Effects of Global Warming on Ancient Mammalian Communities and Their Environments

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Abstract

Background: Current global warming affects the composition and dynamics of mammalian communities and can increase extinction risk; however, long-term effects of warming on mammals are less understood. Dietary reconstructions inferred from stable isotopes of fossil herbivorous mammalian tooth enamel document environmental and climatic changes in ancient ecosystems, including C3/C4 transitions and relative seasonality.

Methodology/Principal Findings: Here, we use stable carbon and oxygen isotopes preserved in fossil teeth to document the magnitude of mammalian dietary shifts and ancient floral change during geologically documented glacial and interglacial periods during the Pliocene (~1.3 million years ago) and Pleistocene (~1.9 million years ago) in Florida. Stable isotope data demonstrate increased aridity, increased C4 grass consumption, inter-faunal dietary partitioning, increased isotopic niche breadth of mixed feeders, niche partitioning of phylogenetically similar taxa, and differences in relative seasonality with warming.

Conclusion/Significance: Our data show that global warming resulted in dramatic vegetation and dietary changes even at lower latitudes (~28°N). Our results also question the use of models that predict the long term decline and extinction of species based on the assumption that niches are conserved over time. These findings have immediate relevance to clarifying possible biotic responses to current global warming in modern ecosystems.

Introduction

Recent global warming alters species distributions, abundances, interactions, and the timing of seasonal activities [1–3]. Bioclimatic ‘envelope’ models examining current warming trends predict the long term decline and extinction of species. Generally, these models are based on an understanding of the modern ecological parameters of species, and often incorporate an assumption of niche conservatism, i.e. the idea that ecological niches are maintained over long time scales [4–6]. The fossil record provides a long-term record from which the effects of past global warming can be assessed. Previous work comparing mammalian communities during the last ~780,000 years has documented only minor declines in small mammal species richness with increased warming [7]. Dietary reconstructions inferred from stable isotopes of mammalian tooth enamel yield minor to no changes between glacial and interglacial periods in both large and small mammals [8,9]. Similarly, there is evidence that the niches of mammalian taxa, based on temperature and precipitation, that persisted during the last glacial to interglacial transition, are conserved [10]. All of these studies suggest that mammalian responses to interglacial warming were generally minor.

Here we present stable carbon and oxygen isotope data of medium to large mammals from a glacial and an interglacial site in Florida. We first compare carbon isotope values and evaluate the hypothesis that dietary niches, inferred from the mean and breadth of carbon isotope values, did not change with interglacial warming. Next, carbon and oxygen isotope data from serially-sampled horse teeth are used to elucidate if and how relative seasonality differed between the glacial and interglacial period, with oxygen isotope data from all taxa documenting changes in relative humidity [11]. This study tests how interglacial warming affected mammalian diets as well as documents the magnitude of climatic differences at these low latitude (~28°N) glacial and interglacial sites.

Stable carbon and oxygen isotopes are incorporated into the tooth enamel of mammalian taxa and are representative, respectively, of the food and water consumed while alive. Furthermore, C3 plants (e.g. trees, shrubs, and cool season grasses) photosynthesize differently from C4 plants (e.g. warm season grasses) and subsequently reflect distinctly lower δ13C ranges [12]. Taking into account the 13C enrichment from food to tooth enamel (~14‰) as well as the decline in δ13C values (~1.5‰) of atmospheric CO2 due to fossil fuel burning over the past two
centuries [13–15], tooth enamel values of less than −8‰ indicate a diet consisting of primarily C_{3} vegetation whereas δ^{13}C values of greater than −2‰ indicate a diet of predominately C_{4} vegetation [12,14]. Additionally, C_{3} grasses are a rare or absent component of the landscape in Florida during the last ~2 million years [16–19], further enabling δ^{13}C values of less than −8‰ to indicate a predominantly browsing diet. Lower δ^{13}C values can also indicate the consumption of browse in denser canopied C_{3} forests [20–22]. By comparing stable carbon isotope values between individuals and populations during a glacial and an interglacial period, we can assess how long-term warming affected mammalian diets. Specifically, we compare the relative consumption of C_{3} browse vs. C_{4} grass, as inferred from δ^{13}C values. In addition, oxygen isotopes in mammalian tooth enamel typically document changes in temperature and precipitation, with $^{18}$O enrichment indicating a warmer and/or drier climate [23–25]. Additionally, when comparing the oxygen isotope values of mammals that obtain a large proportion of their water from plants, relative aridity can be assessed [11,25].

Based on the depth of terrestrial fossils in relation to current sea-levels, the coastal fossil sites of Inglis 1A and Leisey 1A (Figure S1) represent a glacial and an interglacial site, respectively. Inglis 1A (29°0’N, 82°41’W; ~2.0–1.6 Ma) exhibits terrestrial fossils within a sinkhole in the Eocene Inglis Formation at depths of 5 meters below sea-level and completely lacks a marine fauna, indicating lower sea-levels that would have occurred during a glacial period [26]. This glacial interpretation is also supported by the presence of cooler adapted taxa such as the muskrat Ondatra zibethicus and pronghorn Capromeryx arizonensis [26]. The younger Leisey 1A (27°42’N, 82°30’W; ~1.6–1.3 Ma) locality instead has terrestrial and marine fossils intermixed between two shell beds at depths consistent with interglacial levels [26]. Leisey 1A also has taxa indicative of a warmer interglacial period including alligators (Alligator mississippiensis) [26]). These geographically similar terrestrial localities provide the rare opportunity to examine how mammals altered their diets in response to interglacial warming during the late Pleistocene.

All mammalian taxa present within the orders of Artiodactyla, Perissodactyla, and Proboscidia were sampled for enamel stable carbon and oxygen isotopes (n = 115; Table S1 and S2; see supporting information and Materials and Methods). Representing 8 families, these taxa include the following: deer (Odocoileus virginianus), horses (Equus sp.), llamas (Hemiauchenia macrocephala, Palaeolama mirifica), peccaries (Mylohyus fossilis, Platygonus vetus), proboscidians (Cieieronius tropicus, Mammut americanum, Mammutus hayi), pronghorn (Capromeryx arizonensis), and tapires (Tapirus sp., including Tapirus hayi). These mammals were compared both within (Table 1 and 2) and between fossil localities to demonstrate how dietary resources were partitioned. Serial samples (samples taken at a series of intervals perpendicular to the growth axis of the tooth) of the high-crowned horses were also taken from specimens at both localities, enabling comparisons of relative seasonality (n = 23; Table S3).

### Results and Discussion

#### Dietary Partitioning

The glacial Inglis 1A locality represents a C_{3}-dominated community with all taxa, except for Equus, having δ^{13}C values more negative than −9.1‰ (Figure 1 and S2, Table S1 and S2). As C_{3} grasses are a rare or absent component of Florida landscapes during the last ~2 million years [16–19], all ungulate taxa are interpreted to be C_{3} browsers, with the exception of Equus. Resource partitioning within this C_{3}-dominated community is apparent with Odocoileus δ^{13}C values significantly less than all other taxa sampled (with n>1) and Tapirus significantly less than Platygonus and Hemiauchenia (Table 1). Equus is more enriched in δ^{13}C than all other taxa (p<0.0001), indicating a diet consisting mainly of C_{4} vegetation (i.e. warm season grasses, as C_{4} dicots and CAM vegetation with similar δ^{13}C values are rare or absent in Florida [17,27,28]). Thus, this glacial site is dominated by C_{3} browsers, although it is clear from the horse data that C_{4} grasses were present. Due to the reliance of the majority of taxa on C_{3} vegetation and the relative rarity of Equus at Inglis 1A, we hypothesize that C_{4} grasses likely occurred in much lower abundance.

The interglacial fossil site Leisey 1A consists of taxa which display a large range in δ^{13}C values from −14.3 to −2.0‰ (Figure 1 and S2, Table S1 and S2). All genera (with n>1) present at both Leisey 1A and Inglis 1A are significantly more enriched in δ^{13}C at the interglacial site (Equus, p<0.05; Hemiauchenia, p = 0.0001; Odocoileus, p = 0.001; Platygonus, p = 0.0001) with the exception of Tapirus. Increased δ^{13}C values in these taxa demonstrates increased inclusion of C_{4} grasses in their diets, although Odocoileus may instead be browsing from a more open canopied forest during the interglacial period. The lack of dietary changes in tapires is consistent with their morphologically and isotopically inferred dense-canopy browsing diet over time [29,30]. Additionally, the mixed feeders, Hemiauchenia and Platygonus, increased their isotopic niche breadth from a total δ^{13}C range of 3.3‰ and 3.1‰ at the glacial site to 5.5‰ and 5.7‰ at the interglacial site, respectively (Figure 1, Table S1). Leisey 1A potentially has increased ungulate diversity compared to Inglis 1A with the addition of the peccary (Mylohyus fossilis), the llama (Palaeolama mirifica), and two proboscidians (Cieieronius tropicus, Mammutus hayi), but lacks the pronghorn (Capromeryx arizonensis). However, Inglis 1A (~7700)

| Table 1. Significant differences in δ^{13}C values among taxa from Inglis 1A, Florida. |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Inglis 1A, Florida              | Tapirus sp.     | Capromeryx arizonensis | Mammut americanum | Platygonus vetus | Hemiauchenia macrocephala | Equus sp. |
| Odocoileus virginianus          | 0.045           | 0.027             | 0.063            | 0.063           | 0.063           | 0.063           |
| Tapirus sp.                     | 0.447           | 0.438             | 0.010            | 0.010           | 0.010           | 0.010           |
| Capromeryx arizonensis          | 0.862           | 0.255             | 0.092            | 0.092           | 0.092           | 0.092           |
| Mammut americanum              | 0.516           | 0.279             | 0.092            | 0.092           | 0.092           | 0.092           |
| Platygonus vetus               | 0.339           | 0.0001            | 0.0001           | 0.0001          | 0.0001          | 0.0001          |
| Hemiauchenia macrocephala      | 0.0001          | 0.0001            | 0.0001           | 0.0001          | 0.0001          | 0.0001          |

Bold p-values indicate significant differences. doi:10.1371/journal.pone.0005750.0001
Table 2: Significant differences in $\delta^{13}$C values among taxa from Leisey 1A, Florida.

| Taxon                      | $\delta^{13}$C values | $p$-value |
|----------------------------|------------------------|-----------|
| *Mammut americanum*        | 0.711                  | $<0.0001$ |
| *Odocoileus virginianus*   | 0.284                  | $<0.0001$ |
| *Mylohyus fossilis*        | 0.082                  | $<0.0001$ |
| *Hemiauchenia macrocephala*| 0.749                  | $<0.0001$ |
| *Platygonus vetus*         | 0.037                  | $<0.0001$ |
| *Cuvieronius tropicus*     | 0.124                  | $<0.0001$ |
| *Equus sp.*                | 0.578                  | $<0.0001$ |
| *Tapirus bairdii*          | 0.415                  | $<0.0001$ |
| *Palaeolama mirifica*      | 0.145                  | $<0.0001$ |
| *Platygonus sp.*           | 0.578                  | $<0.0001$ |
| *Mammuthus sp.*            | 0.037                  | $<0.0001$ |
| *Mylohyus fossilis*        | 0.124                  | $<0.0001$ |

Bold $p$-values indicate significant differences.

Climate Influence on Mammals

has fewer specimens than Leisey 1A (~22,000) which may bias diversity estimates due to taphonomic processes. Both pecary taxa and both llama taxa show significantly different values. *Mylohyus* has lower $\delta^{13}$C values than *Platygonus* ($p<0.05$; Figure 1, Table 2 and S1). Similarly, *Palaeolama* has low $\delta^{13}$C values as compared to *Hemiauchenia* ($p<0.0001$; Figure 1, Table 2 and S1). Although the proboscideans cannot be statistically compared across sites due to the limited sample size at Inglis 1A, the isotopically inferred C4 grazing proboscideans (*Cuvieronius, Mammutius*) are only present at Leisey 1A while the browsing mastodon (*Mammut*) is found at both localities. Because *Mammutius* has one of its earliest occurrences in North America from Leisey 1A, it was absent from the older Inglis 1A locality regardless of ecological factors. However, *Cuvieronius* was present in the late Pliocene of North America [31] and could have been present at Inglis 1A; thus, its absence may represent an ecological signal.

During the interglacial period represented by Leisey 1A, dietary resource use by the majority of ungulate taxa were significantly different from each other (Table 2). However, the isotopically inferred browsers (*Palaeolama, Tapirus, Mammut*, and *Odocoileus*) lacked significant differences when compared to each other (Table 2). Similarly, the isotopically inferred grazers (*Cuvieronius, Equus*, and *Mammutius*) lacked significant differences from one another (Table 2). This high degree of dietary niche partitioning among the Leisey 1A mammalian community, especially among taxa within the same family, may contribute to its higher diversity (Table 2 and S1). For example, *Palaeolama* and *Mylohyus* may be able to coexist with phylogenetically similar taxa during the interglacial period because they were able to successfully partition food resources. The increased inclusion of C4 grasses by presumed dietary generalists such as *Hemiauchenia* and *Platygonus*, the presence of the C4 grazers *Cuvieronius* and *Mammutius*, and the relative abundance of *Equus* at Leisey 1A likely represents the increased abundance of C4 vegetation and the potential expansion of C4 grasslands during interglacial periods in Florida. However, despite the increased consumption of C4 grasses by ungulates at Leisey 1A, none of the grazers are interpreted to consume only C4 grasses based on the presence of individuals with $\delta^{13}$C values of $<-1.5\%_0$. The lack of obligate C4 grazers during an interglacial period in Florida is somewhat surprising based on modern analogues and further demonstrates the importance of C3 dietary resources for all taxa present during these time periods.

In contrast to our data, Koch et al. (1998) demonstrated minor to no differences in ungulates from a full glacial period to late glacial periods during the Pleistocene. The mastodon (*Mammut americanum*) population from the full glacial West Palm Beach locality (~25,000 BP) has significantly greater $\delta^{13}$C values than at the late glacial Cutler Hammock locality (~11,000 to 9500 BP [8]). However, the remainder of the taxa lack significant dietary differences as inferred from $\delta^{13}$C values [8]. The lack of significant changes in dietary resources may be due to the limited sample sizes of taxa from localities with radiocarbon dates that can be discretely defined as full glacial or late glacial ages. The scope of the Koch et al. (1998) paper was to compare taxa with more specialized diets of either browse or grass; therefore, by excluding potential dietary generalists such as *Platygonus* and/or *Hemiauchenia*, the effects of warming on dietary niches may be less apparent. Lastly, the effects of interglacial warming on mammalian communities and their environments may not have been as profound during the late Pleistocene to the early Holocene, as compared to the late Pliocene to the early Pleistocene.

Paleoclimate and Seasonality

Oxygen isotopes of the fossil mammals present at Leisey 1A have a greater range of $\delta^{18}$O values than those at Inglis 1A,
Figure 1. Carbon isotopic niche partitioning of all sampled taxa. Stable carbon isotope values for all taxa sampled at Inglis 1A (I) and Leisey 1A (L), with dominant C₃ browsers (blue), mixed C₃ and C₄ consumers (red), and dominant C₄ grazers (green) indicated. doi:10.1371/journal.pone.0005750.g001

Figure 2. Stacked histogram of oxygen isotope values for all taxa sampled. Frequency of δ¹⁸O values for taxa from the glacial fossil site Inglis 1A (grey) and from the interglacial fossil site Leisey 1A (black). doi:10.1371/journal.pone.0005750.g002
collectively. Oxygen isotope values range from −3.4 to 0.3‰ at Inglis 1A (total range of 3.7‰) and from −5.1 to 2.9‰ at Leisey 1A (total range of 8.0‰; Figure 2 and S2; Table S1). For mammals that get the majority of their water from food, δ18O values increase with temperature and/or aridity. Based on the aridity index of Levin et al. [11], the increased δ18O range at Leisey 1A indicates a drier climate (Figure 2 and S2; Table S1). These data are in agreement with 50,000-year-old pollen records that indicate drying with interglacial warming in Florida [32]. All genera (with n>1) present at both localities become significantly more enriched in 18O at the warming [33].

Values may indicate an increase in semi-aquatic behavior with temperature and/or aridity. Based on the aridity index of Platygonus interglacial site (Hemiauchenia, p<0.05; Platyrus, p<0.01) with the exception of Tapirus and Equus, the latter of which lacks statistical significance potentially due to sample size. Conversely, Tapirus demonstrates significantly lower δ13C values (p=0.0001) during the interglacial. As modern tapirs are observed to have semi-aquatic behavior, the decline in δ13C values may indicate an increase in semi-aquatic behavior with warming [33].

Serial samples of Equus teeth have significantly greater mean δ13C and δ18O values (p<0.0001, for both) at Leisey 1A (δ13C = −2.4‰, δ18O = 1.3‰) than at Inglis 1A (δ13C = −4.1‰, δ18O = −2.2‰; Figure 3, Table S3). The serial carbon isotope samples at Inglis 1A indicate greater variability than at Leisey 1A, with total δ13C ranges of 2.3‰ and 1.3‰, respectively. Aside from greater δ13C variation at Inglis 1A, the δ13C values oscillate in a predictable manner that correlates with seasonal warming and cooling (i.e., greater δ13C values during the summer and lower δ13C values during the winter; Figure 3). This oscillating pattern is likely the result of seasonal variability in the consumption of C3 and C4 vegetation and/or the 13C enrichment and depletion of vegetation due to seasonal water stress [34,35]. Oxygen isotopes similarly track seasonal variation in temperature and/or precipitation at Inglis 1A. The greater δ18O values at Leisey 1A reflect a warmer and/or drier climate than Inglis 1A. Leisey 1A likely experienced a less seasonally predictable climate as δ18O values do not fluctuate in a predictable oscillating pattern. Variation in these δ18O values may instead be due to precipitation events, with periodic lower δ18O values reflecting increased precipitation [23,24]. Even once patterns of mineralization are accounted for [36–38], the pattern of δ18O variation at the interglacial Leisey 1A site is similar to patterns of δ18O variation in Florida today (Figure S3). These data further support the designations of Inglis 1A and Leisey 1A as a glacial and an interglacial site, respectively, demonstrating that changes in relative seasonality occur with increased warming even at low latitudes of ~28°N.

Concluding Remarks

Contrary to previous studies, we document dramatic dietary and floral changes with interglacial warming. The majority of taxa analyzed increase their mean δ13C values and/or isotopic niche breadth with warming. Additionally, closely related taxa partitioned their dietary resources differently when sympatric at the interglacial site. Our data falsify the initial hypothesis of niche conservatism, instead showing that increased warming resulted in changes in both the type and breadth of resource use in mammals. Although δ13C values reflect only an aspect of an animal’s larger dietary niche, significant differences in δ13C values as seen here, demonstrates considerable differences in a component of the dietary niches of mammalian taxa. These data imply that models which incorporate data under the assumption of niche conservatism may not accurately predict the impacts of global warming on mammalian species. Furthermore, oxygen isotopes in fossil mammal teeth demonstrate increased aridity and decreased relative seasonality with interglacial warming. This study highlights the need for further investigations aimed at understanding paleoecology of species over various time and climatic scales for inferring the future effects of global warming.

Materials and Methods

A total of 115 specimens were sampled for stable isotopes of tooth enamel, the preferred tissue for geochemical analysis as it
reliably reflects original isotopic values [12,14,39]. Late erupting teeth (e.g. fourth premolars and third molars) were preferentially selected for sampling when available; however, due to limited sample availability some early erupting teeth and/or fragmentary specimens were sampled. While the stable carbon and oxygen isotope values of early erupting teeth may be influenced by the consumption of the mother’s milk, possibly resulting in differences in isotopic values, the early erupting and/or fragmentary teeth sampled here have isotopic values that are within the range of variation of late erupting teeth, and we therefore include these specimens in our analysis (Table S1 and S2). Using a low speed dental-style drill and carbide dental burs, bulk samples were taken parallel to the growth axis of the tooth while serial samples were taken perpendicular to the growth axis. All enamel powder was pretreated with 30% hydrogen peroxide for 24 hours and 0.1 N acetic acid for 12 hours to remove organics and secondary carbonates, respectively [40]. Approximately 1 mg of these samples were then run on a VG Prism stable isotope ratio mass spectrometer with an in-line ISO-CARB automatic sampler in the Department of Geological Sciences at the University of Florida. The analytical precision is ±0.1%, based on replicate analyses of samples and standards (NBS-19). Stable isotope data were normalized to NBS-19 and are reported in conventional delta (δ) notation for carbon (δ13C) and oxygen (δ18O), where δ13C (parts per mil, %) = [(Rsample/Rstandard)-1]*1000, and, δ18O (parts per mil, %) = [(Rsample/Rstandard)-1]*1000, and the standard is VPDB (Pee Dee Belemnite, Vienna Convention [41]). All stable isotopes are from the carbonate portion of tooth enamel hydroxylapatite.

All carbon and oxygen isotope values within the same locality were analyzed using Fisher’s LSD multiple comparisons, as all samples from taxa with adequate sample size had δ13C and δ18O values that were normally distributed (Shapiro-Wilk tests). When comparing across genera between localities, t-tests were used. T-values that were normally distributed (Shapiro-Wilk tests). When comparing across localities, the aridity index of Levin et al. (2006) tests were also used to compare all individual serial samples per tooth, between localities. The aridity index of Levin et al. (2006) was used to test if interglacial warming resulted in increased aridity by comparing the total range of δ18O values of the most variable evaporation sensitive taxa (i.e. taxa that obtain a large portion of their water from plants) is captured.

Supporting Information

Table S1 Descriptive statistics of stable carbon and oxygen isotopes from all taxa sampled.

Table S2 All ungulate specimens sampled and their corresponding δ13C and δ18O values.

Table S3 Serial samples and descriptive statistics of Equus sp. teeth from Inglis 1A and Leisey 1A.

Figure S1 Map indicating the location of Inglis 1A and Leisey 1A in Florida, USA.

Figure S2 Stable carbon and oxygen isotope values for all taxa sampled. Blue symbols show taxa from the glacial fossil site Inglis 1A (I) and orange symbols show taxa from the interglacial fossil site Leisey 1A (L). The blue and orange bars indicate the total range of δ18O values for Inglis 1A and Leisey 1A, respectively.

Figure S3 Modern climate data from Tampa and Gainesville, Florida, USA. The oxygen isotope data (rainfall precipitation) are from ISOSCAPES (www.waterisotopes.org) and temperature and precipitation data are from the National Climatic Data Center (www.ncdc.noaa.gov), with mean values from the Tampa International Airport and Gainesville Regional Airport during 1971 to 2000.

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Author Contributions

Conceived and designed the experiments: LRGD RSF. Performed the experiments: LRGD RSF BJM. Analyzed the data: LRGD. Wrote the paper: LRGD. Intellectual support and editorial input: RSF BJM.

References

1. Walther G–R, Post E, Convey P, Menzel A, Parmesan C, et al. (2002) Ecological responses to recent climate change. Nature 416: 349–352.
2. Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change across natural systems. Nature 421: 37–42.
3. Post E, Forchhammer MC (2004) Spatial synchrony of local populations has increased in association with the recent Northern Hemisphere climate trend. Proc Natl Acad Sci USA 101: 9286–9290.
4. Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, et al. (2004) Extinction risk from climate change. Nature 427: 145–148.
5. Thuiller W, Lavorel S, Araujo MB (2005) Niche properties and geographic extent as predictors of species sensitivity to climate change. Global Ecol Biogeogr 14: 347–357.
6. Levinsky I, Skov F, Svenning J-C, Rahbek C (2007) Potential impacts of climate change on the distributions and diversity patterns of European mammals. Biodiversity Conserv 11: 453–462.
7. Baransky AD, Bell CJ, Emslie SD, Goodwin HT, Mardle JH, et al. (2004) Exceptional record of mid-Pleistocene vertebrates helps differentiate climate from anthropogenic ecosystem perturbations. Proc Natl Acad Sci USA 101: 9297–9302.
8. Koch PL, Hoppe KA, Webb SD (1998) The isotope ecology of late Pleistocene mammals in North America, Part 1: Florida. Chem Geol 152: 119–138.
9. Feranec RS (2004) Stable carbon and oxygen isotope analysis of marmot cheek teeth from the Pit Localite. In: Barnosky AD, ed (2004) Biodiversity Response to Environmental change in the Early and Middle Pleistocene: The Porcupine Cave Fauna from Colorado. Berkeley: University of California Press. pp 327–331.
10. Martinez-Meyer E, Peterson AT, Hargove WW (2004) Ecological niches as stable directional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecol Biogeogr 13: 305–314.
11. Levin NE, Cerling TE, Passey BH, Harris JM, Ehleringer JR (2006) A stable isotope aridity index for terrestrial environments. Proc Natl Acad Sci USA 103: 11201–11205.
12. Cerling TE, Harris JM, MacFadden BJ, Leakey MG, Quade J, et al. (1997) Global vegetation change through the Miocene/Pliocene boundary. Nature 389: 153–158.
13. DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42: 495–506.
14. Cerling TE, Harris JM (1999) Carbon isotope fractionation between diet and isotopic exchange in ungulate mammals and implications for ecological and palaeoecological studies. Oecologia 120: 347–363.
15. Friedl H, Lütscher H, Oeschger H, Siegenthaler U, Stauffer B (1986) Ice core record of the 13C/12C ratio of atmospheric CO2 in the past two centuries. Nature 324: 237–238.
MacFadden BJ, Cerling TE, Harris JM, Prado J (1999) Ancient latitudinal gradients of C3/C4 grasses interpreted from stable isotopes of New World Pleistocene horse (Equus) teeth. Global Ecol Biogeogr 8: 137–149.

17. Teeri JA, Stowe LG (1976) Climatic patterns and the distribution of C4 grasses in North America. Oecologia 23: 1–12.

18. Easley MC, Judd WS (1990) Vascular flora of the southern upland property of Paynes Prairie State Preserve, Alachua County, Florida. Castanea 55: 142–149.

19. Huffman JM, Judd WS (1998) Vascular flora of Myakka River State Park, Sarasota and Manatee Counties, Florida. Castanea 63: 25–50.

20. van der Merwe NJ, Medina E (1989) Photosynthesis and 13C/12C ratios in Amazonian rain forests. Geochim Cosmochim Acta 53: 1091–1094.

21. van der Merwe NJ, Medina E (1991) The canopy effect, carbon isotope ratios and foodwebs in Amazonia. J Archaeol Sci 18: 249–259.

22. Cerling TE, Hart JA, Hart TB (2004) Stable isotope ecology in the Ituri forest. Oecologia 138: 3–12.

23. Dansgaard W (1964) Stable isotopes in precipitation. Tellus 16: 273–276.

24. Higgins P, MacFadden BJ (2004) “Amount Effect” recorded in oxygen isotopes of Late Glacial horse (Equus) and bison (Bison) teeth from the Sonoran and Chihuahuan deserts, southwestern United States. Palaeogeogr Palaeoclimatol Palaeoecol 206: 357–353.

25. Kohn MJ (1996) Predicting animal δ18O: accounting for diet and physiological adaptation. Geochim Cosmochim Acta 60: 4811–4829.

26. Morgan GS, Hulbert RC (1995) Overview of the geology and vertebrate biochronology of the Loxey Shell Pit Local Fauna, Hillsborough County, Florida. Bull Fla Mus Nat Hist 37: 1–92.

27. Stowe LG, Teeri JA (1978) The geographic distribution of C4 species of the Dicotyledoneae in relation to climate. Am Nat 112: 609–623.

28. Teeri JA, Stowe LG, Murawski DA (1978) The climatology of two succulent plant families: Cactaceae and Crassulaceae. Can J Bot 56: 1750–1758.

29. DeSantis LRG, MacFadden B (2007) Identifying forested environments in Deep time using fossil taphi: evidence from evolutionary morphology and stable isotopes. Curr Forsh Inst Schenk 236: 147–157.

30. DeSantis LRG, Wallace SC (2008) Neogene forest from the Appalachians of Tennessee, USA: geochemical evidence from fossil mammal teeth. Palaeogeogr Palaeoclimatol Palaeoecol 266: 59–68.

31. Bell CJ, Lundelius EL, Barnosky AD, Graham RW, Lindsay EH, et al. (2004) The Blancan, Irvingtonian, and Rancholabrean mammal ages. In: Woodburn MO, ed (2004) Late Cretaceous and Cenozoic mammals of North America. New York: Columbia University Press. pp 232–314.

32. Grimm EC, Jacobson GL, Watts WA, Hansen RCS, Maasch KA (1993) A 50,000-year record of climate oscillations from Florida and its temporal correlation with the Heinrich Events. Science 261: 198–200.

33. Bocherens H, Koch PL, Mariotti A, Gerauds D, Jaeger JJ (1996) Isotopic biogeochemistry (13C, 18O) of mammalian enamel from African Pleistocene hominid sites. Palaeontogr 11: 306–318.

34. Ehleringer JR, Bowling DR, Flanagan LB, Fessenden J, Heffler B, et al. (2002) Stable isotopes and carbon cycle processes in forests and grasslands. Plant Biol 4: 181–189.

35. Passey BH, Cerling TE (2002) Tooth enamel mineralization in ungulates: implication for recovering a primary isotopic time-series. Geochim Cosmochim Acta 66: 3225–3234.

36. Hoppe KA, Stover SM, Pascoe JR, Amundson R (2004) Tooth enamel biomineralization in extant horses: implication for isotopic microsampling. Palaeogeogr Palaeoclimatol Palaeoecol 206: 335–365.

37. Passey BH, Cerling TE, Schuster GT, Robinson TF, Roeder BL, et al. (2005) Inverse methods for estimating primary input signals from time-averaged isotope profiles. Geochim Cosmochim Acta 69: 4101–4116.

38. Wang Y, Cerling TE (1994) A model of fossil tooth and bone diagenesis: implication for paleodiet reconstruction from stable isotopes. Palaeogeogr Palaeoclimatol Palaeoecol 107: 281–289.

39. Koch PL, Tuross N, Fogel ML (1997) The effects of sample treatment and bone diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. J Archaeol Sci 24: 417–429.

40. Coplen TB (1994) Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. Pure Appl Chem 66: 273–276.