Stable isotope ecology of Cape dune mole-rats (*Bathyergus suillus*) from Elandsfontein, South Africa: implications for C_4 vegetation and hominin paleobiology in the Cape Floral Region

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Abstract

The archaeological and paleontological records from the west coast of South Africa have potential to provide insights into ecosystem dynamics in the region during the mid-Pleistocene. Although the fossil record suggests an ecosystem quite different than that of the region today, we understand little about the ecological factors that contributed to this disparity. The site of Elandsfontein (EFT) dates to between 1.0 and 0.6 million years ago (Ma), preserves *in situ* lithic and faunal materials found in direct association with each other, and provides the rare opportunity to examine the relationship between hominin behavioral variability and landscape heterogeneity in a winter rainfall ecosystem. In this study, we examine the stable carbon isotopic composition of a large sample (n = 81) of Cape dune mole-rats (*Bathyergus suillus*) and contemporaneous large mammals (> 6 kg; n = 194) from EFT. We find that $\delta^{13}C$ values of *B. suillus* are significantly different to those of contemporaneous large mammals from EFT indicating a significant presence of plants utilizing the C_4 photosynthetic pathway during the mid-Pleistocene, in contrast to present C_3 dominated ecosystems along the west coast of South Africa. Additionally, we find that artifact density at EFT localities is positively correlated with $\delta^{13}C$ values in *B. suillus* enamel suggesting that evidence of more intense hominin occupation may be associated with the presence of more C_4 vegetation. Lastly, we hypothesize that this unique distribution of vegetation 1) provided abundant resources for both hominin and non-hominin taxa and 2) may have concentrated hominin and animal behavior in certain places on the ancient landscape.

1. Introduction

1.1 Southern African Paleoecosystems

Differing combinations of climatological factors influence ecosystem dynamics in eastern and southern Africa (Levin, 2015). As a result, placing the rich Quaternary fossil records of these two regions within a resolute ecological framework requires the integration of marine and terrestrial proxies reflective of a variety of spatial and temporal scales (deMenocal, 2004; Behrensmeyer, 2006; Behrensmeyer and Reed, 2013). The last 1 million years of the African fossil record is particularly interesting because it witnesses many important shifts in mammal clades (Vrba, 1995; Faith, 2011; Patterson et al., 2014), as well as the blossoming of what many consider the behavioral repertoire of modern humans (McBrearty and Brooks, 2000; Marean et al., 2007). Although the integration of high-resolution paleoecological data has proved successful at many eastern African localities (Potts et al., 1999; Tryon et al., 2014, 2015; Faith et al., 2015), much less is understood about ecosystems and faunal communities in southern Africa during a critical time period in mammalian evolution. As a result, extrapolating the paleoenvironmental conditions of eastern Africa to concurrent time periods in southern Africa has been especially challenging (Patterson et al., 2014).

In southern Africa, differences in the seasonal distribution of precipitation are largely responsible for the geographic distribution of vegetation (Chase and Meadows, 2007). In the summer rainfall zone (SRZ), the majority of precipitation falls between October and March. In contrast, the winter rainfall zone (WRZ), a narrow band incorporating the western and part of the southern coasts, receives the majority of its rainfall between April and September (Fig. 1). Between these two regions is the year-round rainfall zone (YRZ) that receives rainfall throughout the year. Although the extent of these zones are clearly discernable in contemporary southern Africa, their distribution over the past million years is far from understood. It is, however, becoming increasingly clear that oscillations in atmospheric and oceanic circulation as

well as glacial and interglacial cycles affected the location, duration and intensity of rainfall in these regions during the Quaternary (Chase and Meadows, 2007).

INSERT FIGURE 1

The relationship between precipitation and vegetation in southern Africa is most evident in the distribution of plants utilizing the C_3 and C_4 photosynthetic pathways. Globally, C_4 plants are adapted to low- to mid-elevation tropical systems with high temperatures and warm season precipitation, while C_3 plants are dominant in regions of higher elevation with lower temperatures and cool season precipitation (Tieszen et al., 1979; Ehleringer et al., 1997). In the SRZ, C_4 plants dominate plant communities (Vogel et al., 1978; Rebelo et al., 2006; Radloff, 2008). In the WRZ, however, with the exception of a few common plant communities (e.g., strandveld, renosterveld) that contain species that utilize the C_4 pathway, C_3 vegetation dominates in the form of the low-height, shrubby, fire-adapted fynbos (Cowling, 1992). This unique vegetation system primarily within the WRZ, classified as the Cape Floral Region (CFR), is host to nearly 9,000 plant species, a majority (69%) of which are endemic (Cowling, 1992; Cowling and Lombard, 2002; Goldblatt and Manning, 2002; see Marean, 2010 for summary). Within the CFR, differences in the proportion of C_3 and C_4 vegetation are primarily related to the relative abundance of C_3 and C_4 grasses (Bar-Matthews et al., 2010). C_3 grasses are the most common grasses in the WRZ, while the YRZ contains a mixture of C_3 and C_4 grasses. In the SRZ, C_4 grasses are more abundant. The vegetative diversity within the CFR is not mirrored in mammalian diversity (Klein, 1983). Due to the dominance of nutrient-poor fynbos vegetation, the contemporary CFR does not support a sizable community of large-bodied grazing and browsing ungulates, but rather is dominated by small-bodied, browsing taxa (Skead, 1980; Klein, 1983).

Although C_3 plants are present in high frequencies in the modern vegetative communities in the CFR (Cowling, 1992), this may not always have been the case. The timing and underlying climatological drivers of plant distributions in the CFR remain enigmatic. Marine records from the region beginning in the Miocene indicate an overall increase in aridity with

multiple phases of vegetation change alongside relative stability in moisture availability (Maslin et al., 2012; Hoetzel et al., 2013, 2015). More recent stable carbon isotopic analyses of mammalian enamel suggest the presence of C_4 vegetation in the CFR during certain periods of the Quaternary (Luyt et al., 2000; Hare and Sealy, 2013). Much like elsewhere on the African continent, however, the integration of C_4 vegetation into the CFR plant biome would have likely been highly heterogeneous within a C_3 dominated system (Feakins et al., 2013). This scenario is supported by the lack of evidence for C_4 grasses at Langebaanweg approximately 5 Ma (Ma = million years ago; Franz-Odendal et al., 2002; Rossouw et al., 2009), and evidence of their presence at younger sites of Elandsfontein (Luyt et al., 2002) and Hoedjiespunt (Hare and Sealy, 2013) dating to approximately 1.0 – 0.6 Ma and 0.35 – 0.25 Ma respectively. Thus, although these data suggest that C_4 plants were represented in the CFR during the Quaternary, we understand little about their overall spatial and temporal distribution.

Much of the uncertainty about the relative contribution of C_3 and C_4 vegetation in the CFR during the Quaternary can be attributed to a spatially and temporally discontinuous terrestrial paleoclimatic record (Carr et al., 2006). Although the region is host to a rich record of mammalian fossils spanning the Miocene to Holocene (Singer and Heltne, 1966; Hendey, 1974; Volman, 1978; Klein et al., 2007; Marean et al., 2010; Braun et al., 2013a), robust connections between climate and terrestrial ecosystem dynamics are limited to a few well-studied records that are geographically dispersed throughout the CFR. The fossil record suggests that the CFR was drastically different during the Quaternary and was populated with large grazing and browsing herbivores that are absent from the region today (Klein et al., 2007; Stynder, 2008). In addition, this region was host to some of the earliest populations of humans that exhibited 'modern' behavior in terms of their manufacture of artifacts and utilization of resources (Henshilwood et al., 2002; Marean et al., 2007; Brown et al., 2009). This unique and highly

dynamic system is unlike that of the region today and requires further investigation to provide insights into the ecosystem-level drivers of this disparity.

1.2 Study site

The mid-Pleistocene eolian sediments of Elandsfontein (EFT) present a unique opportunity to investigate the nature of paleoecosystems within the CFR during the past 1 million years (Fig. 1). These deposits (approximately 11 km^2) contain an extensive record of both hominin and non-hominin ecological and behavioral evolution between 1.0 and 0.6 Ma (Braun et al., 2013a). With *in situ* associated fossils and artifacts, EFT presents the prospect of illuminating the ecological dynamics within a WRZ paleocommunity during an enigmatic period in the southern African record (Fig. 2). Although there are localities in the region of older (Franz-Odendaal et al., 2002) and younger age (Berger and Parkington, 1995; Dietl et al., 2005; Matthews et al., 2005; Klein et al., 2007; Faith and Behrensmeyer, 2013; Hare and Sealy, 2013), EFT represents a rare window into the ecosystem and faunal community of the CFR during a period unrepresented at other sites (Klein et al., 2007).

INSERT FIGURE 2

Paleontological and archaeological research at EFT has occurred intermittently over the past 50 years. Initial investigations into the EFT deposits resulted in the recovery of a hominin calvarium referred to as the “Saldanha” or “Hopefield” specimen (Drennen, 1953), a number of large cutting tools from a site called Cutting 10 as well as a tremendous quantity of non-hominin mammalian fossils (Singer and Wymer, 1968; Deacon, 1998; Klein et al., 2007). Subsequent collections during the 1960s and 1980s were the result of non-systematic surface surveys over a relatively small portion (~3 km^2) of the extent of the dunefield at EFT (Avery, 1989; Klein et al., 2007). More recently, analyses were focused on collections of contextually uncertain fossil material from deflation surfaces across the dunefied; this collection is referred to as “Elandsfontein Main” and consists of well over 20,000 identified specimens (Klein, 1988; Klein et

al., 2007). The collection consists of an extremely diverse mammalian fauna dominated by large browsing and grazing ungulates suggestive of a paleocommunity that was drastically different in both diversity and abundance from that present in the CFR today. In addition, an analysis of the stable carbon isotopic signature of mammalian enamel from the Elandsfontein Main collection suggests the presence of a small amount of C_4 vegetation in the diet of ungulates from the site (Luyt et al., 2000; Lehmann et al., *in Review.*). Analyses of the mesowear patterns on these teeth indicate that many large mammals had unexpected dietary adaptations to herbivory based on their taxonomy (Stynder, 2009). Although these investigations suggest a vegetation community different than that of contemporary EFT, due to the lack of precise context, questions regarding the spatial and temporal nature of these patterns remain unresolved.

Most recently, beginning in 2008, systematic excavations and collections were undertaken at EFT to provide a contextual link between environmental and hominin behavioral data (Braun et al., 2013a; 2013b). These recent efforts have produced a high-resolution stratigraphic framework for fossils and artifacts across the EFT dunefield and indicate that 1) there are *in situ* assemblages of mammalian fossils and behaviorally associated artifacts, 2) the majority of these *in situ* deposits are associated with a nodular layer in pedogenically modified sands, 3) there is an older, calcretized sand horizon which also contains mammalian fossils but these fossils are not abundant and are not associated with any artifacts, 4) distinguishing between *in situ* materials and deposits that reflect ancient episodes of deflation is straightforward using systematic excavation procedures and geologic observations (Rick, 2002), and 5) hominin toolmakers transported stone to EFT for the production and use of stone tools (Braun et al., 2013a).

The recent collections at EFT (2008-2015) have resulted in the recovery of a large sample of fossil Cape dune mole-rats (*Bathyergus suillus*), which is the focus of this study. The fossil remains of this relatively large, subterranean rodent (780-955 g; Bennett et al., 2009) are found in substantial frequencies in many excavations in the Pleistocene sediments at EFT and

provide the opportunity to characterize localized vegetative environment at EFT due to the restricted home range of *B. suillus*. Unlike most large mammalian ungulates that range over vast territories in search of seasonally available resources, small mammals live (and die) within a highly restricted space (Andrews, 1990; Reed, 1997). Before employing rodents and other small mammals as indicators of paleoenvironments, however, it is crucial to determine the agent/s of accumulation within a fossil assemblage (Andrews, 1990). Although small mammals may die and be preserved within or close to their home range in life, their remains may be transported away from their original environmental context by mammalian and avian predators (Matthews et al., 2006a; Reed, 2007; Terry, 2007). If the mode of accumulation can be confidently established, small mammals may provide an excellent proxy for localized paleoenvironments. This study uses the stable carbon isotopic composition of *in situ* Cape dune mole-rat enamel to provide the first analysis of the structure of the EFT vegetative environment between 0.6 and 1.0 Ma.

1.3 Modern *Bathyergus suillus* ecology

The genus *Bathyergus* consists of two extant species endemic to southern Africa: *Bathyergus suillus* (the Cape dune mole-rat) and *Bathyergus janetta* (the Namaqua dune mole-rat). *B. suillus* is primarily confined to the coastal soils of the Western Cape Province, with a single record from Rondawel near Groenrivier in the Northern Cape Province (Bennett et al., 2009). *B. janetta* occurs in the Northern Cape Province, particularly in the Namaqualand Hardeveld bioregion, Namaqualand Sandveld bioregion and some parts of the Namib desert (IUCN Red List; Herbst et al., 2004). To date, fossil *B. suillus* remains are only known from sites from within its historic range, the majority of which are younger than 130 Ka (Klein, 1991). Previous authors have attributed fossil mole-rat material from the earlier sites of Elandsfontein (Klein, 1991) and Duinefontein 2 (Klein, 1976) to *B. suillus*.

Bathyergus is largely solitary (Van Daele et al., 2007) with its spatial distribution influenced primarily by resource availability. *B. suillus* abundance varies in coastal fynbos and grassland settings, with high densities in grassland environments (Davies and Jarvis, 1986). Additionally, the species is large-bodied relative to other African mole-rats (780-955 g) (Bennett et al., 2009) and dig extensive burrows, some of which can include >400 m of interconnected tunnels, and typically live within a single burrow system throughout their life (Davies and Jarvis, 1986).

Much like other African mole-rats, *B. suillus* feeds upon the underground storage organs (geophytes) of certain plant species (e.g., *Othonna*, *Wachendorfia*; see Yeakel et al., 2007 for summary). Unlike other African mole-rats, however, which are primarily subterranean feeders, more than 60% of the diet of *B. suillus* originates from aerial vegetation pulled into the burrow via the roots (Bennett et al., 2009). Robb et al. (2012) used stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios to illuminate the diet of extant mole-rats in the CFR. The authors conclude that although geophytes make up a significant proportion of the species' diets, *B. suillus* had a substantially more generalized diet, including C_4 grasses, than the other mole-rat taxa of *Cryptomys hottentotus* and *Georychus capensis* from the CFR.

Bathyergus suillus is preyed upon by avian, mammalian and reptilian predators (Bennett et al., 2009); however, the archaeological record indicates some degree of exploitation by human populations in southern Africa (Henshilwood, 1997). This species is particularly vulnerable to predation when above ground and may be preyed upon by both avian and mammalian carnivores. When underground, *B. suillus* is frequently predated upon by mole snakes (*Pseudapis cana*) and Cape cobras (*Naja nivea*) (Bennett et al., 2009).

1.4 Study Objectives

In this study, we use carbon stable isotope data from *in situ* mid-Pleistocene *B. suillus* remains systematically collected at EFT between 2008 and 2014 and address the following questions:

1. Do $\delta^{13}C$ values of *B. suillus* enamel at EFT reflect the same information about mid-Pleistocene vegetation as the carbon isotope data from large mammals at EFT?
2. Can we use the carbon isotope data from the fossil teeth at EFT to identify spatial patterns in vegetation across the EFT dunefield?
3. What are the implications of these findings for understanding hominin paleobiology in the CFR between 1.0 and 0.6 Ma?

2. Materials and Methods

2.1 Collections

All *B. suillus* material was collected as part of archaeological and paleontological excavations or systematic trenches ("shovel test pits" or STPs) across the EFT dunefield between 2008 and 2014 (see Braun et al., 2013a). Collections were distributed spatially based upon what are referred to as Collection "Bays" which refer to deflation hollows between large modern dune crests (see Braun et al., 2013a; Fig. 3).

INSERT FIGURE 3

From this collection, we selected 150 *B. suillus* upper (maxillary) incisors as candidates for stable isotopic and taphonomic analyses. All *B. suillus* material analyzed here originated from the artifact and fossil-rich zone (see Braun et al., 2013a). Due to their unique morphology (Fig. 4), maxillary incisors can be used to distinguish the isolated incisors of *B. suillus* from those of other relatively large rodent taxa (e.g., *Otomys*) in the EFT collection. We therefore focused on isolated upper incisors for this study. To preclude the potential of comingling of

modern and fossil material, this analysis does not include any specimens recovered from the artifact- and fossil-rich horizons that were in the upper ~10 – 15 cm of the STPs or excavations.

INSERT FIGURE 4

2.2 Taphonomic Analysis

Previous researchers have considered *B. suillus* remains from EFT to be contemporaneous with other fossils and artifacts from the site (Klein, 1991). However, we recognize three possibilities regarding the origin of *B. suillus* fossils within the EFT Pleistocene sedimentary units: 1) *B. suillus* remains were deposited and preserved in primary context with the artifacts and the other associated large mammal fossils as a result of normal mortality of *B. suillus*, 2) *B. suillus* remains were deposited by avian and mammalian predators living at EFT around the time of deposition of other fossils and artifacts from the site and are thus contemporaneous with them and, 3) the *B. suillus* fossils are younger than the other materials in the fossil- and artifact-rich horizons at EFT, as a product of *B. suillus* burrowing into those horizons subsequent to deposition. Given that these three scenarios result in two alternative temporal relationships between *B. suillus* remains and the other archaeological and paleontological collections at EFT, we conducted a detailed taphonomic analysis of a subset of *B. suillus* incisors prior to isotopic analyses.

To investigate the likelihood of secondary deposition of incisors (i.e., that the fossils originated from mammalian scats or avian pellets) within the EFT collection, 33 upper incisors were studied for traces of digestion and rounding on the enamel surface. When animal remains pass through the digestive system of a predator, digestive acids leave a distinct signature on the surface of bone or enamel in the form of etching or rounding, particularly in the area of contact between enamel and dentine (Andrews, 1990; Fernandez-Jalvo and Andrews, 1992). This signature can be easily discerned with a dissecting microscope. For this analysis, we use a systematic protocol for evaluating the degree of etching and rounding on rodent incisors

(Matthews 2002; 2006b; Table 1). This methodology is akin to that of Fernandez-Jalvo and Andrews (1992), however categories used here were specifically developed for the incisors of *Bathyergus* and other southern African rodents. Using this protocol, each incisor within our subset was photographed under magnification and rated on a scale of 0 – 4 based upon the degree of etching and rounding on the enamel surface. To remove the possibility of confusion with other taphonomic processes, such as etching caused by acidic/alkaline soil, specimens were only scored if there was unquestionable evidence of digestion (refer to Table 1). Acid and alkaline soils may also cause corrosion and etching on both enamel and dentine (Andrews, 1990; Fernandez-Jalvo, 1995), and could possibly be confused with digestion (see Fig. 4D, 4E, 4F), although there are generally differences in the manner in which this occurs. To avoid any such errors, analysis erred on the conservative side and only included specimens that showed clear evidence of having passed through the digestive tract of an avian or mammalian predator (see Fig. 4B, 4C).

To further investigate the stratigraphic relationship between the fossils of *B. suillus* and the other materials recovered from systematic excavations at EFT, we reviewed the stratigraphic frequency of *B. suillus* fossils in relation to other materials found in these excavations. Previously we conducted a related analysis to document the fact that similar finds (<1cm) are found in similar frequencies as larger finds (Braun et al., 2013a). This analysis was based on previous work documenting these types of patterns in the Channel Islands (Rick, 2002). Here we test whether the frequency of *B. suillus* fossils track the frequency of other finds in these excavations. We excluded samples recovered from localities where formal standardized excavations were not conducted (i.e., material was recovered from shovel test pits). If the abundance of *B. suillus* fossils through the stratigraphic section closely tracks the frequency of other fossils in the excavations at EFT, it would suggest that the deposition of the *B. suillus* fossils and the other materials were the result of similar processes. If the frequency of these two types of material deviate through the stratigraphic section, however, then there is the

possibility that the *B. suillus* fossils were deposited through either 1) a natural mortality event occurring after mole-rats burrowed down into Pleistocene deposits or 2) deflation of younger sediments that were previously stratigraphically above the Pleistocene sediments.

2.3 Stable Isotopic Analysis

2.3.1 Analytical Methods

A subset of 19 *B. suillus* incisors from EFT was analyzed for carbon and oxygen stable isotope ratios using a laser ablation gas chromatograph system, coupled to a Thermo MAT 253 isotope ratio mass spectrometer in the Department of Earth and Planetary Sciences at Johns Hopkins University. Although typically less precise than conventional, phosphoric acid digestion methods (Passey and Cerling, 2006), laser ablation approaches were first used on the EFT *B. suillus* material because they are less destructive and require less sample material than conventional methods. Because the laser ablation technique samples all material in the laser ablation pit, and does not select for the carbonate component, it is common to attempt removal of surface organics prior to analysis (Passey and Cerling, 2006). Here, we used three different approaches to evaluate the influence of contaminants on the surface of teeth: 1) gentle abrasion of the surface enamel with a high speed rotary drill to remove secondary material, 2) soaking the incisors for 15 minutes in 3% hydrogen peroxide (H_2O_2) to remove organic material and 3) a control group in which nothing was done to the enamel surface. We analyzed a subset of teeth targeted for carbon and oxygen isotopes of tooth enamel using the phosphoric acid digestion method (see methods below) such that we could develop an understanding of the offset in the results between these two methods that is specific to these samples, as is necessary for laser ablation studies of fossil teeth.

In addition to the dataset of incisors analyzed for comparison to the data obtained from laser ablation technique (n = 19), a large dataset of *B. suillus* upper incisors were analyzed using phosphoric acid digestion method (n = 62). As with the laser ablation technique, only

upper incisors were analyzed. All incisors were photographed prior to sampling with a high-speed rotary drill fitted with a diamond bit. Enamel powder was treated for 15 minutes with 3% H_2O_2 to remove organic material and rinsed 3 times with distilled water prior to a 15 minute treatment with 0.1M buffered acetic acid to remove secondary carbonate. Following this treatment, samples were rinsed 3 times with distilled water and dried overnight at 60°C. Samples were then loaded into silver capsules and digested in a 100% phosphoric acid bath at 90°C for 10 minutes. Samples were cryogenically cleaned using a custom-built automated system (Passey et al., 2010) and the resulting CO_2 was analyzed for $\delta^{13}C$ and $\delta^{18}O$ on a Thermo MAT 253 mass spectrometer. An acid fractionation factor of 1.00725 (90°C) was used for tooth enamel following Passey et al., (2007).

Stable isotope ratios for all phosphoric acid digestion and laser ablation samples are reported as δ values relative to Vienna Pee Dee Belemnite (VPDB) using standard per mil (‰) notation, where $\delta^{13}C = (R_{sample}/R_{standard} -1) \times 1000$, and R_{sample} and $R_{standard}$ are the ratios of heavy to light isotopes (e.g., $^{13}C/^{12}C$, $^{18}O/^{16}O$) of the sample and the standard, respectively. During both types of stable isotope analyses, internal working enamel standards were analyzed, normalized to the carbonate standard NBS-19, routinely to monitor instrument performance. For the phosphoric acid method, Carrara marble, normalized to NBS-19, was also routinely measured as an internal working standard. $\delta^{13}C$ standard deviation of internal standards was 0.3‰, while that of $\delta^{18}O$ was 0.2‰.

Lastly, we compare $\delta^{13}C$ enamel values obtained from acid-etched, non-acid etched, laser ablated and phosphoric acid digestion. Although we include the oxygen isotope results for completeness in the tables of this paper, we do not discuss them in depth and instead focus on the carbon isotope data.

2.3.3 Dietary Reconstructions

We use an isotopic dietary mixing model to estimate the potential contribution of C_3, C_4 and Crassulacean acid metabolism (CAM) vegetation to the diet of *B. suillus* at EFT. We use the following equation:

$$\delta^{13}C_{B.suillus} = (fC_3 * \delta^{13}C_{C_3(veg)}) + (fC_4 * \delta^{13}C_{C_4(veg)}) + (fCAM * \delta^{13}C_{CAM(veg)})$$

where *f* indicates the fraction of the different dietary inputs from plants that use the three photosynthetic pathways and $\delta^{13}C$ indicate published average $\delta^{13}C$ values for each (Radloff, 2008; Kohn, 2010; Boom et al., 2014).

To reconstruct the ingested vegetation, we use a diet-tissue fractionation factor ($\varepsilon^*_{enamel\text{-}diet}$) of 11.1‰, which has been shown to be appropriate for small mammals (Podlesak et al., 2008). The incorporation of CAM vegetation into this analysis is especially important given: 1) the broad and often poorly understood isotopic signature of CAM vegetation in southern Africa (Boom et al., 2014), and 2) their well-documented abundance in the CFR (Peters and Vogel, 2005). To incorporate CAM vegetation into our model, we use carbon isotopic values derived directly from CAM vegetation in the CFR. Boom et al. (2014) characterized the isotopic signature of 36 taxa of CAM plants from within the CFR. We use the average $\delta^{13}C$ value for all CAM plants from the CFR (-19.7 ± 4.0‰; Boom et al., 2014) because we do not know the specific CAM plants that were prevalent in the region around EFT during the mid-Pleistocene. For C_3 vegetation we used a $\delta^{13}C$ value of -27.1 ± 1.6‰ obtained from the large (n = 480), global compilation of C_3 plants by Kohn et al. (2010). For C_4 vegetation we used a $\delta^{13}C$ value of -12.8 ± 1.3‰ obtained by Radloff et al. (2008) for C_4 grasses in the CFR.

We estimate the percentage of C_4 vegetation consumed by large mammals at EFT following a two-member version of the above mixing model, assuming that only C_3 and C_4 plants contributed to large mammal diets, where $f_{CAM} = 0$. For these estimates we use a $\varepsilon^*_{enamel\text{-}}$

$_{diet}$ of 14.1‰ following Cerling and Harris (1999) and compare these values to those obtained from the *B. suillus* model ($\varepsilon^*_{enamel\text{-}diet}$ = 11.1‰; Podelsak et al., 2008) that also considers the influence of CAM vegetation.

3. Results

3.1 Taphonomic Analysis

In the taphonomic sample (n = 33), 18% of EFT *B. suillus* incisors in our taphonomic subsample (n = 33) showed extreme signs of enamel and dentine etching as a result of predation (Fig. 4; Table S1). Of the etched specimens, 5 scored greater than 1, with scores of 3 being the most prevalent. Many specimens, especially within the unetched category showed clear signs of root marks (etching) as well as small, circular areas where both enamel and dentine were dissolved (see Fig. 4). The latter could be related to intestinal etching, soil microbes, or soil acidity, but additional actualistic studies are needed to confirm this possibility.

Our analysis of the frequency of specimens through the stratigraphic sequence suggests that the fossils remains of *B. suillus* and those of other fossils from EFT are the result of similar depositional processes. A clear indication of differences in depositional context is when smaller specimens increase in frequency while larger specimens decrease (Rick, 2002). The upper 40 cm of the excavation at the 0313 locality shows this pattern suggesting the upper part of this excavation is representative of a variety of depositional processes. In all other localities in this analysis, however, the abundance of *B. suillus* fossils tracks that of large mammals at the EFT Collection Bays (Fig. 5). Braun et al., (2013a) used the relationship between large and small mammal remains within EFT excavated localities to suggest that there is little evidence of deflation at certain localities. There have been previous suggestions that the fossiliferous sediments at EFT represent multiple episodes of deflation and reburial in the past (Klein et al., 2007). The fact that the frequency of *B. suillus* fossils follows the patterns exhibited by the larger fossils suggest that 1) these assemblages do not represent ancient deflated surfaces and 2)

that the depositional processes that are responsible for the burial and preservation of the large mammal fossils is also responsible for the presence of the *B. suillus* fossils. If the *B. suillus* fossils represented instances where younger (or modern) mole-rats burrowed down into the older Pleistocene sediments and died there, it is highly unlikely that they would preferentially be buried in the same horizons that also had the highest frequencies of fossils.

INSERT FIGURE 5

3.2.1 Laser Ablation vs. Acid Digestion

Nearly all enamel surfaces sampled by laser ablation charred significantly, which suggests a high proportion of impurities on the enamel surface as well as within the enamel matrix. $\delta^{13}C$ values obtained by laser ablation and phosphoric acid digestion of EFT *B. suillus* enamel (n = 19) are compared in Table 2. Average isotopic enrichment ($^{13}C\varepsilon^*_{laser\text{-}acid}$) was -5.9 ± 2.2‰ and ranged from -9.5‰ to -2.4‰. Acceptable values, as detailed in Passey and Cerling (2006) are: $^{13}C\varepsilon^*_{laser\text{-}acid}$ = -0.5 ± 0.8‰. The majority of the $\delta^{13}C$ values for EFT *B. suillus* incisors fall outside of the acceptable values obtained by Passey and Cerling (2006). This was true even for samples treated prior to sampling with either diluted H_2O_2 or abrasion of the enamel surface. As a result, we do not use any of the laser ablation data in any of the following analyses. Due to the specific preservation circumstances of the *B. suillus* fossils at EFT, laser ablation is an inappropriate technique for isotopic analysis. The standard deviation of $\delta^{13}C$ of JHU internal tooth enamel standards analyzed in the same laser ablation sessions as the EFT *B. suillus* teeth was 0.9‰ for $\delta^{13}C$ and 0.5‰ for $\delta^{18}O$, which suggests that the poor performance of EFT *B. suillus* incisors is related to the characteristics of the EFT *B. suillus* teeth themselves and not related to the performance of the laser ablation system. Enamel standards analyzed on the system had an average $^{13}C\varepsilon^*_{laser\text{-}acid}$ of -1.2 ± 0.3‰. The poor performance on the laser system may be due to the nature of preservation of fossil teeth at EFT. Previous analyses have noted the low carbonate content of EFT fossil teeth (Luyt et al., 2000; Lehmann et al., *In Review*). This serves as an instructive example that not all samples are appropriate for analysis by laser

ablation approaches. All subsequent analyses will be based on data obtained from phosphoric acid digestion.

3.2.2 Phosphoric Acid Digestion

INSERT FIGURE 6

EFT *B. suillus* $\delta^{13}C$ enamel values (n = 81) average -7.9 ± 1.4 ‰ and range from -10.4 to -4.1‰ (Tables 3, S2), while $\delta^{18}O$ enamel values (n = 81) average -0.8 ± 1.2 ‰ and range from -4.1‰ to 2.6‰. When these samples are pooled by Collection Bay, we do not observe a significant correlation between median $\delta^{13}C$ value and latitude (p = 0.35; Spearman's Rank Correlation) or longitude (p = 0.69; Spearman's Rank Correlation) values at EFT (Fig. 6 A,B). We do, however, recognize statistically significant differences between $\delta^{13}C$ ratio distributions (p = 0.01, Kruskal-Wallis test of equal medians) across Collection Bays, which suggests significant isotopic heterogeneity across the dune field. It is important to consider, however, that sample sizes for some Bays are especially low (Table 3) and additional targeted sampling is needed to further confirm these patterns.

We find no statistically significant differences in the mean (p = 0.32, ANOVA; p = 0.32, Wilcoxon-Mann-Whitney Rank Sum Test) or variance (p = 0.52, F test for equal variance) of $\delta^{13}C$ values between the subset of acid-etched and unetched incisors (Fig. 6C). $\delta^{13}C$ of etched incisors (n = 6) average -6.7 ± 1.2 ‰ and range from -8.2 to -5.0‰, while unetched incisors (n = 27) average -7.4 ± 1.2 ‰ and range from -10.1 to -4.1 ‰. Additionally, we find no difference in the mean (p = 0.41, ANOVA; p = 0.28, Wilcoxon-Mann-Whitney Rank Sum Test) of $\delta^{18}O$ values of acid-etched and unetched incisors. We do, however, find a significant difference in the variance (p = 0.003, F test for equal variance) in $\delta^{18}O$ values of acid-etched and unetched incisors. The similarities in isotopic values between the etched and unetched specimens further

support the assertion that all of the EFT *B. suillus* incisors analyzed here originated from the same fossil population.

INSERT FIGURE 7

Fossil EFT *B. suillus* incisors are significantly ($p < 0.001$, ANOVA; $p < 0.001$ Wilcoxon-Mann-Whitney Rank Sum Test) enriched in $\delta^{13}C$ when compared to contemporaneous large mammals (n = 194; Luyt et al., Lehmann et al., *In Review.)* from the site (Fig. 7). $\delta^{13}C$ values of large mammals average -10.2 ± 1.3‰ and range from -13.3‰ to -6.9‰. The Lehmann et al. (*In Review*) large mammal dataset from EFT consists of samples from taxonomically (i.e., 8 families) and ecologically (i.e., browsers and grazers) diverse taxa.

3.2.3 Estimates of C_4 dietary contribution

Even when considering the potential contribution of CAM vegetation, we find that the mean $\delta^{13}C$ value (-7.9‰) for *B. suillus* teeth at EFT would require diets between 20 and 52% C_4 vegetation (Fig. 7). This is consistent with dietary estimates based upon stable isotopic analyses for modern *B. suillus* obtained by Robb et al. (2012). It should be noted that the $\delta^{13}C$ values for the modern mole-rats may indicate the consumption of grasses that are not native to the CFR. This variable diet is consistent with descriptions of modern populations in southern Africa (Bennett et al., 2009) and agrees with previous studies that indicate the presence of at least some C_4 vegetation within the EFT vegetative community (Luyt et al., 2000; Lehmann et al., *In Review*).

3.2.4 Implications for Hominin Paleobiology

The isotopic variation in the fossil *B. suillus* specimens likely reflects some variation in vegetation in the past. To better understand the relationship between this variation in ancient vegetation and hominin behavior we investigate the frequency of excavated artifacts at EFT and the $\delta^{13}C$ signature of *B. suillus* from the various localities at EFT. We find that there is a positive

relationship (Kendall's Tau = 0.54; p = 0.05) between artifact density (count/m^2) and the median *B. suillus* $\delta^{13}C$ signature when binned by Collection Bay (Fig. 8). We use the non-parametric Kendall's Tau correlation due to its conservative significance estimates with small sample size (refer to Table 3).

INSERT FIGURE 8

4. Discussion

4.1 Taphonomic history of *B. suillus* at EFT

The taphonomic data demonstrate that at least 18% of *B. suillus* incisors from EFT display evidence of digestion (i.e., acid etching), indicating that they were prey items of avian or mammalian carnivores and became associated with the site through the deposition of pellets or scats (Fig. 4). The $\delta^{13}C$ values from the acid-etched incisors are indistinct from $\delta^{13}C$ values of teeth for which there is no evidence of acid digestion (Fig. 4C). This is also the case for $\delta^{18}O$ values. We conclude that the material analyzed here appears to have originated from a fossil population that has a similar depositional history as the other fossils and artifacts at EFT. This finding, originally suggested by Braun et al. (2013a), is supported by our analysis of the relative stratigraphic abundance of *B. suillus* and large mammal fossils at EFT (Fig. 5). We note that we cannot completely rule out the possibility that some of the fossil *B. suillus* material at EFT represents geologically later incursions into older deposits.

4.2 Vegetative variability at EFT during the mid-Pleistocene

The $\delta^{13}C$ signature of *B. suillus* suggests significant vegetative variability (i.e., plants utilizing the C_3, C_4 and CAM photosynthetic pathways) at EFT during the mid-Pleistocene. The ubiquity of *B. suillus*, a species with high dietary flexibility (Bennett et al., 2009), at the site,

combined with $\delta^{13}C$ values spanning approximately 6‰ suggest the ancient local ecosystems varied significantly. For comparison, the range of $\delta^{13}C$ values for *Aepyceros melampus*, a wide-ranging mixed-feeding bovid, in eastern Africa is approximately 10‰ (Cerling et al., 2003). The diet of *A. melampus* is directly related to the proportional representation of C_3 and C_4 vegetation across ecotones, such that as these proportions change, so does the diet of *A. melampus*. Thus, $\delta^{13}C$ variation in *B. suillus* from EFT is consistent with findings in modern representatives (Robb et al., 2012) and suggests that the taxon was a relatively opportunistic feeder in ancient times and incorporated an isotopically diverse range of vegetation into its diet.

Our analyses of the $\delta^{13}C$ signature of *B. suillus* (Fig. 6) suggest that the distribution of vegetation at EFT was highly heterogeneous across space. The spatial distribution of vegetation types at EFT could be related to highly localized landscape features (e.g., springs). The heterogeneous nature of the environment at EFT, and the resources available within it, is supported by the diversity of the large mammal fauna (Klein et al., 2007; Braun et al., 2013a). Alternatively, the variation that we have identified may be related to the particular taphonomy of this region. This is attributable to a combination of two possible factors: 1) some degree of time averaging within the assemblages, and 2) a majority of *B. suillus* material originated from avian pellets or mammalian scat that were deposited in locations a distance away from the area in which the material was caught. Although there are clear fossil horizons at EFT (Braun et al., 2013a), the depositional time represented by these horizons across the dunefield remains unclear. Dynamic climatic and geologic variables may have resulted in shifting ecotones at EFT; therefore a fossil sample originating from within one Collection Bay at EFT potentially represents an accumulation of time-averaged sediment as is the case with almost all Pleistocene archaeological sites (Shick 1987). Thus, each locality likely represents a unique window into the ecosystem at a particular time in the dunefield's depositional history. Secondly, predators may have transported the remains of *B. suillus* across the EFT dunefield, thus

532 decreasing the spatial fidelity of the sample. We suggest that it is likely that a combination of
533 these factors contributed to the lack of spatial patterning in the $\delta^{13}C$ signature of *B. suillus* at
534 EFT.
535
536 **4.3 Large mammals versus *Bathyergus suillus* at EFT**
537 The $\delta^{13}C$ data indicate significant dietary differences between large mammals and *B.*
538 *suillus* at EFT (Fig. 7). Based upon our dietary mixing model, even after considering the
539 potential contribution of CAM vegetation, *B. suillus* at EFT consumed significant quantities of C_4
540 vegetation. To obtain the mean EFT *B. suillus* $\delta^{13}C$ value (-7.9± 1.4 ‰), the diets of individual
541 mole-rats would have had to included 20 - 52% C_4 vegetation. In contrast, $\delta^{13}C$ values from
542 large mammals at EFT indicate that individuals had diets with 0-35% C_4 vegetation (Lehmann et
543 al., *In Review*), which is significantly less than that of contemporaneous *B. suillus*. This
544 comparison clearly demonstrates that mole-rat diet at EFT was different than that of large
545 mammals. Although it is difficult to assess the particular types of plants that contributed to the
546 C_4 component to *B. suillus* diets (e.g., grasses or sedges), the diet of extant *B. suillus* from the
547 CFR can potentially shed light on this issue. Although the diet of the species is especially
548 variable relative to other African mole-rat genera, more than 60% of the diet of modern *B. suillus*
549 is derived from the blades and rhizomes of *Cynodon dactylon*, a C_4 grass (Davies and Jarvis,
550 1986; Bennett and Jarvis, 1995, Smith and Winter, 1996; Yeakel et al., 2007). Although
551 *Cynodon dactylon* in not endemic to South Africa, it does suggest that *B. suillus* readily
552 consumes C_4 resources if available on the local landscape. Thus, we suggest that it seems
553 more likely that C_4 grasses and sedges, rather than CAM plants, were the primary source of
554 relatively high $\delta^{13}C$ values in *B. suillus* teeth relative to those of large mammals at EFT.
555 It is also important to consider how variation in the carbon isotope diet-tissue
556 fractionation factor ($\varepsilon^*_{\text{enamel-diet}}$) affects dietary reconstructions, especially between large and
557 small mammals that potentially have different digestive physiologies (Passey et al., 2005). Here

we use a $\varepsilon^*_{\text{enamel-diet}}$ of 11.1‰ which has been suggested appropriate for small mammals (Podelsak et al., 2008). It is also important to consider, however, a scenario where $\varepsilon^*_{\text{enamel-diet}}$ for *B. suillus* was closer to that proposed for large mammals (i.e., 14.1‰; Cerling and Harris, 1999). If the $\varepsilon^*_{\text{enamel-diet}}$ for *B. suillus* were 14.1‰, then *B. suillus* at EFT during the mid-Pleistocene consumed slightly greater proportions of C_4 vegetation than we suggest in Section 3.2.3 (Fig. S1). Thus, the estimates provided here for the proportion of C_4 vegetation in the diet of *B. suillus* are conservative, minimum values given uncertainties in $\varepsilon^*_{\text{enamel-diet}}$ for *B. suillus* and other mole-rats.

The carbon isotope data presented here indicate that *B. suillus* consumed significantly more C_4 vegetation than large mammals at EFT in the mid-Pleistocene. We consider this to be reflective of elevated concentrations of C_4 vegetation at EFT relative to the surrounding, C_3 vegetation dominated, CFR. Because large-bodied mammals migrate seasonally and have more expansive home ranges, their isotopic signature is likely to reflect the vegetation in a larger geographic region than that of *B. suillus*. Given the relatively small spatial extent of EFT (~11 km^2), it is likely that large mammals ranged both within and outside of site and as a result incorporated vegetation from outside of the bounds of EFT. Even considering post-mortem predatory transport estimates for avian predators of 1.5 km^2 (Colvin, 1984; Taylor, 1994), the $\delta^{13}C$ data from *B. suillus* at EFT represents vegetation from a more limited geographic range than that of the larger mammals, which in some cases could be greater than 50 km^2 (Klingel, 1969). It is difficult to assess the impact of mammalian carnivore predation on the distribution of *B. suillus* remains at EFT, but it is unlikely that small carnivores transported mole rats far from the area in which they were caught. Previous work at EFT suggests a high diversity of mammalian carnivores at the site (Klein et al., 2007). Although mammalian carnivores can have extensive ranges based upon body size, metabolic requirements, habitat and diet (Gittleman and Harvey, 1982), our taphonomic analysis revealed that less than 20% of *B. suillus* incisors showed definitive evidence of digestion. Therefore, we find it implausible that the $\delta^{13}C$ values of

584 fossil EFT *B. suillus* incisors reflect a geographic space equivalent in size to that of the home
585 range of large mammalian carnivores.
586 An additional possibility is that the C_4 component of *B. suillus* diet is related to the
587 consumption of C_4 sedges rather than C_4 grasses. Existing work by Mucina et al., (2006) and
588 Radloff et al., (2008) indicates that wetlands within the WRZ support locally abundant C_4
589 biomass. Spring features on the ancient EFT landscape could have provided the water needed
590 to fuel the growth of C_4 sedges during hot summer months in the CFR. Wetlands associated
591 with spring features could have also supported C_4 grasses and it has been demonstrated that
592 certain large ungulate taxa in the CFR preferentially target these grasses when available
593 (Radloff, 2008). If this behavior was consistent in the past, the presences of C_4 grasses at EFT
594 may have concentrated large ungulate taxa at the site and may explain the C_4 component of
595 EFT large mammal diet reported by Lehmann et al., (*In Review*). If these wetland areas,
596 however, supported only C_4 sedges, which are less likely to be consumed by large herbivores, it
597 may explain the significantly enriched $\delta^{13}C$ values of *B. suillus* relative to those of EFT large
598 mammals.
599 **4.4 C_4 vegetation in the Cape Floral Region**
600 Although the contemporary CFR lies well within the WRZ and is dominated by C_3
601 vegetation, we understand little about the evolution of this climatic system throughout the
602 Quaternary (Chase and Meadows, 2007). Previous research suggests that C_4 vegetation was
603 not a major component of CFR ecosystems at 5 Ma (Franz-Odendaal et al., 2002; Rossouw et
604 al., 2009; Dupont et al., 2011, 2013; Hoetzel et al., 2013, 2015), however analyses of enamel
605 from large mammals (Luyt et al. 2000; Hare and Sealy, 2014; Lehmann et al., *In Review*)
606 suggest a minor presence of C_4 vegetation in the mid-Pleistocene, potentially related to
607 decreased atmospheric pCO_2 conditions during glacial periods. Our study suggests that a C_4
608 signal within the CFR during this period may be somewhat masked by the wide-ranging nature
609 of large mammals. The carbon isotope data from *B. suillus* at EFT, which sample relatively

610 small geographic regions (<1.5 km^2) indicate that some regions in the CFR potentially had
611 greater proportions of C_4 vegetation than is indicated by carbon isotope data from large
612 mammals alone.

613 It is important to consider the effect of glacial and interglacial climatic cycles on the $\delta^{13}C$
614 signatures of herbivores at EFT (Hare and Sealy, 2013). The crossover model of Ehleringer
615 (1997) and Cerling (1998) predicts that during glacial periods, atmospheric pCO_2 is lower and
616 C_4 plants should have a distinct advantage over C_3 plants. Thus, it is hypothesized that during
617 glacial periods in the CFR, C_4 vegetation would have been a more significant proportion of the
618 plant biome than during interglacial periods (Hare and Sealy, 2013). Current geochronological
619 models of EFT make it impossible to ascertain if the sediments at EFT represent a glacial or
620 interglacial period. Both large and small mammals were collected from within a single fossil- and
621 artifact-rich horizon at EFT that could represent glacial or interglacial cycles or a combination of
622 both. Regardless of the specific time period represented, EFT large and small mammals
623 represent similar depositional circumstances and were likely aggregated over a similar time
624 interval (Fig. 5).

625 Previous research has demonstrated that in addition to atmospheric pCO_2, growing
626 season temperature is the dominant climatic parameter that determines the abundance of C_4
627 vegetation within an ecosystem (Terri and Stowe, 1976; Epstein et al., 1997). These studies
628 suggest that more elevated growing season temperatures result in higher proportions of C_4
629 plants within a particular system. As with all plants, however, water availability is crucial for the
630 initiation of plant growth (Ehleringer et al., 1997). We hypothesize that the consistent presence
631 of water near springs at EFT evident from spring deposits (Braun et al., 2013a) may have
632 created conditions in which a significant proportion of C_4 vegetation could thrive during the hot,
633 dry summers of the WRZ. We further hypothesize that the prevalence of C_4 vegetation would be
634 elevated in areas with low-lying topography in close contact with the water table (i.e., spring
635 features). This relationship between spring features and elevated C_4 vegetation has been

636 demonstrated in eastern Africa (Garrett, 2015). In the contemporary CFR, increased C_4
637 biomass, specifically *Sporobolus virginicus* and *Stenotaphrum secundatum*, has been
638 documented in conjunction with estuaries and wetlands (Mucina et al., 2006; Radloff, 2008).
639 Thus, it is highly plausible that spring features and the resulting availability of water during the
640 dry summer months resulted in localized instances of C_4 vegetation at EFT during the mid-
641 Pleistocene.

642 It is also important to consider that the C_4 vegetation component of *B. suillus* enamel
643 values may have been affected by seasonal variation in the EFT ecosystem. Breeding in *B.*
644 *suillus* has been shown to be highly seasonal and tied to periods elevated rainfall (Hart et al.,
645 2006). The shorter life spans and enamel maturation periods in *B. suillus* relative to those of
646 large mammals, means that the $\delta^{13}C$ data from *B. suillus* is representative of relatively shorter
647 periods of time compared to the $\delta^{13}C$ data of large mammals at EFT. If the time of enamel
648 maturation in *B. suillus* corresponds to a seasonal period in which C_4 vegetation is more
649 abundant, then the EFT mole-rat $\delta^{13}C$ data could represent a bias towards this particular aspect
650 of the ecosystem. Carbon isotopic data from large mammals at Hodjiespunt (Hare and Sealy,
651 2013) and EFT (Lehmann et al., *In Review*) however, suggest that the differential winter rainfall
652 seen in the modern winter rainfall zone was active during the mid-Pleistocene. Thus, C_3
653 vegetation is more likely to have increased in the WRZ during instances of increased rainfall.
654 This scenario would manifest in the enamel of *B. suillus* that would reflect greater amounts of C_3
655 vegetation during these periods. This is the opposite of the pattern exhibited in the *B. suillus*
656 specimens in this study.

657 The connection between C_4 vegetation and standing water could represent an important
658 insight into the ecological mechanisms behind the elevated diversity and abundance of
659 mammalian fossils at EFT (Klein et al., 2007). The consistent presence of water would have
660 been an extremely valuable resource for animals, especially the obligate drinkers during the
661 relatively long, hot and dry summers in the WRZ. In turn, the seasonal consumption of

vegetation from these areas at EFT could be responsible for the small amount of C_4 vegetation in the diet of large mammals from the site (Luyt et al., 2000; Lehmann et al., *In Review.*).

4.5 Implications for hominin ecology at EFT

The fossil and archaeological deposits at EFT provide a rare glimpse into hominin behavior between 1.0 and 0.6 Ma, a period of human history that is poorly understood in Africa (Patterson et al., 2014). Previous research suggests that hominin occupation at EFT can be best explained by the complex interplay of availability of stone to make artifacts and the variability in food resources (Archer and Braun, 2010; Braun et al., 2013a). Our findings suggest a previously undocumented diversity of vegetative resources at EFT and support this conclusion on two fronts: 1) EFT likely represented a rare, resource-rich landscape within a broader regional ecosystem that was relatively resource poor, and 2) this landscape presented an adaptive scenario for mid-Pleistocene hominins in the Western Cape that is substantially different from the summer rainfall ecosystems represented in the vast majority of similarly aged deposits on the African continent.

Although we understand little about the position of mid-Pleistocene hominins within the broader mammalian community in the CFR, EFT provides important clues into hominin paleoecology during this period. Directly associated artifacts and fauna at EFT (Braun et al., 2013a) suggests that hominins capitalized on meat resources and were likely drawn to EFT by what may have been consistently available water and vegetation. Additionally, the incredible diversity of mammalian carnivores preserved at EFT (Klein et al., 2007; Braun et al., 2013a), suggests that hominins were a part of the large carnivore guild by this time, a process that potentially began at least 1 million years earlier on the continent (Werdelin and Lewis, 2013). Recent work by Forrest et al. (2015) suggests a higher frequency of cut marked bones which is likely an underestimate due to poor bone surface preservation resulting from the Aeolian

687 depositional setting at the site, at EFT than that indicated by previous studies (Klein et al.,
688 2007).
689 The isotopic disparity between EFT *B. suillus* and EFT large mammals suggests a
690 landscape that provided hominins with locally distinct and consistent resources (i.e., water and
691 associated C_4 vegetation) during periods of resource scarcity in the broader CFR, particularly
692 during the dry summer months. Although the CFR may have been climatically dynamic during
693 the mid-Pleistocene (Chase and Meadows, 2007), we hypothesize that the resources available
694 at EFT may have provided a buffer against broader environmental, and resource instability in
695 the CFR.
696 Lastly, our analysis contributes to our understanding of intra-landscape hominin behavior
697 at EFT. Although lithic evidence indicates that hominin behavior varied in intensity across the
698 EFT dunefield (Braun et al., 2013a), we know little about the ecology of these patterns.
699 Preliminarily, our analyses suggest that the presence of C_4 resources, could have contributed to
700 this concentration. Our data indicate a positive relationship between artifact density and median
701 $\delta^{13}C$ of *B. suillus* from EFT. This finding suggests that the unique environmental conditions
702 suitable for C_4 vegetation (i.e., water during the summer months) may have also contributed to
703 the resultant discard of stone artifacts by hominin toolmakers at similar points on the landscape.
704
705 **5. Conclusion and future directions**
706 We used a large sample (n = 81) of fossil *B. suillus* incisors to assess the distribution of
707 vegetation at EFT. Our findings suggest that the paleolandscape of EFT contained a unique
708 mixture of C_4, C_3 and CAM vegetation relative to the broader fynbos-dominated C_3 ecosystem
709 of the CFR. $\delta^{13}C$ values of *B. suillus* are significantly different from those of contemporaneous
710 large mammals from EFT and suggest a plant community with a significant presence of plants
711 utilizing the C_4 photosynthetic pathway, even when the contribution of CAM vegetation in the
712 diet of *B. suillus* is considered. We hypothesize that this geographically restricted landscape

provided abundant resources for both hominin and non-hominin taxa and potentially buffered these populations against larger environmental fluctuations and resource instability in the Cape Floral Region.

Future studies at EFT hope to increase the resolution with which we understand both hominin and large mammal behavior in the CFR. Strontium isotopic analysis of both large and small mammals at the site promises to provide insight into ranging patterns and the opportunity to further test many of the hypotheses presented here. In addition, geochemical sourcing of raw materials utilized by EFT hominins can potentially offer insights into the utilization of regionally available lithic resources (Braun et al. 2008). Lastly, increasing the chronological resolution of the EFT deposits is crucial to testing climatic hypotheses, especially the impact glacial and interglacial cycles on the CFR.

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Figure Captions

Figure 1. Modern rainfall seasonality in southern Africa. Inset: location of Elandsfontein (EFT) and other important archaeological locations along the west coast of southern Africa (rainfall data: www.worldclim.org; Inset: modified from Braun et al., 2013a).

Figure 2. Temporal distribution of WCP sites. Refer to Figure 1 for spatial distribution.

Figure 3. A) Map of EFT Collection Bays and small mammal collection strategies. B) Shovel test pit (STP) in Bay 0710; refer to Braun et al., (2013a) for further descriptions of geological context of EFT; C) 0313 excavation.

Figure 4. A) Modern *B. suillus* skull (NMNH 344067) from Mosselbaai, South Africa; B) WCRP 46140 (acid etch score = 3); C) WCRP 46138 (acid etch score = 3); D) WCRP 45684 (acid etch score = 0); E) WCRP 45642 (acid etch score = 2; note potential root etching); F) WCRP 45548 (acid etch score = 0); Arrows indicate anterior direction of specimen. Note differences in enamel surface modification in 3B, 3C, 3D, 3E, 3F. 3D, 3E and 3F could be related to soil acidity, microbes or both.

Figure 5. Altimetric analysis of the relationship between *B. suillus* fossils and large mammal fossils from EFT Collection Bays. EFT *B. suillus* fossils depicted with red triangles. EFT large mammal fossils depicted with black circles.

Figure 6. A) *B. suillus* $\delta^{13}C$ values arranged by Collection Bay from north to south, B) *B. suillus* $\delta^{13}C$ values arranged by collection Bay from east to west, C) Comparison of $\delta^{13}C$ and $\delta^{18}O$ values of etched and unetched incisors. Center line represents the sample median, box represents the 25^{th} and 75^{th} percentiles, whiskers represent the sample range exclusive of outliers, circles represent outliers defined at 1.5 times the interquartile range.

Figure 7. Comparison of EFT large mammals and EFT *B. suillus*. Models of 100% C_3, CAM and C_4 represent are associated with the diet of *B. suillus*, not EFT large mammals. Darker green,

765 hashed areas represent overlap between the two distributions. EFT large mammal grazer and
766 browser mean values from Lehmann et al. (*In Review*).
767
768 **Figure 8.** Relationship between Collection Bay median *B. suillus* $\delta^{13}C$ values and Bay artifact
769 density. Line represents best fit line from median *B. suillus* $\delta^{13}C$ values – artifact density linear
770 model.
771
772 **Figure S1.** $\varepsilon^*_{\text{enamel-diet}}$ affect on EFT large mammal and EFT *B. suillus* distributions. A) Small
773 mammal $\varepsilon^*_{\text{enamel-diet}}$ (11.1‰) following Podelsak et al., 2008, B) Large mammal $\varepsilon^*_{\text{enamel-diet}}$
774 (14.1‰) following Cerling and Harris (1999).
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785 **List of Tables:**
786
787 **Table 1**. Protocol used for assigning EFT *B. suillus* upper incisors to acid-etching categories
788

Table 2. $^{13}C_{\varepsilon\text{ laser-acid}}$ and $^{18}O_{\varepsilon\text{ laser-acid}}$ for EFT *Bathyergus* enamel. ^{13}C Offset[1] and ^{18}O Offset[1] refer to difference between values obtained in this study and those of Passey and Cerling (2006)

Table 3. Summary of $\delta^{13}C$ and $\delta^{18}O$ EFT *B. suillus* upper incisors arranged by Collection Bay

Table S1. Taphonomic analysis of EFT *B. suillus* upper incisors. Refer to Table 1 for etch scoring protocol.

Table S2. $\delta^{13}C$ and $\delta^{18}O$ values of EFT *B. suillus* upper incisors.

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Figure 1. Modern rainfall seasonality in southern Africa. Inset: location of Elandsfontein (EFT) and other important archaeological locations along the west coast of southern Africa (rainfall data: www.worldclim.org; Inset: modified from Braun et al., 2013a).

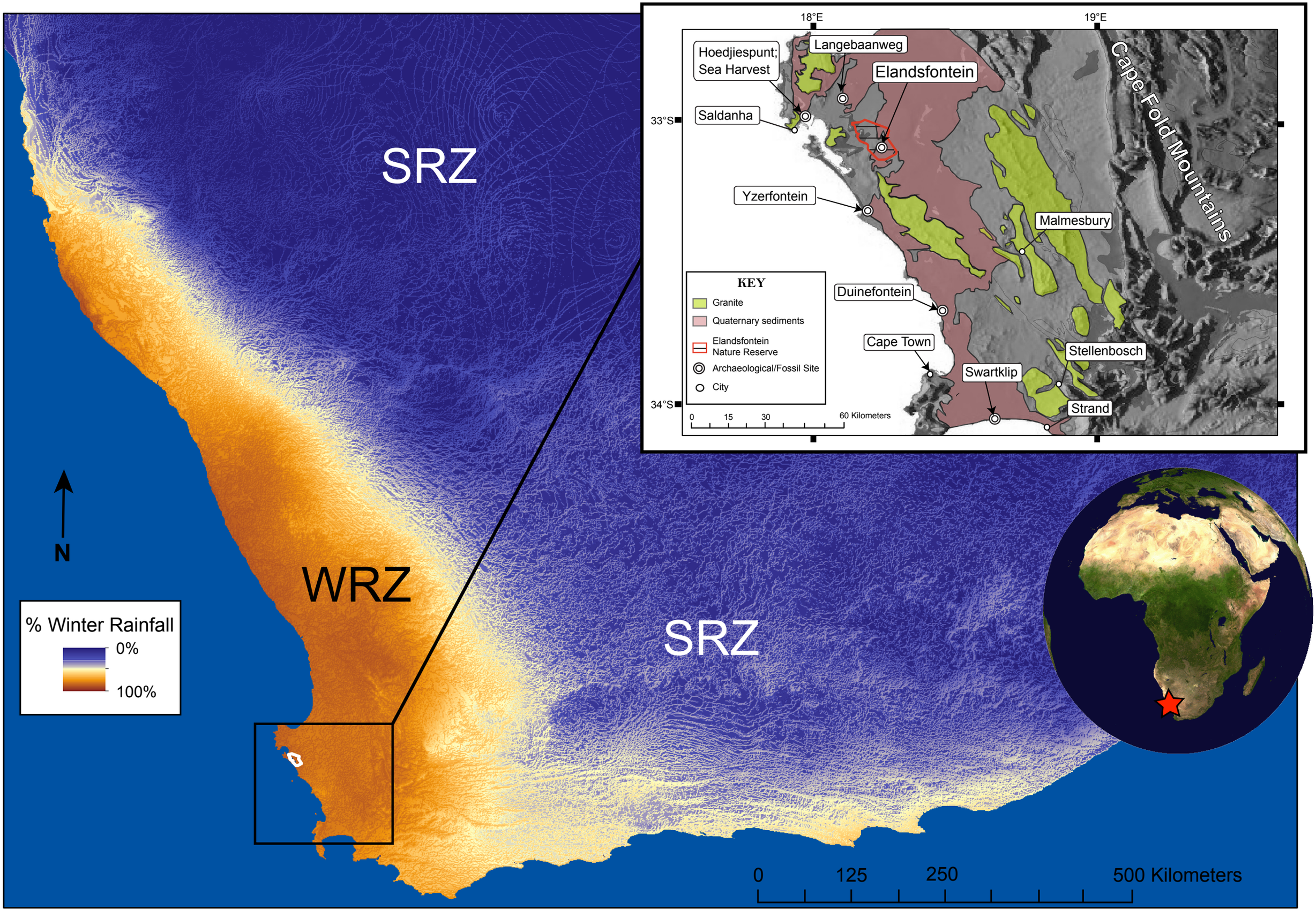


Figure 2. Temporal distribution of WCP sites. Refer to Figure 1 for spatial distribution.

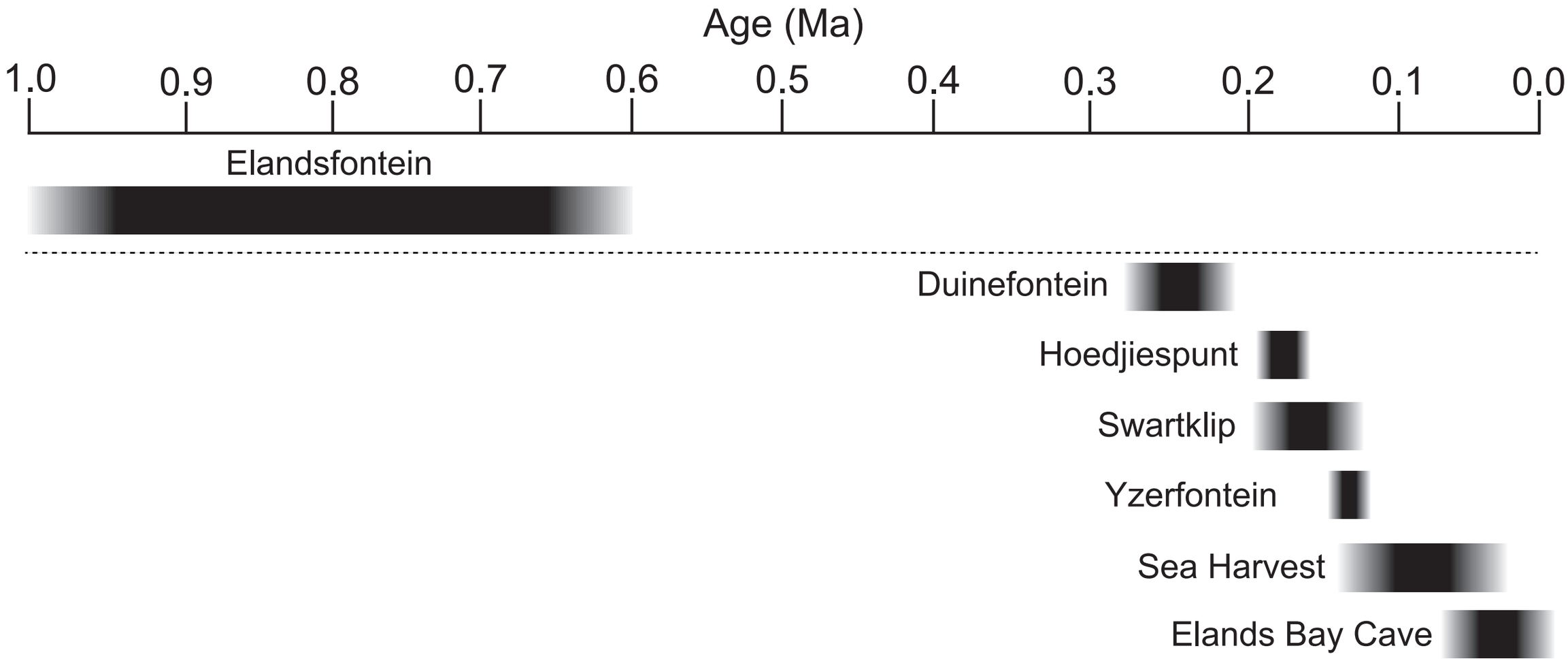
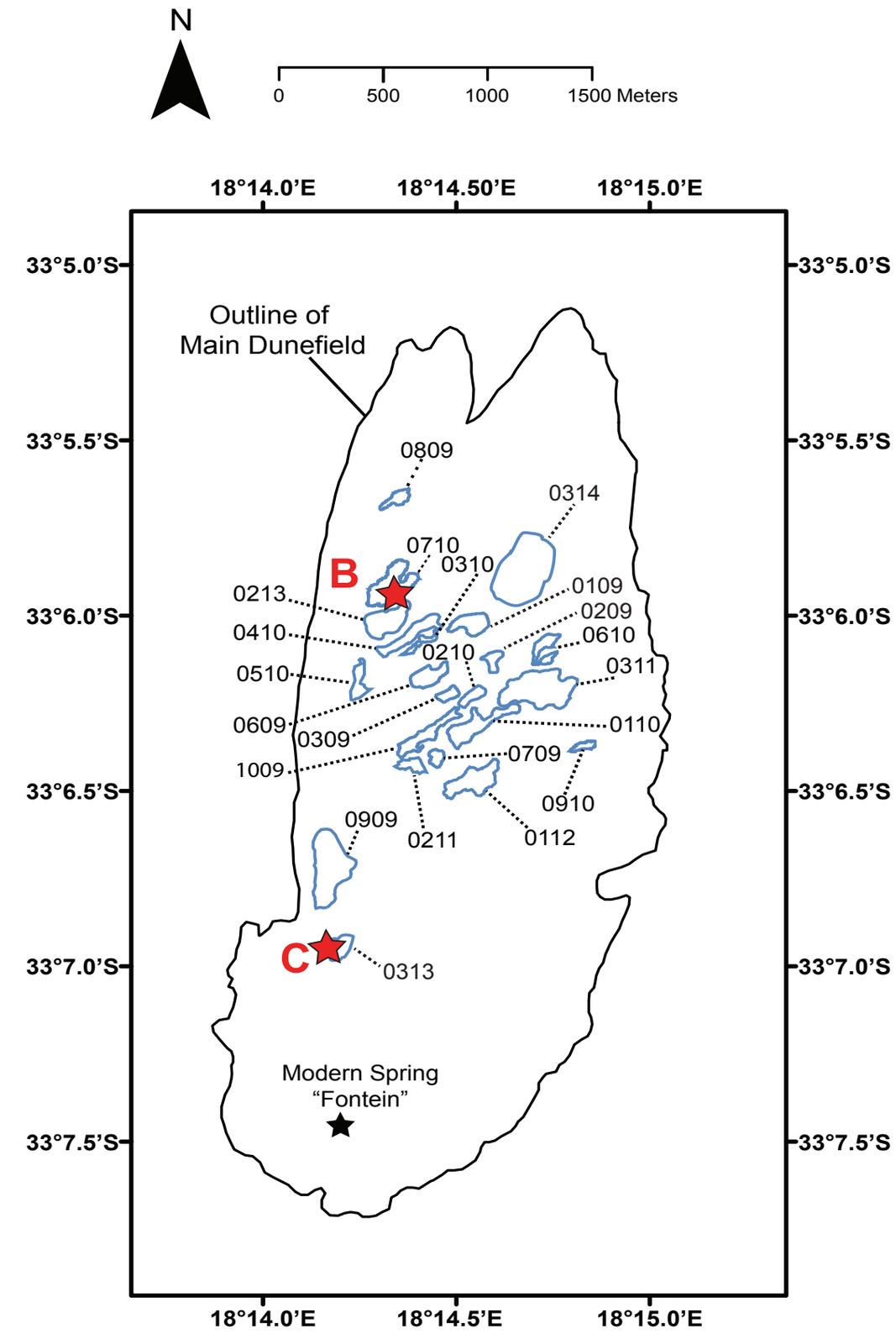


Figure 3. A) Map of EFT Collection Bays and small mammal collection strategies. B) Shovel test pit (STP) in Bay 0710; refer to Braun et al., (2013a) for further descriptions of geological context of EFT; C) 0313 excavation.



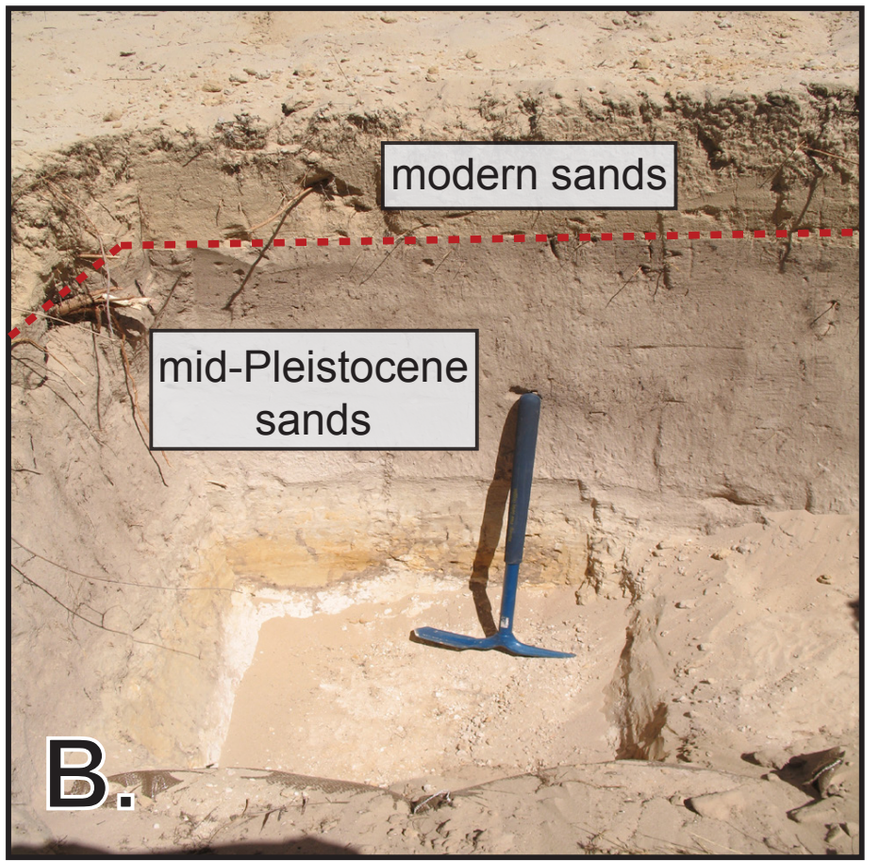


Figure 4. A) Modern *B. suillus* skull (NMNH 344067) from Mosselbaai, South Africa; B) WCRP 46140 (acid etch score = 3); C) WCRP 46138 (acid etch score = 3); D) WCRP 45684 (acid etch score = 0); E) WCRP 45642 (acid etch score = 2; note potential root etching); F) WCRP 45548 (acid etch score = 0); Arrows indicate anterior direction of specimen. Note differences in enamel surface modification in 3B, 3C, 3D, 3E, 3F. 3D, 3E and 3F could be related to soil acidity, microbes or both.

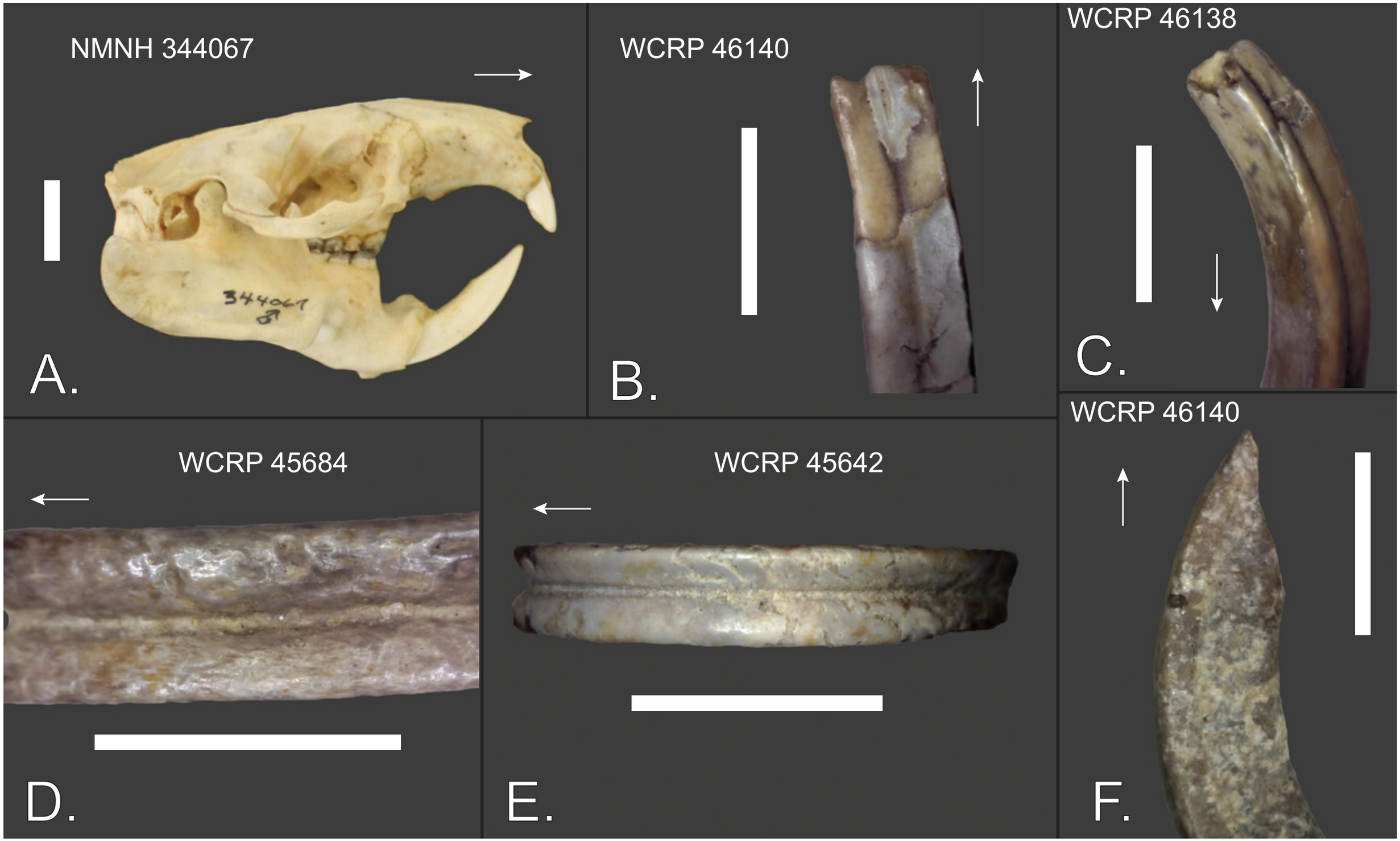


Figure 5. Altimetric analysis of the relationship between *B. suillus* fossils and large mammal fossils from EFT Collection Bays. EFT *B. suillus* fossils depicted with red triangles. EFT large mammal fossils depicted with black circles.

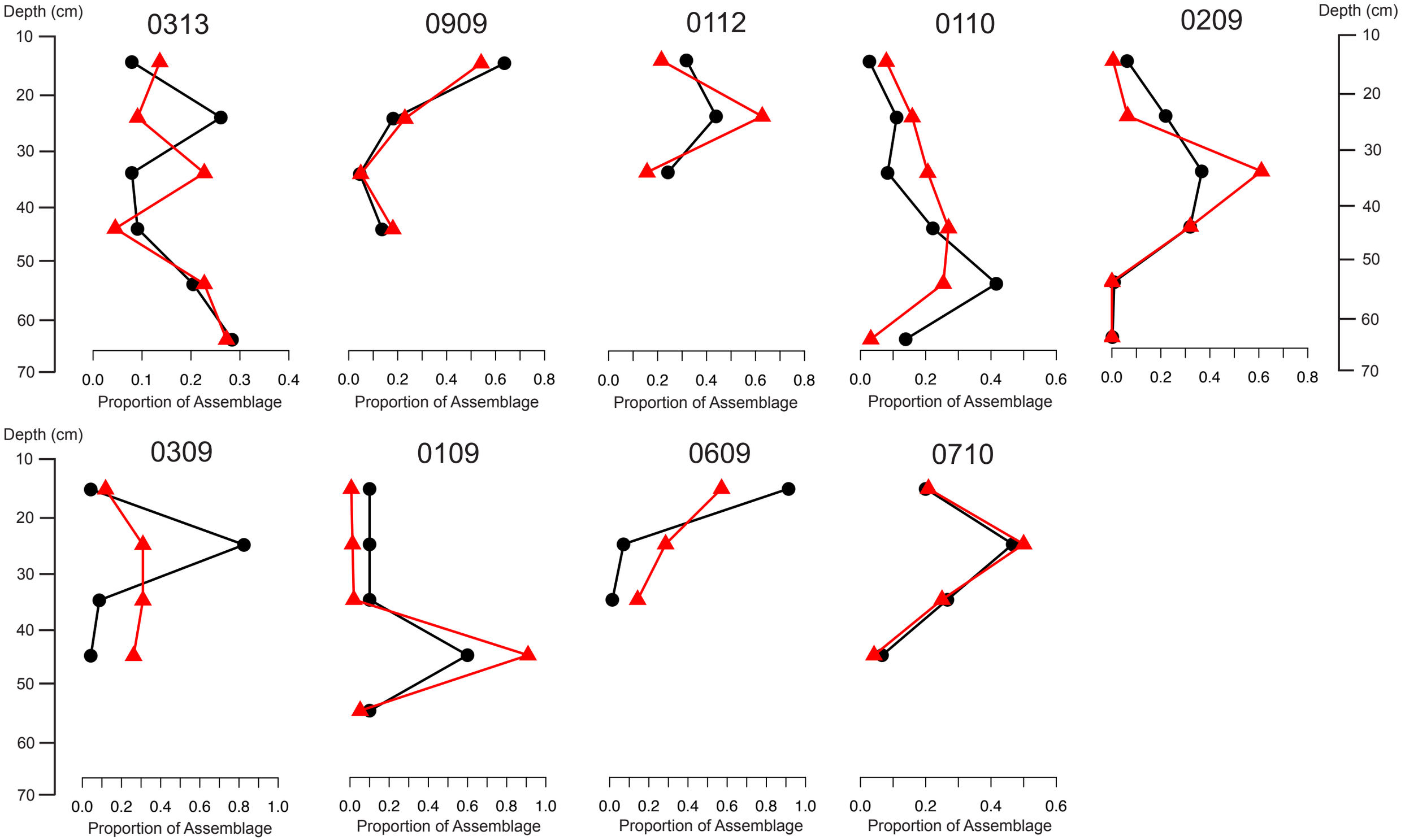
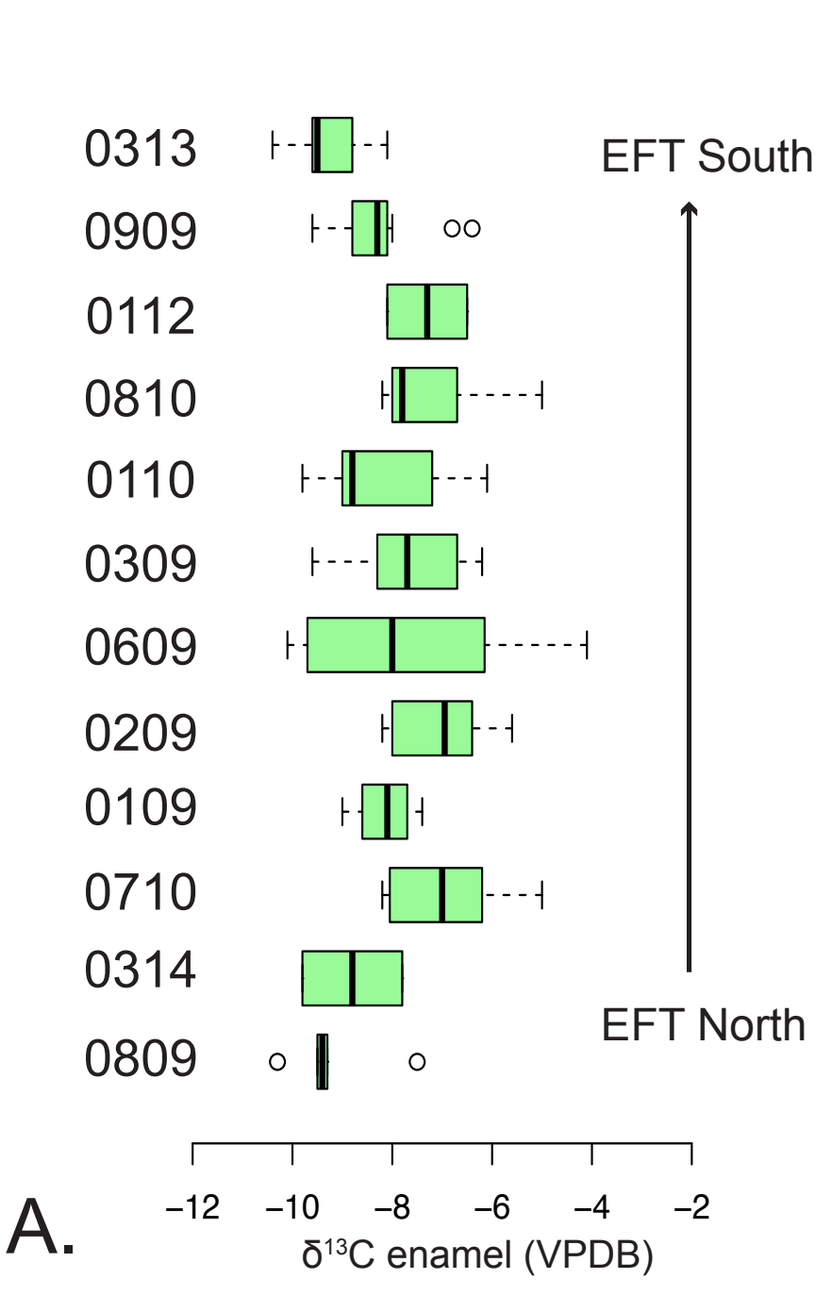
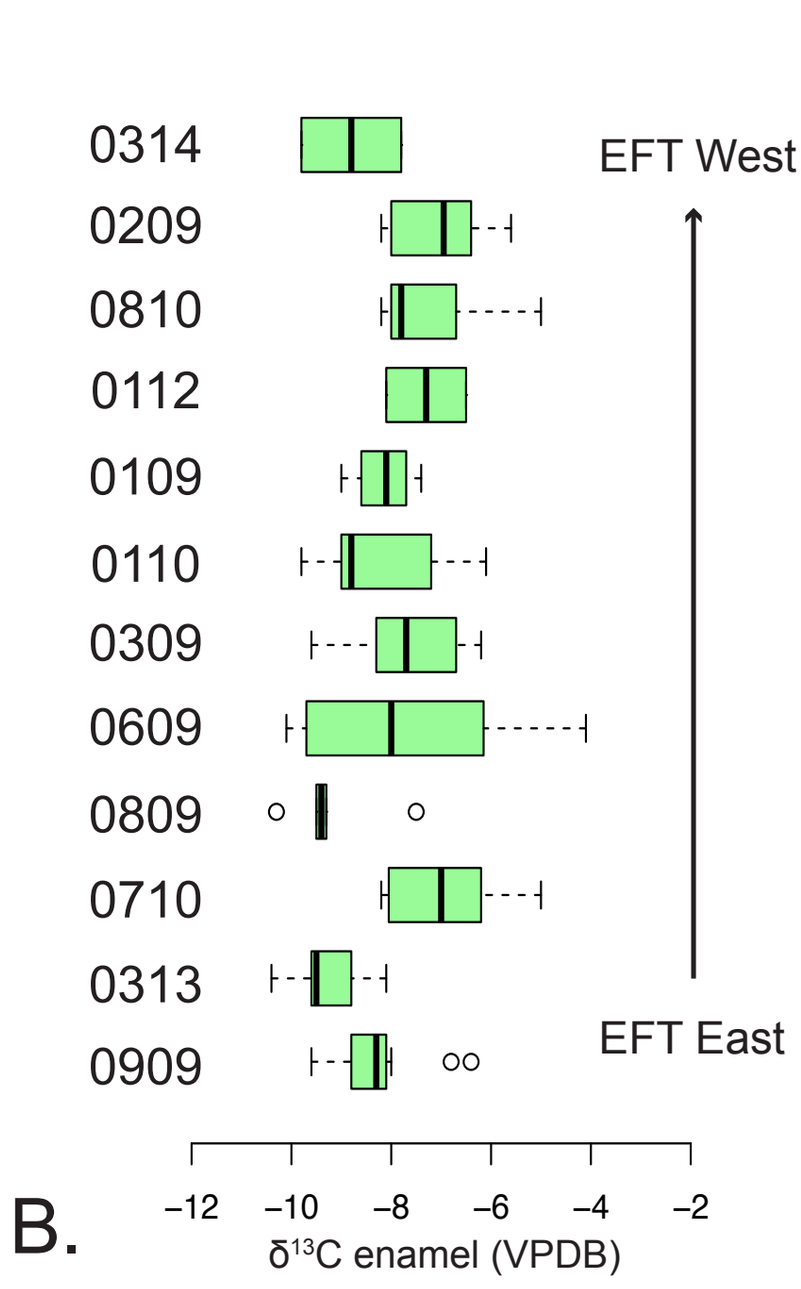
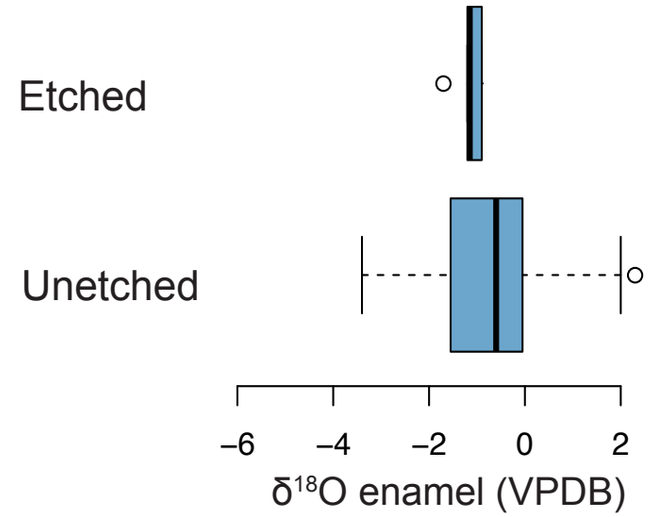


Figure 6. A) *B. suillus* $\delta^{13}C$ values arranged by Collection Bay from north to south, B) *B. suillus* $\delta^{13}C$ values arranged by collection Bay from east to west, C) Comparison of $\delta^{13}C$ and $\delta^{18}O$ ratios of etched and unetched incisors. Center line represents the sample median, box represents the 25th and 75th percentiles, whiskers represent the sample range exclusive of outliers, circles represent outliers defined at 1.5 times the interquartile range.







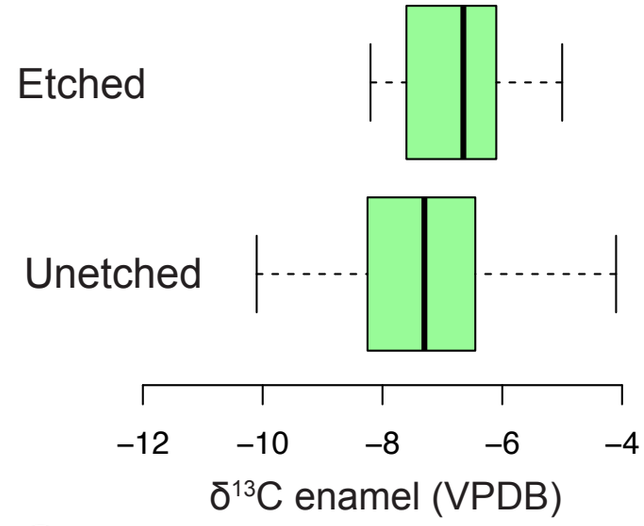


Figure 7. Comparison of EFT large herbivores and EFT *B. suillus*. 100% C_3, CAM and C_4 represent are associated with the diet of *B. suillus*, not EFT large herbivores. Darker green, hashed areas represent overlap between the two distributions. EFT large mammal grazer and browser mean values from Lehmann et al. (*In Review*).

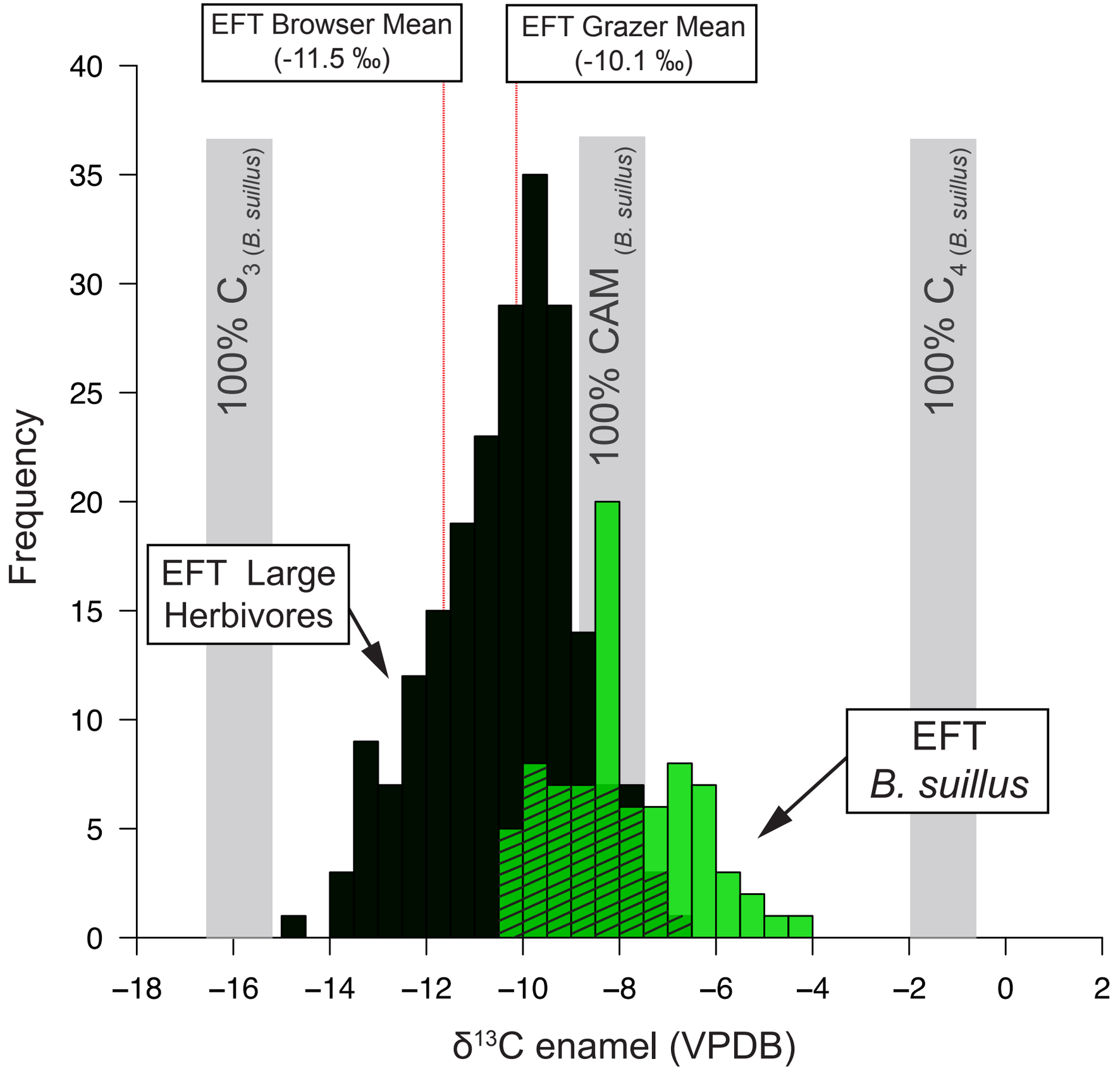


Figure 8. Relationship between Collection Bay median *B. suillus* $\delta^{13}C$ values and Bay artifact density. Line represents best fit line from median *B. suillus* $\delta^{13}C$ values – artifact density linear model.

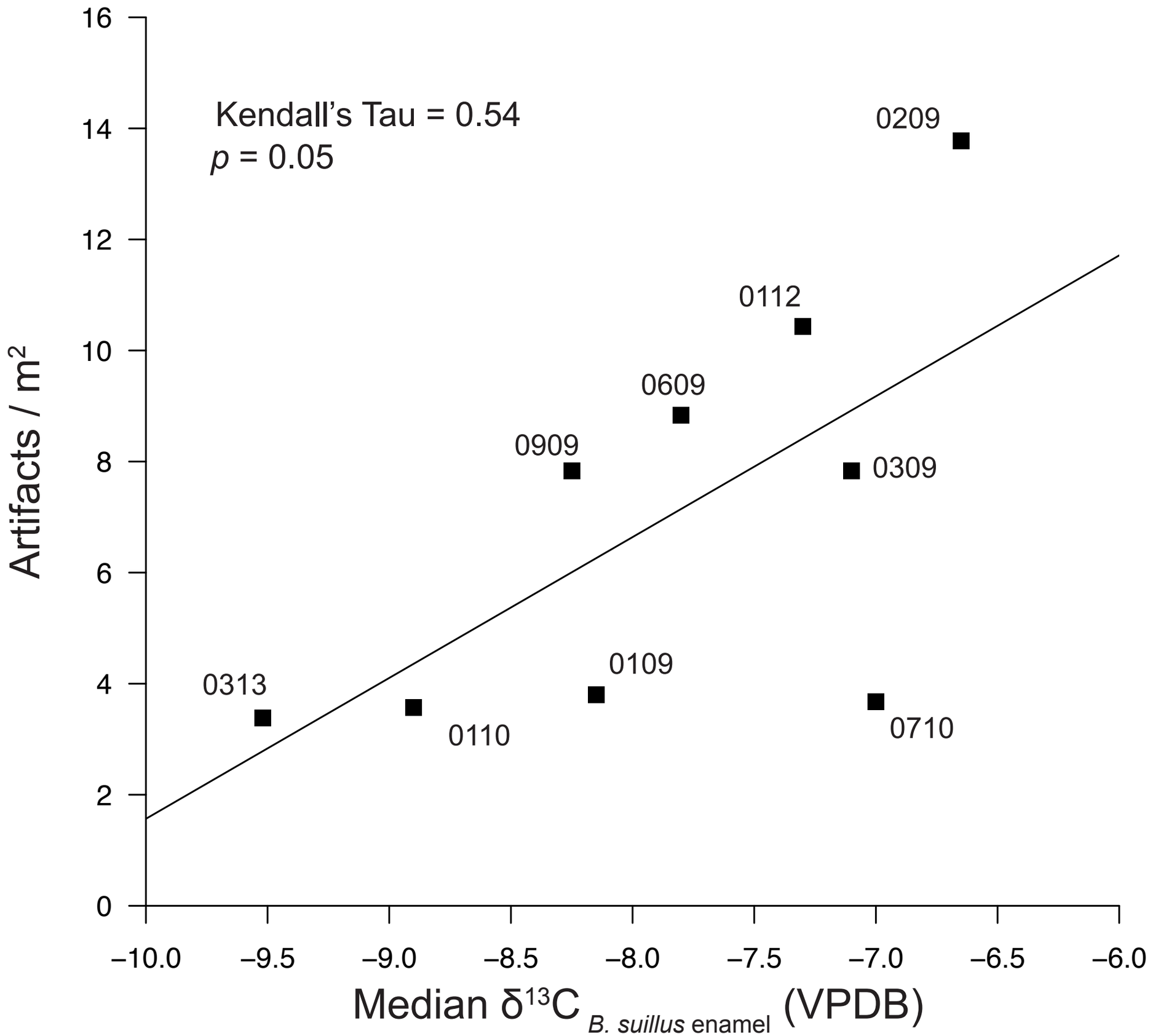


Figure S1. $\varepsilon^*_{\text{enamel-diet}}$ affect on EFT large herbivore and EFT *B. suillus* distributions. A) Small mammal $\varepsilon^*_{\text{enamel-diet}}$ (11.1‰) following Podelsak et al., 2008, B) Large mammal $\varepsilon^*_{\text{enamel-diet}}$ (14.1‰) following Cerling and Harris (1999).