchronous increases in North American mammal diversity (Woodburne et al., 2009, but see Dutchak, 2010). Insect communities from the Okanagan Highlands were also species rich during the Early Eocene, but with high beta diversity being attributed to low temperature seasonality rather than global climate change (Archibald et al., 2013). Following the EECO, the initiation of global cooling (Zachos et al., 2001) coincided with an abrupt decline in mammal diversity (termed the "Bridgerian Crash", 50-47 Ma) and the second major turnover in Western Interior floras (Wilf, 2000; Woodburne et al., 2009). This pattern is attributed to decreasing mean annual temperatures and increased precipitation seasonality (Wilf, 2000; Woodburne et al., 2009, but see Smith et al., 2008).

If the diversity of plants and vertebrates changed during the early and middle Eocene, why are similar patterns not evident for Green River beetles? One possibility is that the threshold, or "tipping point", required to catalyze significant directional change in richness and evenness differs between plants, insects, and vertebrates. Ideally, one way to test this hypothesis would be to examine the diversity and turnover of plants collected alongside the lower and upper locality beetles, but, unfortunately, fossil leaves are relatively scarce at these sites. An alternative approach would be to apply the methods used in this study to the latest Eocene beetles of the nearby Florissant Formation and make comparisons between the Green River and Florissant faunas. A pattern of decreasing herbivory during this time interval (~49-34 Ma) has been previously shown from the Green River and Florissant floras and may reflect diminishing diversity and/or abundances of insect herbivores (Smith, 2008), but this prediction has yet to be directly tested.

Later in the Cenozoic, Arctic beetle faunas experienced decreased richness and dramatic turnover beginning in the late Pliocene (~3 Ma) (Elias & Matthews, 2002; Elias et al., 2006) during the onset and intensification of Northern Hemisphere glaciation (Maslin et al., 1998). Changes included the disappearance of herbivorous species from high latitude beetle communities with cooling, followed by decreased diversity of beetle faunas as a whole (Elias et al., 2006). The loss of herbivorous beetles was specifically attributed to the migration of host plants with cooling (Elias et al., 2006; Elias & Matthews, 2002). However, in contrast to Green River beetles, which did not show any change in richness during gradual global cooling, Pliocene-Pleistocene beetle communities may have been altered by more rapid climatic oscillations (Shackleton, 2000; Zachos et al., 2001), which points to the role of rate of change when climate mechanistically drives diversity. Additionally, annual temperature ranges (coldest versus warmest months) occurring at Arctic latitudes may have been more extreme, thereby placing different physiological demands on Plio-Pleistocene beetles than the more equable conditions of the middle Eocene (MacGinitie, 1969). While the early to middle Eocene was generally characterized by low seasonality (i.e. narrow annual temperature range), which may have contributed to high insect diversity at mid-high latitudes in North America (Archibald et al., 2013), lower cold month temperatures were eventually achieved by the end of the Eocene

(Wolfe, 1994). This and previous examples lead to one of the most important findings of this study: while the potential for beetle communities to change is clear, the threshold at which change is initiated is not. Comparison to additional fossil insect assemblages will be necessary to develop a more thorough understanding of how prolonged and rapid global climate change have affected beetle communities through time.

In a related vein, there is another plausible explanation for the lack of diversity change shown in Green River beetles with time and cooling: perhaps the magnitude of global temperature change experienced by this community was not great enough to impart significant change to its overall richness or evenness. The maximum possible magnitude of this change approximates to a ~4°C decrease in benthic marine temperatures (Fig. 4), but because Lake Uinta was situated near the continental interior, its surrounding environment was effectively isolated from the direct influence of marine temperatures. It is also possible that Western Interior climates were influenced by regional topographic features, elevation gradients, and global climate patterns that operated differently during the Eocene (Rea, 1994; Rea et al., 2000). A possible "benchmark" for terrestrial temperatures at this time comes from the early Bridgerian (~50 Ma) Little Mountain flora from the Green River Formation of Wyoming. The MAT estimated from this flora ($\sim 19.6^{\circ}$ C) was interpreted to be slightly cooler than those of earlier Eocene floras from the Western Interior (Wilf, 2000). MacGinitie (1969) estimated a similar MAT for the Green River paleoenvironment (MAT ~16-21°C) with a relatively frostless winter (CMMT>13°C). While this interpretation of cooling agrees with the marine isotope record, the same sequence of floras also suggest increasing precipitation seasonality during this time (Wilf, 2000), but not without controversy, as other workers have suggested that the Little Mountain flora may reflect either localized conditions or short-term (<10 kyr) climatic perturbations (Smith et al., 2008). These authors also assert that the recurring deposition of evaporites in Lakes Uinta and Gosiute cannot be taken as evidence for increasing aridity following the EECO (Smith et al., 2008). Further, the influx of sediment eventually leading to basin infilling may have been driven by both climate and tectonism (Tänavsuu-Milkeviciene & Sarg, 2012), although uplift of nearby topographic highs occurred prior to the deposition of the beetle assemblages assessed here (Smith et al., 2008). If aridity in this area became progressively more severe during the early middle Eocene near in the Western Interior, this component of climate could have affected Green River beetles; for example, community diversity could have decreased in response to host plant stress (Cuartas-Hernández & Gómez-Murillo, 2015) and/or by causing beetles to fluctuate in abundance (Pinheiro et al., 2002). However, how these patterns would translate to the time scale in question is uncertain, and the interaction between insect diversity and precipitation (among other climatic drivers) is understudied relative to temperature (Andrew et al., 2013). Despite these potential confounding factors, the depositional sequence of the Green River Formation within the Piceance Creek Basin is believed to closely reflect global climate in the early to middle Eocene (Tänavsuu-Milkeviciene & Sarg, 2012). It also seems reasonable to believe that inland temperatures followed a similar pattern to the deep sea, but possibly with lessened intensity, as the interior location of the lake system and associated local climatic aberrations may have muted or delayed the magnitude of temperature change experienced by beetle communities, thereby explaining the lack of change in their diversity.

For beetles, it may very well be that the thresholds of change not only vary between the components of diversity and community composition, but also between the components of climate itself. Returning to the suggested comparison to other fossil insect assemblages, similar to the Green River and Florissant floras (MacGinitie, 1969), the Florissant beetle fauna should

represent a derivative of the original Green River community. This continuity, combined with the added magnitude of global cooling (~6-7°C) occurring between the deposition of the two formations (Zachos et al., 2001), would make comparison between these two beetle assemblages particularly instructive in relating changes in community-level diversity and composition to the magnitude of global temperature change. That said, unlike comparisons of Green River beetles, contrasting fossil assemblages from the Green River and Florissant Formations could be complicated by differences in elevation of >1000 m (Wolfe, 1994). Similar compositional affinities have been shown between middle and late Eocene marine faunas, with reduced diversity and turnover respectively coinciding with the middle-late Eocene and Eocene-Oligocene boundaries (Ivany et al., 2003). This work therefore serves as a starting point to which further comparisons can be made across time and space.

CHAPTER 5:

Conclusion

I hypothesized that beetle diversity changed in response to global cooling during the middle Eocene in western Colorado. To test this hypothesis, patterns of richness and evenness were assessed using three beetle groups, the Carabidae, Staphylinidae, and Curculionoidea (weevils) from two end-member assemblages coincident with the onset of global cooling. When all beetle abundances were pooled together and separated by feeding guild and taxon, no significant changes in richness or evenness were detected. These results did not align with the directionality of change predicted for both components of diversity. There is evidence that the abundances and compositions of herbivorous and non-herbivorous feeding guilds did change with time, but further effort is needed to completely sample and identify the beetles from both localities before these trends can be quantitatively verified and their underlying ecological nuances further interpreted.

One important finding of this study was that the Green River beetle community was considerably undersampled at both localities despite a sampling effort of 90 collecting days that produced 580 specimens categorized to morphospecies. Complete representation of total species richness was not obtained, as less than half of the total estimated species were observed at each fossil locality. Extrapolation of sample-based abundance data estimates that observed sampling intensity must be greatly increased (>3x) before all species of carabids, staphylinids, and weevils can be recovered. However, increasing sampling effort should not affect the directionality or strength of emerging patterns produced by rarefaction analyses (Gotelli & Colwell, 2001), and the observed species included in this study likely represent a small subset of an exceptionally diverse beetle fauna that once lived in Eocene Colorado.

By using individual-based rarefaction to make comparisons between beetle assemblages, it was shown that patterns of richness may be highly sensitive to community components in terms of their ecological preferences and taxonomic identity. The removal of singleton species further demonstrated that "rare" individuals comprised a significant proportion of total beetle richness, as removing them from analyses imparted significant differences in richness between localities, but did not affect evenness. These results indicate that patterns derived from coarsegrained data sets (e.g. all beetle data combined by locality) may not be as informative as those produced by analyses with more fine-grained control on ecological or taxonomic resolution when studying community response to global warming.

Comparison of diversity patterns in the Green River beetle community to previous studies of plants and mammals lead to questions regarding the thresholds necessary to drive changes in the diversity of different organisms. Climate, like diversity, can be distilled into multiple components, and the results presented herein point to the significance of the rate and magnitude of climate change in defining these thresholds for different organisms. For middle Eocene beetles, it appears this tipping point was not achieved during the interval of time following the EECO and preceding Piceance Creek Basin infilling (~50-48 Ma). Applying the methods used here to additional fossil insect assemblages across longer or more abrupt intervals of global warming or cooling may better constrain the thresholds necessary to drive change in the components of diversity.

Community composition can also be discussed relative to thresholds. That beetle species and their relative abundances did change with time aligns with patterns observed in modern insect and arthropod communities, which were not shown to change in richness, abundance, or community structure over a 4.3°C terrestrial temperature gradient, but still maintain potential for component species to be transient in response to warming or cooling (Andrew & Hughes, 2004, 2005a, 2005b). This finding also agrees with the "fingerprints" of climate change defined by recent meta-analyses, which have shown that current global warming of <2°C has driven significant distributional changes of species populations across continents and taxa (Parmesan & Yohe, 2003; Root et al., 2003). However, while the magnitude of global climate change experienced by middle Eocene beetles is similar to forecasts for the 21st century, future species extinctions (Urban, 2015) and community reorganizations are predicted to occur in response to much more rapid global temperature change (Williams & Jackson, 2007).

Obtaining beetle identifications below subfamily or tribe would enable further testing of new predictions, in turn allowing this study's hypotheses to be further addressed. For instance, one could assess differential turnover of taxa with warm- and cool-adapted life strategies in addition to compositional beta diversity, which are both predictions with accumulating support. Many specimens from the Green River beetle faunas are new species awaiting description, not only among carabids, staphylinids, and weevils, but also within the Coleoptera as a whole. Further refinement of "who's-who" in these assemblages would permit more detailed exploration of taxon-specific life history traits driving the patterns occurring within these beetle communities.

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APPENDIX

Appendix A. Preliminary beetle identifications. Note that individuals designated as the same species (e.g. morphospecies "Carabid5") may not, in fact, be the same species at both localities. Further work will be necessary to refine these results before compositional overlap can be assessed in detail. Singletons species are listed by UCM catalog number.

Coleoptera: Carabidae									
Morphospecies	Identification	Lower	Upper						
Carabid5	Bembidion sp. 1	16	1						
Carabid2	<i>Lebia</i> sp.1	6	16						
Carabid3	<i>Dyschirius</i> sp.	6	4						
Carabid8	Harpalini sp. 1	6							
Carabid7	Bembidion sp. 2	5	13						
Carabid9	Harpalini sp. 2	5	4						
Carabid11	Bembidion sp. 4	3	6						
Carabid2A	<i>Lebia</i> sp. 2	1	1						
Carabid1	Pinacodera?	1	1						
38368		1							
38942		1							
39297		1							
39907		1							
54425		1							
54795		1							
55659		1							
55665		1							
55822		1							
56105		1							
56644		1							
56875	Bembidion sp. 5?	1							
57178		1							
57475		1							
79798		1							
Carabid10	Bembidion sp. 3		4						
76849			1						
77437			1						
79491			1						
80218			1						
81010			1						
81240			1						
81328			1						
Total		64	57						

Manukanada	Lindification	T	T I
Morphospecies	Identification	Lower	Upper
Staphylinid4	Paederinae	39	5
Staphylinid5a		10	11
Staphylinid5		7	3
Staphylinid4a	Paederinae?	6	
Staphylinid1	Pinophilus?	5	
Staphylinid3	Stenus sp. 1	5	1
Staphylinid6	Cryptobiina	4	
Staphylinid1a	Procirrina?	2	
Staphylinid3	Stenus sp. 2	2	7
Staphylinid4b	Aleocharinae?	2	
Staphylinid5b		2	1
Staphylinid8		2	1
Staphylinid2	Tachyporinae	1	6
Staphylinid3	Stenus sp. 3	1	
Staphylinid7		1	1
Staphylinid8b	Platydracus sp.	1	1
42386	Philonthus sp.	1	
57082	-	1	
57480	<i>Aleochara</i> sp.	1	
56874	Tachyporinae	1	
56001		1	
54825ab		1	
Staphylinid4c			3
Staphylinid4d			2
Staphylinid8a	<i>Carpelimus</i> ? sp.		3
76772	Aleocharinae		1
76910			1
78145			1
Total		96	48

Coleoptera: Staphylinidae

Coleo	ptera: Curculior	loidea	
Morphospecies	Identification	Lower	Upper
Curculionid10	Entiminae sp. 2	48	
Curculionid11		46	
Curculionid10	Entiminae sp. 1	23	
Curculionid8	Baridinae	17	1
Curculionid3	Ceutorhynchinae	11	
Curculionid10	Entiminae sp. 3	9	
Curculionid3C		8	
Curculionid4	Nemonychidae	7	5
Curculionid5	Entiminae sp. 7	7	
Curculionid6		6	
Curculionid7	Molytinae	6	5
Curculionid8A		6	
Curculionid1		3	1
Curculiionid2A	Apioninae	3	7
Curculionid2B		3	
Curculionid9		3	
Curculionid15B	Magdalidini	3	1
Curculionid2	Apioninae	2	3
Curculionid5A		2	
Curculionid16		2	
Curculionid3A	Baridinae	1	2
Curculionid3B	Ceutorhynchinae	1	1
Curculionid3D		1	1
39301	Baridinae	1	
39434	Molytinae	1	
41763	Entiminae sp. 8	1	
44071		1	
44419		1	
54009	Nemonychidae	1	
55729	Ceutorhynchinae	1	
57586	Curculioninae	1	
58123		1	
58251	Molytinae?	1	
78304	2	1	
Curculionid3CP			2
Curculionid10	Entiminae sp. 4		2
Curculionid11	Entiminae sp. 5		17
Curculionid11A	Entiminae sp. 6		3
Curculionid12	Nemonychidae		4
Curculionid13	2		10
Curculionid14			7

Coleontera: Curculionoidea

Curculionid15	Curculioninae?		4	
Curculionid15A			2	
75855			1	
75889	Molytinae		1	
76121			1	
80221			1	
81011			1	
81021			1	
81031			1	
81295	Otiorhynchini		1	
Total		229	86	