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Isotopic niche modelling of the Pondaung mammal fauna (middle Eocene, Myanmar) shows microhabitat differences. Insights into paleoecology and early anthropoid primate habitats

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The late Middle Eocene Pondaung Fm. is a window to understand the environment and ecosystem dynamics of a past greenhouse world and the paleoenvironments where modern mammal clades such as anthropoid primates originated. Previous studies focused on the overall climate and vegetation of this Eocene habitat and provided first evidence for an early monsoon onset before the orogenesis of the Himalayan-Tibetan range. Here, we wanted to investigate how the mammal fauna used this habitat and which different ecological niches and microhabitats they occupied. We analyzed the carbonate fraction of dental enamel of a fossil mammal assemblage from various localities of the Pondaung Fm. in Myanmar. Bayesian niche modelling of the δ^{13}C and δ^{18}O values allowed us to quantify aspects of the ecological core niches occupied by these taxa, to calculate niche overlap and to use these data to infer directional competition potential in this mammal assemblage. Furthermore, comparison of different areas of the Pondaung Fm. revealed two different microhabitats whose distribution is consistent with existing vegetation models. Most primate taxa were found in both described environments, which gives a first indication about their ecological flexibility.

KEYWORDS

isotopic niche, Pondaung Formation, Anthracotheriidae, anthropoid primates, competition potential, Eocene, paleoecology

1. Introduction

The climate today is changing fast and towards conditions never before experienced by humans. Some geological time periods might however be important analogues for possible climate scenarios in the future. One of these epochs is the Eocene that spans from 56 to 34 Ma (million years ago). The Eocene Earth was a greenhouse world with mean annual temperatures around 5°C higher than today in the Late Eocene (Zachos et al., 2001; Pagani et al., 2005). It was a world not unlike the possible man-made greenhouse world in our future (Burke et al., 2018;

Tierney et al., 2020). Studying this time period, the paleoenvironments, and the organization of fossil mammal communities can therefore provide valuable information to better understand various scenarios of future environments on Earth. In addition, it was also the period when modern mammals started their ecological radiation (e.g., Coster et al., 2018; Ducrocq et al., 2019; Jaeger et al., 2020). Here we want to focus on one mammal community, characterize its habitat and niche partitioning and explore if and to what extent approaches from ecology such as directional competition potential and individual specialization can be applied to paleoecology.

The mammal assemblage we focus on is from the late Middle Eocene Pondaung Formation (Fm.) located in modern day Myanmar. Southeast Asia is a hotspot for understanding mammal evolution during that time, as many radiations of important clades such as early anthropoid primates (Jaeger et al., 2020) and anthracotheres that are believed to be ancestral to the extant hippopotamids (Lihoreau et al., 2015), but also ruminants, pigs and hystricognath and anomalurid rodents took place there (Marivaux et al., 2005; Beard, 2016; Coster et al., 2018). The Pondaung Fm. is one of the fossil formations that document the rich biodiversity in this important biogeographic region. In this study we report the first substantial sample of isotopic data from herbivorous mammals and we correlate it to previously studied paleoenvironmental proxies. Our research questions can be structured around three topics: paleoseasonality, microhabitat differences, and niche partitioning from which we try to infer competition potential of the Pondaung mammal fauna with a focus on the Anthracotheriidae.

It has been thought that the Tibetan-Himalayan orogenesis was a prerequisite for a strong monsoonal climate in Southeast Asia, which could therefore not have originated earlier than 25 to 22 Ma. Studies on different climatic proxies including stable isotope analysis of gastropod shells and mammal teeth from the Pondaung Fm. revealed however that a monsoon-like climate was already present in the Eocene (Licht et al., 2014c; Toumoulin et al., 2022; Huang et al., 2023). With our larger data set, covering some of the localities represented in the previous study by Licht et al. (2014c) and more, we will try to test whether the same pattern is present. Furthermore, we investigated possibilities to compare monsoon intensity. For this we are comparing the Eocene data to a specimen of modern *Bos* from the Central Myanmar Basin (Habinger et al., 2022). δ^{18}O values of the Eocene mammals as low or lower than in the modern specimen together with a sinusoidal variation pattern would be evidence for a seasonal precipitation regime similar or even more pronounced as in Myanmar today. Our goal is not only to substantiate the hypothesis of an early onset Eocene monsoon-like precipitation regime, but also to characterize the environmental conditions linked to this kind of climate in more detail.

The localities of the Pondaung Fm. represent a terrestrial paleoecosystem with several river channels. They are situated in the Central Myanmar Basin (17–21°N, 92–96°E) west of the Chindwin River and northwest of the Irrawaddy River. However, in the late Middle Eocene the Pondaung Fm. was part of the Trans-Tethyan arc and therefore located farther south close to the equator (Westerweel et al., 2019, 2020). According to paleoenvironmental reconstructions, the ancient Eocene coastline with its mangrove forests lay farther to the west of the fossil localities. The vertebrate fossil bearing area was located further inland in a deltaic plain with reconstructed environments ranging from littoral to riparian forests and open-forested seasonal wetlands to dry dipterocarp and Schima forests in the upstream areas (Licht et al., 2013, 2014a, 2015; Gentis et al., 2021). Morphological adaptations to leaping in the primate taxa suggest that the Eocene forest density was high enough to allow for such a locomotive repertoire for example in the medium sized sivaladapid *Kytchaungia takaii* (body mass 1.6–1.8 kg; Kay et al., 2004; Beard et al., 2007; Marivaux et al., 2008a,b). The elevated temperatures during the Eocene led to a northward expansion of tropical and subtropical climatic zones, where rainforests could grow (Morley, 2018). We will test if microhabitat differences between the three geographic clusters of localities—the Bahin, Pangan, and Mogaung areas (Figure 1)—can be detected. Based on their geographic distribution and the vegetation model published by Licht et al. (2015) we have formulated two hypotheses. First, as the Mogaung area is further upstream the paleoriver system we are expecting the habitat there to be more densely forested and humid, as suggested by the different modelled vegetation regimes described above. Thus, both the δ^{13}C and δ^{18}O values of the mammals from this areas should be lower than at the other two areas. Second, should we detect microhabitat differences the probability that these differences are in fact correlated with spatial factors and not differences in exact dating of the localities of the different areas rise, if the Bahin and Pangan areas are more similar to one another than to the Mogaung area, and if they exhibit higher δ^{13}C and δ^{18}O values than the mammals from Mogaung.

As described above, the paleoenvironment of the Pondaung Fm. has already been characterized using different approaches, from ecomorphology to vegetation modelling based on fossil plant remains (Licht et al., 2015). However, to our knowledge no studies on niche partitioning and habitat use of this mammal fauna have been conducted yet. Increasing our knowledge on the organization of this fossil mammals has also implications on our knowledge about the palaeoecology of the earliest anthropoid primates, which makes studying it so important. Though these primates are not directly part of the data set used in this study, they were part of this same fossil mammal assemblage occurring sympatric with them in all three areas with fossil localities (see Supplementary Table SI 4). Reconstructing the paleoecology and niche partitioning among other members of this mammal fauna forms the basis on which we can discuss the paleoecology of the anthropoid primates in more detail. With our approach we can model aspects of the ecological niche of a taxonomic group reflecting the habitat and its use as well as dietary ecology. Should we detect microhabitat differences, but have some of the fossil primates occur in more than one this indicates a certain degree of ecological flexibility in these taxonomic groups.

Many open questions remain also regarding the anthracotheres, a group widely considered to be ancestral to hippos (Lihoreau et al., 2015), which are of special interest given their abundance and diversity in the Pondaung mammal fauna and the possibility to detect an ecological transition from a fully terrestrial to a semi-aquatic lifestyle around that time. As of today, three genera are known in this fossil assemblage. The taxonomy of this clade has been discussed and revised several times (Tsubamoto et al., 2002; Lihoreau and Ducrocq, 2007; Soe, 2008). With our isotopic data, we want to characterize aspects of their ecological niches at the genus and species level to see if there are any notable differences. In addition, we will calculate the niche overlap and explore the possibility to infer directional competition potential from these calculations. To our knowledge, this approach used by ecologists (Ogloff et al., 2019) has not yet been applied to fossil mammal communities. We expect that anthracothere taxa with higher body mass

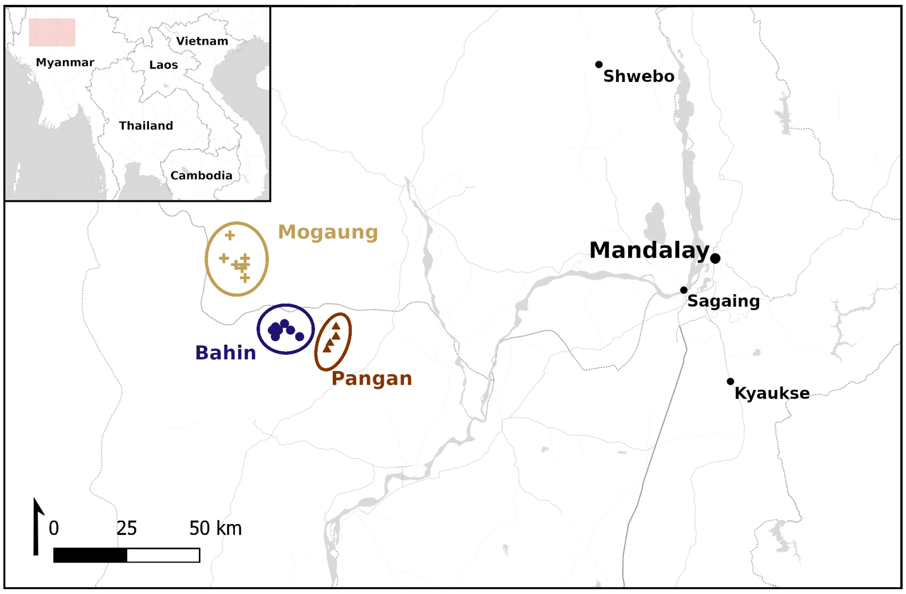

FIGURE 1
Map showing the location of the different localities of the Pondaung Fm. and their division into the three area clusters. Coordinates for all the localities from which samples were analyzed in this study are reported in Supplementary Table SI 1. The location of the detailed map is marked in the overview with a colored rectangle. Map tiles by Stamen Design, under CC BY 3.0. Data by OpenStreetMap, under ODbL.

share more of their niche space with other anthracotheres, as they can balance the higher degree of competition potential this implies with their size. For several medium to large sized anthracotheres from periods younger than the Eocene, such as *Arretotherium*, *Merycopotamus*, and *Libycosaurus* with body masses ranging from 150 to 1,000 kg, semi-aquatic lifestyle similar to extant hippos has been inferred (Orliac et al., 2013). They also displayed morphological adaptation to such a lifestyle that have often been referred to as hippo-ecomorph (Clementz et al., 2008), such as elevated orbits, external nares at the top of the snout, and massive limbs with high bone density (Lihoreau and Ducrocq, 2007). None of these morphological adaptations is present in the anthracotheres from the Pondaung Fm. We nevertheless wanted to test if their oxygen isotopic abundances already indicate semi-aquatic behavior before morphological adaptations to this lifestyle are visible. To do so we will test, if their $\delta^{18}O$ values are lower than the ones of the other taxonomic groups and if the variation in these values is reduced. Similar studies have been conducted on Eocene early whales (Thewissen et al., 2007; Cooper et al., 2016).

To answer all of these questions, we conducted stable isotope analysis on the carbonate fraction of fossil tooth enamel on the terrestrial mammal fauna from the Pondaung Fm. Due to its high content of inorganic hydroxyapatite and the fine and dense crystalline structure, enamel is very resistant to diagenetic changes. In addition, the Pondaung sediments that we analyzed are low in carbonate content, thus reducing the probability of diagenetic alteration of the original biological isotopic signal in the fossil teeth (for details see Methods section).

2. Materials and methods

2.1. The geological context

The mammal fauna that we analyzed for this study originates from the Pondaung Fm. in the Central Basin of Myanmar. During annual fieldwork campaigns of the French-Myanmar expedition, the fossils were collected from different localities that can be attributed to one of three areas—Bahin, Pangan, and Mogaung (Figure 1).

The Middle Eocene Pondaung Fm. is framed by the underlying Early Eocene Tabyin and the overlying Late Eocene Yaw Fm., both of which are marine deposits (Bender and Bannert, 1983). The Pondaung Fm. itself is up to 2 km thick (Bender and Bannert, 1983) with a succession of marine to terrestrial sediments (Stamp, 1922), but only the upper part (Upper Member) with a thickness of around 500 m (Oo et al., 2015) yielded significant amount of fossils representing a terrestrial mammal fauna. The stratigraphic positions of the different fossil localities to one another has not been studied in depth as of today. Nevertheless, the fossiliferous sediments of some localities from the Bahin area (PK1, PK2, PK3, PK4, PK5, and PK8) belong to the same traceable claystone named Ayoedawpon Taung Claystone ranging in thickness from 8 to 20 m. It is underlain directly by another widely traceable sediment, the Ayoedawpon Taung Sandstone. For two other fossil localities from the same region, the stratigraphic relationship is well constrained. The fossil outcrops at PK9 are part of the Nyaungpinle Claystone, which is stratigraphically lower than the Ayoedawpon Taung Claystone. The claystones at the PK12 locality on the other hand overlay directly the sandstones above the Ayoedawpon Taung Claystone (Maung et al., 2005; Suzuki et al., 2006). It has been dated to 40.31 ± 0.65 Ma and 40.22 ± 0.86 Ma using LA-ICP-MS, U–Pb zircons on tuffaceous sandstones from the Bahin area (PK4 and PK8; Zaw et al., 2014). This means that the Pondaung Fm. dates to around 40 Ma, which corresponds to the late Middle Eocene or Bartonian.

Its depositional environment was characterized by fluvial sediments of meandering river channels and is mostly comprised of sandstone with interspersed silt/clay bands. Fossils are mostly associated with lithofacies indicative of small fluvial or crevasse channels, swale fills and point bar deposits. Some evidence of peat layers and coal seams might indicate peat swamp formation of the inter-channel areas (Soe et al., 2002).

In their magnetostratigraphic study on a 319 m thick section of the Upper Member of the Pondaung Fm., Benammi et al. (2002) detected a single normal polarity. Although this homogenous paleomagnetism makes correlation with a specific Bartonian chron difficult, it indicates a high sedimentation rate of the floodplain (>0.3 mm yr.$^{-1}$; Licht et al., 2014b) as the maximum length of the possible Bartonian polar chron is smaller than 1 Myr (Benammi et al., 2002). This inference can be further substantiated by the results of another study on sedimentation rates in Asia (Métivier et al., 1999). Given this high sedimentation rate and the observed homogeneity of the fauna documented notably by rodents, amynodontids, anthracotheres and primates, we will consider that the Pondaung fossil remains correspond to a contemporaneous mammal fauna assemblage (Ducrocq et al., 2019). We give a detailed evaluation of sympatry of the different taxa in our sample per locality and area in Table SI 1.

2.2. The Pondaung mammal fauna

The fossil mammal fauna preserved in the Pondaung Fm. is famous for its unique and diverse primate assemblage. Two Sivaladapid adapiformes (*Kyitchaungia takaii*, and *Paukkaungia parva*), one Eosimiiforme (*Afrasia djijidae*), one Eosimiidae (*Bahinia pondaungensis*), a yet undescribed tarsid and most notably three different Amphipithecidae (*Ganlea megacanina*, *Pondaungia cotteri*, and *Myanmarpithecus yarshensis*) were found there (Marivaux et al., 2008b; Chaimanee et al., 2012; Fleagle, 2013; Jaeger et al., 2020). The phylogenetic position of the amphipithecids has been highly debated in the past century, but these primates are now firmly established as stem anthropoids by cranial, postcranial, and phylogenetic evidence (Jaeger et al., 2020). The high diversity in species underlines the importance of the Pondaung Fm. and Southeast Asia as the biogeographic region of early diversification and origin of this clade. This fact, together with the co-occurrence of three different stem anthropoid species together with eosimiids, which are basal anthropoids, and other primate taxa raises the interest in the paleoenvironment in which they all existed.

The diet of the Pondaung primates has been inferred from both dental morphology as well as dental microwear analysis. *Pondaungia* was likely predominantly frugivorous and also included some hard items in its diet. *Myanmarpithecus* subsisted on a mix of fruit and leaves (Kay et al., 2004; Ramdarshan et al., 2010). Although the unique tooth morphology of *Ganlea* complicates the dietary interpretations, this amphipithecid likely also ingested a mixture of leaves and fruit, but also engaged in seed predation (Beard et al., 2009; Jaeger et al., 2020). For the smaller primates *Bahinia* and *Paukkaungia* an insectivorous diet has been suggested (Kay et al., 2004; Ramdarshan et al., 2010). Only few primate postcranial remains have been found from the Pondaung Fm. Both *Pondaungia* and *Ganlea* have been described as active arboreal quadrupeds (Marivaux et al., 2003, 2010; Jaeger et al., 2020). For the Sivaladapidae a generalized locomotor profile as an arboreal quadruped has been suggested as well (Kay et al., 2004; Beard et al., 2007), with some evidence for leaping capabilities due to hip and pelvis morphology in *K. takaii* (Beard et al., 2007; Marivaux et al., 2008a,b). Given the small size of the teeth and their importance and rarity it was not possible to sample any of the Eocene anthropoid primates for stable isotope analysis.

Four large herbivore groups make up the majority of our sample of the Pondaung mammal fauna. The numbers in brackets correspond to the number of specimens sampled. There are three groups of perissodactyls, Brontotheriidae ($n = 24$), Amynodontidae ($n = 16$), Rhinocerotoidea indet. ($n = 27$), and the artiodactyl Anthracotheriidae ($n = 56$). Of these tooth specimens, 38 were sampled serially (9 Brontotheriidae, 9 Amynodontidae, 8 Rhinocerotoidea indet., and 12 Anthracotheriidae), hence providing a time series across the mineralization time of the fossil enamel allowing the investigation of seasonal variations. Brontotheriidae are described as being obligate browsers due to their brachydont teeth with bunoselenodont morphology and therefore preferring forest to woodland habitats in warm temperate to subtropical environments (Mader, 1998). Some of the brontotherids in our data set have been identified as *Bunobrontops* a more primitive genus in comparison to two other known genera, *Metatelmatherium* and *Sivatitanops*, from the Pondaung Fm. (Holroyd and Ciochon, 2000). Most of the Rhinocerotoidea are probably Amynodontidae, the most abundant family in the Pondaung Fm., but the fragmentary nature of the sampled fossils did not allow for an assignment of this taxonomic label with enough certainty. Previous work on fossil Rhinocerotoidea from Late Eocene sites in Vietnam characterized them as forest dwellers with their brachydont teeth and as being obligate browsers as well (Böhme et al., 2013). These brief descriptions of two of the main herbivorous taxonomic groups at the Pondaung Fm. reveal once more the lack of systematic studies especially on the Perissodactyl fauna. In addition, the tapiromorph *Bahinolophus* ($n = 2$), Eomoropidae ($n = 1$), and Ruminantia ($n = 2$) are also part of our data set. In four cases two teeth were sampled per individual (*Siamotherium* PNG-20 M2/M3 and PNG-141 M2/M2, *Anthracokeryx tenuis* PNG-22/23, *Anthracotherium crassum* PNG-56/57, and Amynodontidae PNG-92/93). In general, the ungulate fauna in the Pondaung mammal fauna is considered to be representative of the original living community, while a sampling bias is likely in the case of rodents and other small mammals including primates. This is due to the fieldwork method applied by the different teams of researchers, which mainly conduct surface prospecting in the area (Tsubamoto et al., 2005).

The Pondaung Fm. has also yielded some creodont (Egi and Tsubamoto, 2000; de Bonis et al., 2018), fish, reptile (crocodilian, lizard, and turtle; Hutchison et al., 2004; Tsubamoto et al., 2006a; Head et al., 2013) and bird fossils (Tsubamoto et al., 2006b). However, no extensive systematic studies on this material exist as of now and it has therefore not been included in our data set for isotopic analysis.

2.3. The anthracotheres

In the Pondaung Fm., we find a high diversity of anthracothere taxa. This comes as no surprise, as this taxonomic group likely originated in Southeast Asia and experienced a radiation there in the late Middle Eocene. Later on, anthracotheres spread from Asia to Europe, Africa, and North America. Three different anthracothere genera are known from the Pondaung Fm.—*Anthracotherium*, *Anthracokeryx*, and *Siamotherium*. In contrast to the perissodactyls from the Pondaung mammal fauna that were strictly herbivorous according to their tooth morphology, anthracotheres were more opportunistic feeders. They likely had a much more diversified diet that included leaves, fruits, roots, and invertebrates.

Anthracotherium ($n = 20$) was a medium to large sized anthracothere and the largest of the three genera found at the Pondaung Fm. It has bunodont teeth suitable for crushing tougher food like roots or even scavenge carcasses from time to time. Hence, its cranio-dental morphology indicates a more generalist diet not unlike the one of extant pigs (Ducrocq, 1999). Therefore, we hypothesize that it occupied more open forests than the other two and probably lived closer to the river system, meaning that it was more water dependent than the other anthracothere genera known from the Pondaung Fm. Two species could be identified in our sample, the smaller *A. crassum* ($n = 5$) and the larger *A. pangan* ($n = 11$).

The second genus, *Anthracokeryx* ($n = 13$) with the two species, the larger *Anthracokeryx birmanicum* ($n = 4$) and the smaller *A. tenuis* ($n = 4$), represents a more typical forest dweller with bunoselenodont teeth. These are typical for a more specialized herbivorous foraging ecology (Ducrocq, 1999). It has a body mass, of about 20–25 kg (Lihoreau and Ducrocq, 2007). This and its cranio-dental morphology are consistent with dwelling in denser forests and having a more specialized folivorous diet.

Siamotherium ($n = 4$) is the smallest and most primitive of the three genera with an estimated body mass of 7.5 kg for *S. pondaungensis*. It was a small, slender animal with a short snout showing first signs of selenodonty on its molars (Ducrocq et al., 2001; Soe et al., 2017; Ducrocq et al., 2021). Its subsistence strategy has been described as more omnivorous including occasional scavenging, and it is thought to have lived in open forested areas (Soe et al., 2017). For this study, we could sample four teeth from two individuals.

2.4. Sample preparation and analysis

We sampled the specimens during a museum visit to the National Museum in Nay Pyi Taw in February 2020 and the fieldwork campaign in the following weeks. The specimens were cleaned from dust and sediment using ethanol and the outermost layer of fossil enamel was removed on the sampling site as these would be most susceptible to diagenetic alteration. During sampling 6–12 mg of fossil enamel powder were drilled using a portable diamond coated micro drill station. Dentine samples from these specimens were also sampled using the same sampling methodology. Sediment attached to the specimens was also collected in some instances, depending on availability. Both of these tissue types were used to assess diagenesis (see SI). They are reported in Supplementary Table SI 3.

The pretreatment and analysis in the IRMS (isotopic ratio mass spectrometer) was conducted in the laboratories of the Biogeology working group (Department of Geosciences) at the University of Tübingen using a modified Koch method (Bocherens et al., 1994; Koch et al., 1997; Wright and Schwarcz, 1999). We added 1.35 ml of NaOCl at a concentration of 2.5% to each of the powdered samples and left it react for 24 h to remove organic matter that might be present in the sample. Then the liquid was removed and after rinsing the samples three times with distilled water, 1.35 ml of 1 M acetic acid buffer solution (CH_3COOH) was added to the enamel and dentine samples and let to react with the samples for 24 h. Given difference in crystalline structure between enamel and other exogenous sources of carbonates, the latter ones were removed by this step. The samples were once again rinsed three times with distilled water and then dried at 35°C for 72 h. With each set of samples two internal standards of elephant and hippo enamel were treated following the same protocol. Prior to analysis one internal (LM = Laaser Marmor) and two international (IAEA-603, NBS-18) pure carbonate standards were added to the data set after every 15 samples. These were not subjected to any pretreatment prior to analysis.

For the analysis with the Elementar IsoPrime 100 IRMS 2.5–3 mg of enamel or 0.1 mg of pure carbonate were reacted with 99% phosphoric acid (H_3PO_4) at 70°C for 4 h. The isotopic ratios of the resulting CO_2 gas were measured four times for each sample over a time span of 15 min. This allowed us to monitor measurement precision by calculating the mean and standard deviation of these repeated measurements for each sample (Szpak et al., 2017). In addition, measurement uncertainty was assessed using the standards. It is reported for each sample in Supplementary Table SI 2. Isotopic ratios are reported using the δ-notation (in per mill). The calculation is based on formula (1) (Coplen, 2011; Bond and Hobson, 2012) where j marks the heavier and i the lighter isotope.

$$\delta^{j/i}X = \frac{\left({}^{j}X/{}^{i}X\right)_{sample}}{\left({}^{j}X/{}^{i}X\right)_{standard}} - 1 \qquad (1)$$

With the internal enamel standards the isotopic ratios were calibrated relative to VPDB (Vienna Pee Dee Belemnite). Oxygen isotopic ratios have been subsequently converted to $\delta^{18}O_{VSMOW}$ values (Vienna Mean Ocean Water) using the formula (2) by (Coplen, 1988).

$$\delta^{18}O_{VSMOW} = \left(1.03091 \times \delta^{18}O_{VPDB} + 30.91\right) \qquad (2)$$

In Supplementary Tables SI 2, SI 3 we also report the $CaCO_3$ content of each sample. It was calculated with the Ion Vantage software based on an estimated elemental composition with sample weight, peak area and the internal LM standard as variables. The resulting $CaCO_3$ values are subsequently scaled up until one of the international pure carbonate standards reaches 100%. $CaCO_3$ content of sediment samples from various Pondaung localities was too low when we used the regular amount of 0.1 mg of powdered sediment sample in the IRMS. Even when we raised the sample size to 2.5–3 mg of powdered sample, $CaCO_3$ content remained very low for the Pondaung sediments (Supplementary Table SI 3). We discuss the results of the sediment and dentine samples in the Supplementary Information to evaluate the risk of diagenetic alteration of the original biogenic isotopic signal in our data set.

2.5. Data correction and statistical analysis

Prior to data analysis and isotopic niche modelling two types of data corrections were applied to account for differences in enrichment of $\delta^{13}C$ values between diet and bioapatite as well as changing $\delta^{13}C$ baselines, due to shifts of the isotopic composition of CO_2 in the atmosphere. All the data before and after the corrections were applied as well as the specific enrichment factor used to calculate $\delta^{13}C_{diet}$ values are reported in Table 1.

In the past one uniform enrichment factor of 14‰ for the carbon isotope ratio from diet to apatite in dental enamel has been used for all medium to large bodied herbivores (Cerling and Harris, 1999). Recent studies however showed, that many different factors such as body mass and digestive physiology influence this enrichment factor (Passey et al., 2005; Tejada-Lara et al., 2018). Conducting an experimental study to establish a specific ε^* for a species is only possible for extant animals. For our study we therefore apply the regression formula (3) proposed by Tejada-Lara et al. (2018) to account for differences of ε^* due to variations in body mass. This is the conservative formula, which is not specific to foregut or hindgut fermenters.

$$\varepsilon^* = e^{\left[2.4+0.034(\mathrm{BM})\right]}. \tag{3}$$

Here, BM stands for the log transformed (ln) body mass in kg. The resulting enrichment factor is in per mill (‰), which can then be applied to the data prior to isotopic modelling (Table 1) to calculate $\delta^{13}C_{diet}$ values (4).

$$\delta^{13}\mathrm{C}_{\mathrm{diet}} = \delta^{13}\mathrm{C}_{\mathrm{apatite}} + \varepsilon^*. \tag{4}$$

Instead of correcting the individual $\delta^{13}C$ values for changes in $\delta^{13}C_{CO2}$ of the atmosphere, which is the pool from which plants extract the carbon in their tissue during photosynthesis, we chose to apply the corrections to the thresholds used for the interpretation of vegetation type and density. Post-1,930 the $\delta^{13}C_{CO2}$ values were −8‰ (Zachos et al., 2001; Cerling et al., 2010 but see Keeling et al., 2005 for fluctuations within this time period). Tipple et al. (2010) reconstructed Cenozoic $\delta^{13}C_{CO2}$ values based on stable isotope analysis of benthic foraminifera. For the middle Eocene at 40 Ma their model suggest higher $\delta^{13}C_{CO2}$ values than today with an estimate of −5.5‰ (ranging from −6‰ to −5.2‰ at a confidence interval of 90%). Thus, we corrected the modern thresholds by +2.5‰ before interpreting the Eocene data.

Following the Hutchinsonian niche concept (Hutchinson, 1957, 1978), we calculated core ecological niches for each taxonomic group using the R package SIBER (version 2.1.6; Jackson et al., 2011). For this study, we quantify niches using standard ellipse area corrected for small sample sizes (SEA_C). They correspond to a confidence interval (CI) of 40%. As this modelling approach is based on a maximum likelihood estimation in a Bayesian framework, the limiting effect of small sample sizes on statistical power of our analysis is counteracted to a certain extent. Should the sample size of a taxonomic group be below five individuals we mention it explicitly during the interpretation of the results.

For the evaluation of niche packing and directional competition potential, we calculated three metrics to quantify niche overlap between two taxonomic groups. These are the percentage of the total niche space of the two taxa that is shared between them (% overlap), which is calculated with formula (5; Ogloff et al., 2019), the percentage of niche area of taxon A (A_A) that overlaps the niche space of taxon B (A_B), and vice versa. The latter two are reported as A_A–A_B and A_B–A_A, respectively. A_O which is the area shared between taxon A and taxon B was acquired by using the maxLikOverlap() function of the SIBER package. A_A and A_B are calculated using A_O and the unitary method.

TABLE 1 Summary of the body mass (BM) estimates and the modelled isotopic enrichment factor based on formula (3).

Taxonomy	BM (kg)	ε* (‰) Tejada-Lara et al. (2018)	Reference for BM estimation
Anthracotheriidae		−12.5	
Anthracotherium		−13.1	
Anthracotherium pangan	237	−13.3	Tsubamoto et al. (2005)
Anthracotherium crassum	131	−13.0	Tsubamoto et al. (2005)
Anthracokeryx		−12.3	
Anthracokeryx birmanicum	59.4	−12.7	Tsubamoto et al. (2005)
Anthracokeryx tenuis	16.1	−12.1	Tsubamoto et al. (2005)
Anthracokeryx (lower limit)	20	−12.2	Lihoreau and Ducrocq (2007)
Anthracokeryx (upper limit)	25	−12.3	Lihoreau and Ducrocq (2007)
Siamotherium pondaungensis	7.5	−11.8	Ducrocq et al. (2021)
Rhinocerotoidea		−13.6	
Amynodontidae indet.	154	−13.1	Tsubamoto et al. (2005)
Paramynodon		−13.8	
Paramynodon cotteri	1,010	−13.9	Tsubamoto et al. (2005)
Paramynodon birmanicus	441	−13.6	Tsubamoto et al. (2005)
Brontotheriidae		−14.1	
Sivatitanops birmanicus	5,110	−14.7	Tsubamoto et al. (2005)
Sivatitanops cotteri	2,080	−14.3	Tsubamoto et al. (2005)
Bunobrontops sp.	512	−13.6	Tsubamoto et al. (2005)
Bunobrontops savagei	987	−13.9	Tsubamoto et al. (2005)
Ruminantia		−12.2	
Artiodactyla indet	9.47	−11.9	Tsubamoto et al. (2005)
Indolophus guptai	20.7	−12.2	Tsubamoto et al. (2005)
Bahinolophus birmanicus	51.6	−12.6	Tsubamoto et al. (2005)
Eomoropidae indet.	18.4	−12.2	Tsubamoto et al. (2005)
Eomoropus pawnyunti	15.2	−12.1	Tsubamoto et al. (2005)

For specimen where a taxonomic identification to species level was not possible, the mean modelled enrichment factor the highest taxonomic resolution possible was applied. In this table, whenever no body mass estimate is given, the enrichment factor corresponds to the mean value of the taxonomic groups marked by color. The specific value for the calculation of the $\delta^{13}C$ value of each specimen is reported with the calibrated data before corrections in Supplementary Table SI 2.

$$\%\mathrm{overlap} = \frac{A_O}{A_A + A_B - A_O} \times 100 \tag{5}$$

Based on the modelled ecological niches we also calculated the relative individual niche (RINI; Sheppard et al., 2018) for the individuals from which serial samples were taken. RINI is a metric that relates the individual niche area to the population niche area. Here, it expresses the proportion the SEA_Cs (CI = 40%) of an individual that is shared with the union of all the SEA_Cs of the serially sampled individuals from a taxonomic group. For this we used the siberKapow() function that is part of the SIBER package. Code examples can be found in the explanatory vignettes at the SIBER Github repository.

Given the small sample sizes we are working with and the fact that normal distribution of our data cannot be attested in all cases non-parametric Wilcox rank sum tests are used to test for statistically significant differences in this study. To screen for relationships between δ^{13}C and δ^{18}O values in the specimen where intra-individual serial samples were taken, we performed Spearman correlation analyses. Habinger et al. (2022) identified one statistical outlier in the modern *Bos* data we also use in our study. This outlier was not included in the statistical analysis, but is shown in the plots. Statistical significance is ascribed to test results where $p = <0.05$. In cases where several statistical tests were run on the same data set, value of ps have been adjusted with the Bonferroni correction, a conservative method to correct for multiple comparisons (Bonferroni, 1936). All statistical tests and models were run in R version 4.1.2.

3. Results

A comparison of the δ^{18}O values of the modern bovid from the Central Basin of Myanmar and the fossil mammals from the Pondaung Fm. showed a significant difference ($W = 0$, value of $p < 0.001$), with the Eocene δ^{18}O values being lower. Sinusoidal patterns were present in both the modern and the fossil specimen. Two of the 38 specimens that were sampled serially are plotted together with the modern *Bos* in Figure 2. Figures of all the serially sampled individuals are provided in the Supplementary Information. We also tested if there was a correlation between the δ^{13}C and δ^{18}O values, which would indicate a consistent influence of seasonal precipitation on the plants consumed. We found no constant relationship of these values across all the mammal data (rho = 0.10, $S = 2{,}366{,}301$, $p = 0.106$). However, when we sorted the specimen based on taxonomy (family level), we found significant positive correlation in Anthracotheriidae (rho = 0.56, $S = 9{,}147.2$, $p = 2.28\text{e-}05$) and Amynodontidae (rho = −0.37, $S = 125{,}705$, $p = <0.001$) as well as significant negative correlation in Rhinocerotoidea (rho = 0.33, $S = 18{,}683$, $p = 0.015$). Only in the Brontotheriidae no statistically significant correlation was present (rho = 0.1923064, $S = 35{,}280$, $p = 0.128$). The negative correlation in the modern *Bos* also was not statistically significant (rho = −0.34, $S = 1{,}299$, $p = 0.170$).

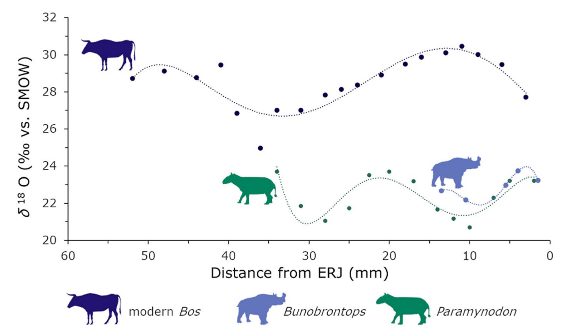

FIGURE 2
Visualization of some exemplary serially sampled specimen, the modern bovid and two of the Eocene specimen from the Pondaung Fm. (*Bunobrontops* PNG-47, *Paramynodon* PNG-119), illustrating different seasonal precipitation regimes. The distance from the ERJ (enamel root junction) on the x-axis has been inverted. This way it represents the values in an intuitive temporal sequence from the oldest ones to the left to the youngest ones to the right. The statistical outlier (lowest δ^{18}O value) in the modern *Bos* is included in this figure, but has been excluded from the statistical analysis. Silhouettes *via* Phylopic under CC 3.0 license (modern *Bos* by T. Michael Keesey, *Bunobrontops* and *Paramynodon* by Zimices).

The different localities where the fossil specimens analyzed in this study have been found can be separated into three areas. Therefore, we wanted to test if the isotopic ratios indicate a difference in environment between them. Visual inspection of the δ^{13}C and δ^{18}O values per area (Figure 3) showed some inter-area differences. The comparison of δ^{13}C and δ^{18}O values from the Bahin and Pangan localities using Wilcox rank sum tests showed no significant difference ($p = 1$ in both cases). Hence, these two areas will be grouped together for the ecological niche modelling. We then conducted a Wilcox rank sum test, to see if the δ^{13}C and δ^{18}O values were significantly different in the Mogaung area than in the Bahin and Pangan ones. All of these test results showed significant differences (Mogaung—Bahin C: $p = 0.001$, O: $p = 0.001$; Mogaung—Pangan C: $p = 0.003$, O: $p = 0.110$). Hence, we modelled the ecological niches separately for the mammals from the Mogaung localities.

The Bahin and Pangan areas (δ^{13}C: −27.2 to −20.7‰; δ^{18}O: 26.2 to 19.8‰) do not only have significantly higher δ^{13}C and δ^{18}O values, the variation of these data is also smaller than in the Mogaung area (δ^{13}C: −29.2 to −21.2‰; δ^{18}O: 25.9 to 18.1‰). Bulk and averaged serial sampling are visualized in Figure 4. Summary statistics for the mammal communities from the Bahin/Pangan and Mogaung area are reported in Table 2 and results of the niche overlap calculations in Table 3. The median % overlap of the Bahin/Pangan area is higher (17.8%) than in the Mogaung area (16.3%). This difference is not statistically significant ($W = 9$, value of $p = 0.786$). The median SEA_C is almost identical in both areas with 3.6 in Bahin/Pangan and 3.5 in Mogaung.

Additionally, we calculated the RINI for the individuals that were sampled serially. A first visual inspection of the patterns between taxonomic groups shows that in Brontotheriidae, as well as the Amynodontidae and Rhinocerotoidea most individuals cluster closely together except for only two or three (Figure 5). In the Anthracotheriidae the individual niches plot more continuously without an apparent split in discrete clusters. It also looks as if the modelled ecological niches of the Anthracotheriidae are slightly bigger than the ones of the other taxonomic groups. This is confirmed when we look at the different median SEA_Cs (Table 4). There we also see that they also have the highest median RINI of all the taxonomic groups. However, these differences are not significant (SEA_C: $W = 162$, value of $p = 0.863$; RINI: $W = 155$, value of $p = 0.280$).

4. Discussion

4.1. Paleoseasonality

The δ^{18}O values including the minimum values, which represent the seasonal precipitation maxima in tropical environments (Dansgaard, 1964; Sun et al., 2021), of the modern bovid are higher than the Eocene (Figure 2) ones even though the temperatures nowadays are around 5°C lower than they were back then. The temperature effect leads to higher δ^{18}O values under warmer

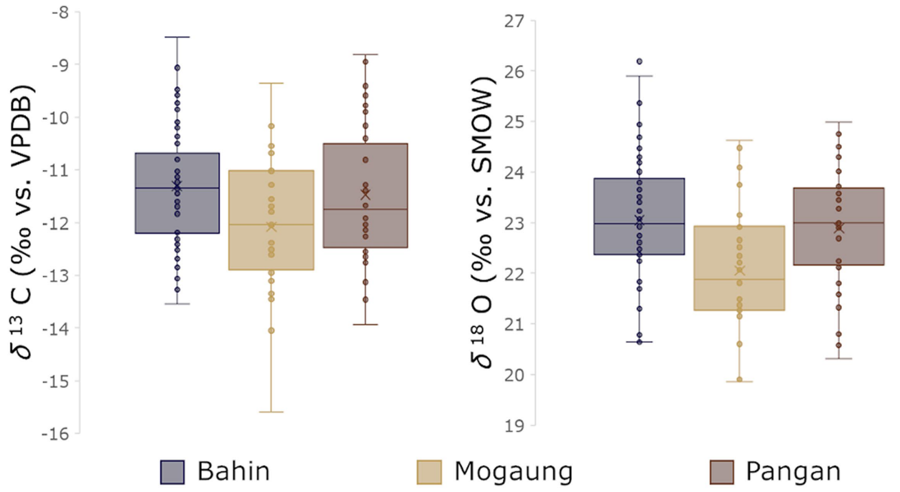

FIGURE 3
Box plots of the compiled $\delta^{13}C$ (left) and $\delta^{18}O$ (right) values per area. The Mogaung values are lower for both isotopes which is consistent with a difference in microhabitats.

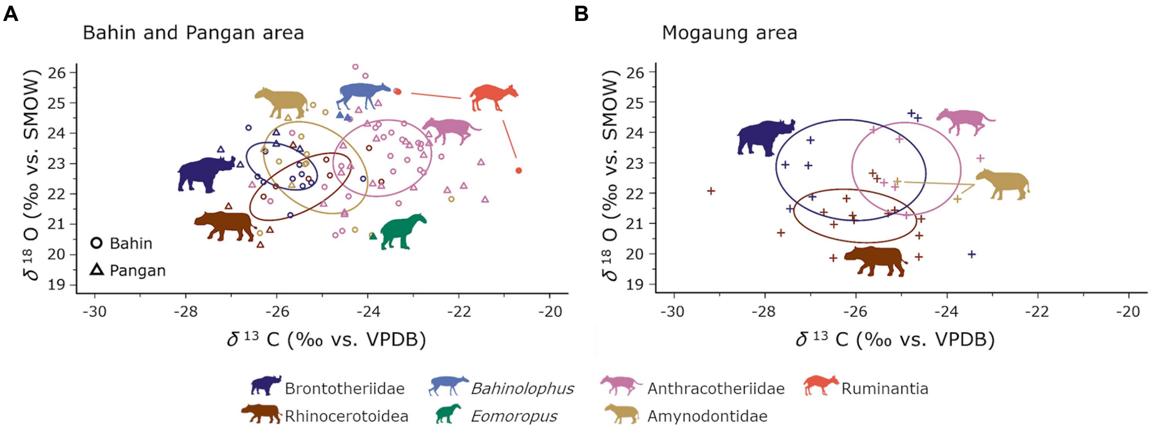

FIGURE 4
Ecological niche modelling of the Bahin/Pangan **(A)** and Mogaung **(B)** mammal communities based on all bulk and averaged serially sampled specimen. Ellipses represent the modelled core ecological niches. Silhouettes are from Phylopic under CC BY 3.0 license by Zimices.

conditions (Dansgaard, 1964). However, the pattern in the comparison of the modern bovid with the Eocene mammals is reversed. This would be consistent with a generally wetter, more humid climate in the Eocene than in Myanmar today. Consistently lower minimum $\delta^{18}O$ might even indicate an increased monsoon intensity in the Eocene, although they could have also been influenced by the possible closer paleogeographic proximity of the fossil localities to the coast at 40 Ma (Westerweel et al., 2019, 2020).

We screened for a correlation between the $\delta^{13}C$ and $\delta^{18}O$ values of the serially sampled specimen; as such a relationship would be consistent with an influence of seasonality on variation in the diet (e.g., the type of plant or plant part ingested) or habitat. We do see that there is a statistically significant correlation between seasonal precipitation and diet/habitat in the Anthracotheriidae, Amynodontidae, and Rhinocerotoidea as opposed to the Brontotheriidae. This relation however is not uniform across the taxonomic groups. This pattern is consistent with an interpretation of different strategies of the taxonomic groups to react to seasonal habitat changes such as for example adapting their subsistence strategy or migration. As there is no correlation of the $\delta^{13}C$ or $\delta^{18}O$ values diagenesis is likely not the cause for these correlations (see discussion in the Supplementary Information). The correlation in Anthracotheriidae and Amynodontidae is positive, whereas it is negative in Rhinocerotoidea. This difference between Amynodontidae and Rhinocerotoidea is surprising, since as stated earlier, most specimens which are classified as Rhinocerotoidea are likely amynodonts as no other genus from this superfamily has been described yet. Of course, this difference could be introduced by a sampling bias. If not, it could indicate that either there are two groups of amynodonts that have different ecological strategies to cope with seasonality or that these different ecological strategies also coincide with a taxonomic distinction on a generic level that has not been described as of yet. As there are no experimental studies that focus on this relationship, we cannot precisely characterize the difference

TABLE 2 Summary statistics from the isotope data used for ecological niche modelling (bulk and averaged intra individual serial samples).

Taxonomy	$n°$	$\delta\ ^{13}C_{diet}$ (‰ VPDB)		$\delta\ ^{18}O$ (‰ VSMOW)		TA (‰^{2})	SEA$_C$ (‰^{2})
		Mean	SD	Mean	SD		
Bahin/Pangan							
Brontotheriidae	16	−25.9	0.7	22.9	0.7	4.4	1.7
Anthracotheriidae	50 (46)	−23.7	1.1	23.2	1.2	16.6	4.2
Anthracotherium	19 (18)	−23.4	0.8	22.9	0.9	5.7	2.2
A. crassum	5 (4)	−23.3	0.5	23.6	0.6	0.6	0.6
A. pangan	11	−23.6	1.0	22.5	0.9	4.6	2.5
Anthracokeryx	15 (14)	−23.5	1.0	23.2	1.2	8.2	4.0
A. birmanicum	5	−24.0	0.7	23.7	1.2	1.7	2.4
A. tenuis	4 (3)	−23.2	1.3	23.6	1.0	3.1	5.8
Amynodontidae	14 (13)	−25.1	1.1	22.9	1.4	11.4	5.1
Rhinocerotoidea	11	−25.5	1.0	22.2	1.0	6.1	3.0
Siamotherium pondaungensis	4 (2)	−23.2	1.1	23.5	0.4	1.1	2.0
Bahinolophus	2	−24.5	0.1	24.5	0.1	-	-
Eomoropidae	1	−23.9	-	20.6	-	-	-
Ruminantia	2	−22.0	1.9	24.1	1.8	-	-
Mogaung							
Brontotheriidae	8	−26.1	1.6	22.8	1.6	11.3	9.1
Anthracotheriidae	6	−24.9	0.8	22.8	1.1	3.3	3.5
Anthracotherium	5	−24.9	0.9	22.6	1.1	-	-
A. crassum	1	−25.4	-	22.3	-	-	-
Anthracokeryx birmanicum	1	−25.0	-	23.8	-	-	-
Amynodontidae	2	−24.4	0.9	22.1	0.4	-	-
Rhinocerotoidea	15	−26.0	1.2	21.2	0.8	8.2	3.3

The numbers under $n°$ correspond to number of specimen, which were used to calculate the summary statistics. In cases where multiple teeth from the same individual have been sampled the number of individuals is given in brackets. All specimens from levels of higher taxonomic resolution (anthracothere genus and species level) are included in the calculation and modelled groups at a lower taxonomic level (anthracothere genus and family level) for summary statistics, niche modelling and niche overlap calculations. Total area (TA; Layman et al., 2007) corresponds to the convex hull area of a taxonomic group whereas SEA$_C$ is the modelled core ecological niche area corrected for small sample sizes (CI = 40%).

between a positive versus a negative correlation of $\delta^{13}C$ and $\delta^{18}O$ values in plants or herbivorous animals.

Nevertheless, the occurrence of significant correlation of $\delta^{13}C$ and $\delta^{18}O$ values can be interpreted as an increased influence, e.g., due to the reconstructed monsoon intensity in the Eocene, of seasonality on the diet/habitat on some of the mammal groups from the Pondaung Fm when compared with the modern cow. Two important limitations of this interpretation are the small sample size for modern *Bos*, which is only represented by one individual and the fact that we are comparing wild Eocene mammals with a modern domestic *Bos*, whose precise diet is unknown. But even the statistically significant correlations of $\delta^{13}C$ and $\delta^{18}O$ values in the Eocene alone are another indication of an intense Eocene monsoon.

4.2. Paleoenvironmental differences between the Bahin, Pangan, and Mogaung areas

The Pondaung Fm. was a habitat with only C_3 plants present. When we consider the changes in $\delta^{13}C_{CO2}$ values of the atmosphere discussed in the Methods section, modern C_3 plants would lead to $\delta^{13}C_{diet}$ values of −17.5 to −34.5‰ (modern thresholds from Kohn, 2010). Hence, $\delta^{13}C_{diet}$ values higher than −17.5‰ would be evidence for the presence of C_4 plants in the Eocene. The $\delta^{13}C$ values of all the mammals in the data set used in this study range from −20.7 to −29.2‰, and thus falling within the range of Eocene C_3 plants. As C_4 plants with their photosynthetic pathway adapted to dry and hot climatic conditions did not evolve and spread to Asia until the Late Miocene (Cerling et al., 1993, 1997) we did not expect to find any values that high in our data set. In Myanmar, the first evidence of the presence of C_4 plants based on isotopic data is from 6 Ma (Thein et al., 2011; Habinger et al., 2022).

The variation of $\delta^{13}C_{diet}$ values that we observed within and between the two study areas is caused by differences in vegetation structure. Due to the canopy effect, including factors such as low irradiance and carbon recycling, $\delta^{13}C$ values decrease with an increased canopy density (van der Merwe and Medina, 1989; Jackson et al., 1993; Bonal et al., 2000; Leffler and Enquist, 2002; Bonafini et al., 2013). This effect is less pronounced high up in the canopy and more open patches of a habitat. In these microhabitats C_3 plants yield delta-values of −18.5 to −24.5‰, whereas $\delta^{13}C_{diet}$ values of −29‰ and

TABLE 3 Summary of the results of the niche overlap in the Bahin/Pangan and Mogaung mammal communities.

Species order (A_A–A_B)	A_O	% Overlap	A_A–A_B	A_B–A_A
Bahin/Pangan				
Amynodontidae—Rhinocerotoidea	2.0	32.9%	39.2%	67.0%
Amynodontidae—Brontotheriidae	1.3	23.5%	25.4%	76.3%
Amynodontidae—Anthracotheriidae	0.9	10.4%	17.1%	20.9%
Rhinocerotoidea—Brontotheriidae	0.7	17.8%	23.7%	41.7%
Rhinocerotoidea—Anthracotheriidae	0.3	3.8%	8.7%	6.2%
A. pangan—A. crassum	0.3	8.7%	10.0%	40.1%
A. pangan—A. tenuis	1.1	15.7%	44.5%	19.5%
A. pangan—S. pondaungensis	0.4	10.6%	17.2%	21.8%
A. pangan—A. birmanicum	0.1	2.5%	4.7%	5.0%
A. crassum—A. birmanicum	0.2	6.4%	28.6%	7.6%
A. crassum—S. pondaungensis	0.4	19.8%	69.1%	21.8%
A. crassum—A. tenuis	0.6	10.9%	99.9%	10.9%
S. pondaungensis—A. tenuis	2.0	34.0%	98.6%	34.1%
S. pondaungensis—A. birmanicum	0.6	16.8%	31.5%	26.4%
A. tenuis—A. birmanicum	1.7	27.3%	30.3%	73.5%
Anthracotherium—Anthracokeryx	2.2	53.1%	98.6%	53.5%
Anthracotherium—Siamotherium	0.9	27.2%	40.8%	44.8%
Anthracokeryx—Siamotherium	1.6	35.5%	39.2%	79.3%
Mogaung				
Rhinocerotoidea—Brontotheriidae	1.7	16.3%	52.5%	19.1%
Rhinocerotoidea—Anthracotheriidae	0.0	0.4%	0.9%	0.8%
Brontotheriidae—Anthracotheriidae	2.5	24.8%	27.5%	71.6%

A_0 is the area of the niche space shared between two taxonomic groups (‰^{2}). % overlap is the percentage of the total niche space of the two taxa that is shared between them. A_A—A_B is the percentage of niche area of taxonomic group A that is shared with taxonomic group B. A_B—A_A is the same metric, but it gives the percentage of shared niche area of taxonomic group B. The three overlap metrics were calculated for each pair of taxonomic groups whose core ecological niches overlap. All specimens from levels of higher taxonomic resolution (anthracothere genus and species level) are included in the calculation and modelled groups at a lower taxonomic level (anthracothere genus and family level) for summary statistics, niche modelling and niche overlap calculations.

below are indicative for the understory of a closed canopy forest (modern thresholds from Kohn, 2010). δ^{13}C values from both the Bahin/Pangan (−20.7 to −27.2‰) and the Mogaung area (−21.2 to −29.2‰) are consistent with open-forested seasonal woodlands, like the ones reconstructed for the upper deltaic plain by Licht et al. (2015). These woodlands were denser in the Mogaung area, given the significantly lower δ^{13}C values (Figure 3), and with specimen with the lowest $\delta^{13}C_{diet}$ values falling just below the threshold for closed canopy vegetation. This possibly indicates proximity to the more closed dipterocarp forests in the upstream areas from the same vegetation model (Licht et al., 2015). An interpretation of the microhabitat differences as being caused by such spatial factors is also consistent with the paleoenvironmental similarities of the geographically close Bahin and Pangan areas with one another. However, given the currently available dates and correlations of the stratigraphic sequences of the different fossil localities of the Pondaung Fm. we cannot rule out the possibility of the two microhabitats representing a changing environment at two different late Middle Eocene time intervals completely.

The significant difference in the δ^{18}O values between the Bahin/Pangan and the Mogaung area is consistent with a more humid climate in the latter. As the Mogaung area was probably more densely forested as well, the data are also consistent with a consumption of drinking water from water sources that are more protected from direct sunlight. Water sources that are subjected to evaporation would have higher δ^{18}O values as the lighter oxygen isotope would evaporate more readily. However, there is no significant difference in the ranges of δ^{18}O values of the intra-individually sampled individuals between the Bahin/Pangan and the Mogaung area ($W = 104$, value of $p = 0.07336$). Range here is defined as the minimum δ^{18}O value subtracted from the maximum one. This indicates that there is no difference in the intensity of the seasonality.

Considering the occurrences of fossil primates (Supplementary Table SI4) in relation with these two different habitat types, we see that so far for only two of the four genera of the anthropoid Amphipithecidae have been found at all three localities, *Aseanpithecus* and *Pondaungia*. So at least for these two amphipithecid genera we can propose a certain degree of ecological flexibility. A more detailed discussion of the fossil primate occurrences and how they relate to the localities and the other mammal taxa in our data set can be found in the Supplementary Information.

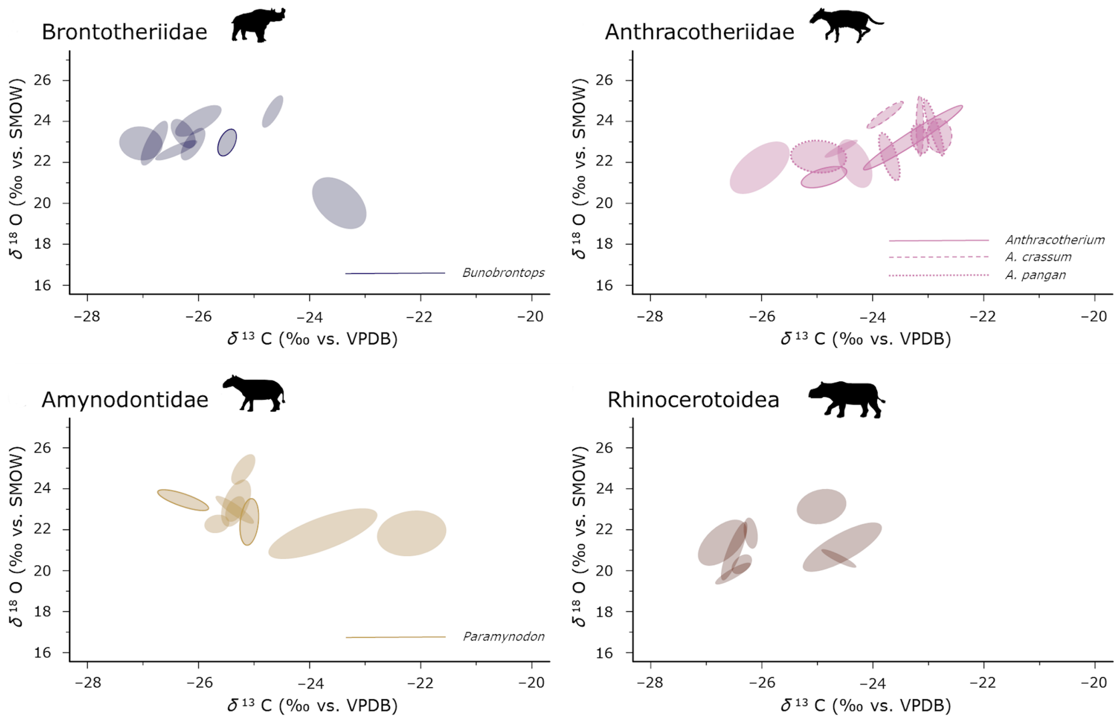

FIGURE 5
Modelled ecological niches of the serially sampled specimen in separate graphs per taxonomic group. Each ellipse corresponds to the modelled core ecological niche represented by SEA_C of one individual (CI=40%) visualizing different clustering patterns especially between the Anthracotheriidae and the other three taxonomic groups. Silhouettes are from Phylopic under CC BY 3.0 license by Zimices.

4.3. Niche partitioning and directional competition potential

An evaluation of differences in size of combined ecological niches on taxonomic family level, which potentially consist of multiple species, and their % overlap showed no significant differences between the two areas. In addition to these similarities the relative positions of the taxonomic groups to one another are very similar as well (Figure 4). Anthracotheriidae were occupying the more open patches of the habitat, which is most apparent in the Bahin/Pangan area. However, the high δ^{13}C values that would indicate a more open vegetation in the anthracothere habitat can also be partly influenced by their more omnivorous subsistence strategy. As the Anthracotheriidae are more omnivorous than the other taxonomic group they had an ecological advantage there. They were able to reduce competition potential as evidenced by the indication of their use of more open habitats in the Bahin/Pangan area than in the more closed Mogaung habitat. Brontotheriidae, Rhinocerotoidea, and in the Bahin/Pangan area also Amynodontidae shared their aspects of their ecological niches as modelled by the carbon and oxygen isotopes in parts of the paleolandscape. The differentiation between the Brontotheriidae and Rhinocerotoidea niche space is mostly due to the δ^{18}O, which would be consistent with the former drinking from more evaporated water sources than the latter. Given all these similarities in the relative positioning of the different taxonomic groups to one another, the differences that we saw between the paleoenvironments between the Bahin/Pangan and the Mogaung area, apparently did not translate to a different organization of the habitat use of the mammal communities there.

We took our analysis of the niche modelling of the Pondaung mammal fauna one step further and looked at the serially sampled individuals (Figure 5) separately. This revealed different patterns of the distribution of modelled ecological niches especially in the Anthracotheriidae. While the Anthracotheriidae appear to share the modelled aspects of their ecological niches, there is more diversity in the Brontotheriidae, Amynodontidae, and Rhinocerotoidea. This makes sense as the taxonomic resolution in the Anthracotheriidae is better (Figure 5), where all but two individuals could be identified as to at least belonging to the genus *Anthracotherium*, whereas potentially multiple genera or species with different ecologies could be included in the sample for the other taxonomic groups. Several individuals of the Brontotheriidae, Amynodontidae, and Rhinocerotoidea seem to have occupied different microhabitat niches than the other specimen of these groups. Given that this approach requires multiple samples per individual, it becomes apparent why the species diversity in Anthracotheriidae is not reflected here in its entirety as this sampling technique could only be applied to larger teeth, such as the two *Anthracotherium* species and some undetermined Anthracotheriidae.

Based on the ecological niche modelling on the individual level for the four main taxonomic groups we calculated a metric used in ecology to differentiate generalist from specialist individuals. Large modelled niche areas for a taxon or a taxonomic group are consistent with an overall generalist behavior. It can however, be caused by two different reasons. It can result either from many specialist individuals with different ecologies that would have a low RINI, or from generalist individuals that all more or less use the entire niche space of their taxonomic group and thus having a high RINI. As the total modelled

TABLE 4 Summary of the calculation of RINI for the specimen from which intra-individual serial samples were taken.

Specimen ID	n°Samples	SEA$_C$	RINI	Speciemen ID	n°Samples	SEA$_C$	RINI
Brontotheriidae				**Amynodontidae**			
Bahin/Pangan				*Bahin/Pangan*			
A6	3	0.54	-	A1	9	0.31	0.06
PND-8	13	0.71	0.19	A10	7	0.46	0.09
PNG-109	8	0.32	0.08	A2	17	2.15	0.44
PNG-47	5	0.30	0.08	PNG-35	7	0.82	0.17
PNG-76	9	0.41	0.11	PNG-50	8	0.31	0.06
PNG-78	5	0.42	0.11	PNG-61	5	0.32	0.06
Mean		*0.45*	*0.11*	PNG-75	5	0.39	0.08
SD		*0.16*	*0.04*	*Mean*		*0.68*	*0.14*
Mogaung				SD		*0.67*	*0.14*
A9	10	0.31	0.08	*Mogaung*			
PND-18	6	1.74	0.45	A5	11	2.56	0.52
PNG-106	5	1.00	0.26	PNG-119	13	0.56	0.12
Mean		1.01	0.26	*mean*		1.56	0.32
SD		0.71	0.19	SD		1.41	0.29
Anthracotheriidae				**Rhinocerotoidea**			
Bahin/Pangan				*Bahin/Pangan*			
A4	3	1.76	-	A7	4	1.16	0.30
PNG-21	4	1.20	0.37	PND-22	8	0.24	0.06
PNG-31	3	0.18	-	PND-34	13	1.27	0.33
PNG-34	5	1.02	0.31	*Mean*		*0.89*	*0.23*
PNG-36	4	0.33	0.10	SD		*0.56*	*0.15*
PNG-42	6	0.50	0.15	*Mogaung*			
PNG-45	5	0.36	0.11	A3	4	1.64	0.43
PNG-51	4	0.27	0.08	PND-19	5	0.27	0.07
PNG-56	4	0.33	0.10	PND-1	8	0.56	0.15
PNG-57	4	0.56	0.17	PND-31	7	0.29	0.08
Mean		*0.65*	*0.18*	PND-33	6	0.19	0.05
SD		*0.51*	*0.11*	*Mean*		0.59	0.15
Mogaung				SD		0.60	0.16
A8	4	1.00	0.31				
PNG-115	4	0.55	0.17				
Mean		0.77	0.24				
SD		0.32	0.10				

For each individual we report the number of samples taken, the SEA$_C$ (‰^{2}) corresponding to a CI of 40% and the RINI as well as the median and standard deviation for these two metrics.

niche area of the taxonomic groups is based on higher level taxa (families) there is the possibility of an overestimation of the isotopically modelled niche aspect, if there are big differences in habitat preferences and use in the lower level taxa. Hence, the RINIs could be lower in these cases. Both SEA$_C$ and RINI were not significantly different between Anthracotheriidae and the rest of the taxonomic groups. The fact the same pattern is present in both metrics is an indication that no particular generalist or specialist individuals were present, and that the bias towards an underestimation of the RINIs has no significant effect on this comparison. The clustering pattern in Anthracotheriidae seems to be different than in the other three taxonomic groups. The lack of individuals plotting apart from the main cluster of modelled ecological core niches without overlapping them is consistent with a more continuous variation of ecological requirements in this group whereas the pattern in Brontotheriidae, Amynodontidae, and Rhinocerotoidea indicates more discrete ecological niches reflecting aspects of habitat use and dietary ecology.

4.4. Paleoecology of the Pondaung Anthracotheriidae

Although the localities are located along a paleo river system, none of the taxonomic groups has δ^{18}O values low enough to suggest semi-aquatic behavior. Previous studies showed that depending on the humidity of the terrestrial habitat, this offset can be 2–4‰ lower in freshwater living semi-aquatic species than in terrestrial ones (Clementz et al., 2008). An additional indication of semi-aquatic behavior in a taxonomic group is a reduced standard deviation (SD) of ≤0.5‰ (Yoshida and Miyazaki, 1991; Clementz and Koch, 2001). In our dataset such low SDs are only present in *S. pondaungensis*, *Bahinolophus*, and Amynodontidae from Mogaung (Table 2). These are all taxonomic groups with very low sample sizes (MNI = minimum number of individuals = 2). Therefore, we do not consider the low SD as an indication for semi-aquatic behavior in any of these cases. Differences in δ^{18}O values can however result from the use of different water sources. The lower δ^{18}O values in Rhinocerotoidea in comparison to Brontotheriidae would be consistent with them drinking from less evaporated water sources. This could mean shaded water or flowing and not stagnant water.

Between the three different anthracothere genera found in the Pondaung Fm. there is a lot of niche overlap (Figure 6), which was already suggested by the niche modelling of the serially sampled anthracotheres (Figure 5), although none of the smaller genera (*Anthracokeryx* and *Siamotherium*) were in this sample group. Apparently, the three genera did share habitats with similar ecological characteristics. Hence, the different feeding ecologies and habitat preferences in regard to forest density inferred from tooth and bone morphology (Ducrocq, 1999) do not translate to different habitats occupied by them based on the modelled core ecological niches. No clear patterns are visible that would differentiate the anthracothere genera based on canopy closure or isotopically different water sources. We described the hypothetical ecology of *Anthracotherium* as being both more water dependent and more reliant on open spaces in the habitat for their subsistence. *Anthracotherium* however does not have significantly higher δ^{13}C values or lower δ^{18}O values than the other genera, thus the isotopic data are not consistent with this hypothesis.

Anthracotherium shares almost all of its modelled ecological core niche space with *Anthracokeryx* (Figure 6B). This can indicate that *Anthracotherium* experienced a higher competition potential for its ecological niche than *Anthracokeryx* (Ogloff et al., 2019). However, the larger body mass of *Anthracotherium* counteracts this effect. The

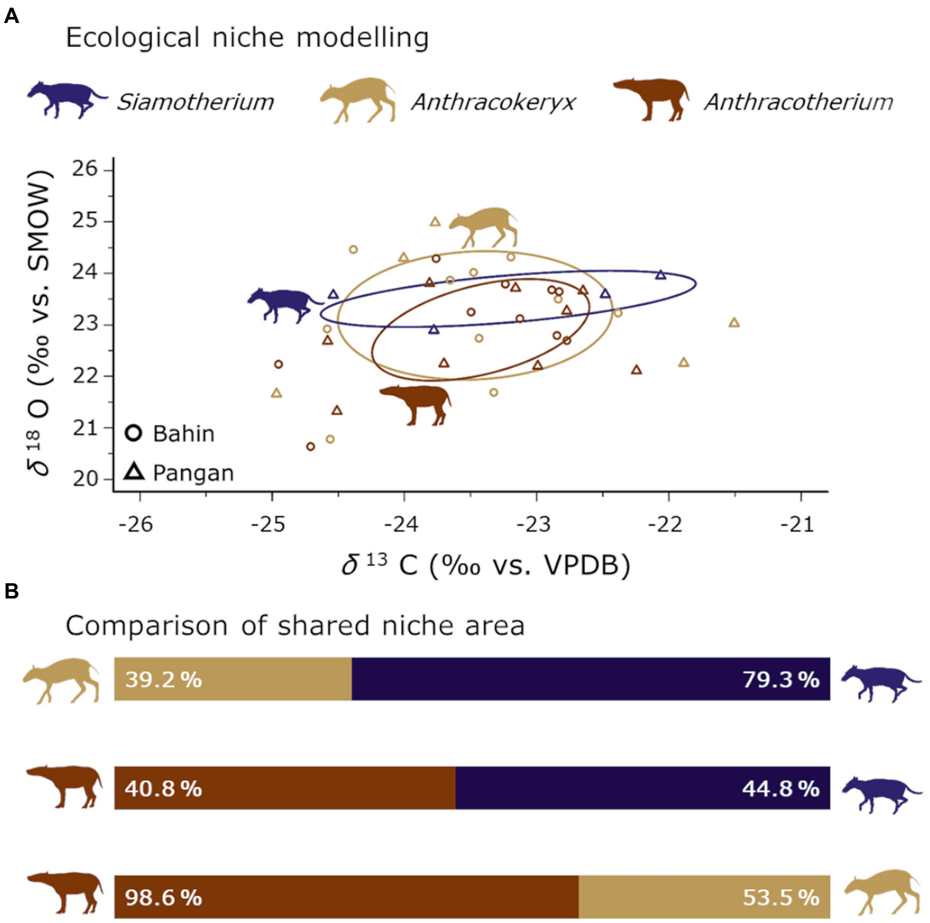

FIGURE 6
Ecological niche modelling of the anthracotheres from Bahin/Pangan per genus **(A)**. Ellipses represent the core ecological niches. In **(B)** the results of the shared niche area (A_A—A_B, and A_B—A_A) between each taxonomic group are visualized. Silhouettes are from Phylopic under CC BY 3.0 license (*Anthracotherium* by Zimices, *Anthracokeryx* by Nobu Tamura and vectorised by T. Michael Keelsey, and *Siamotherium* is Public Domain).

higher %overlap of the *Anthracotherium* with the *Anthracokeryx* niche could also mean that the advantage of being larger and more generalist in its diet enabled *Anthracotherium* to use more of the *Anthracokeryx* niche space (Schoener, 1983; Persson, 1985; Law et al., 1997). A similar pattern is also visible in the comparison of *Anthracokeryx* and *Siamotherium*, which would be consistent with similar interpretations. However, it is important to keep in mind that the *Siamotherium* niche is based on only two individuals, with two sampled teeth each, which differ vastly in δ^{13}C values, and further interpretations will depend on a larger sample size for *Siamotherium*.

The limitation of sample size of course is even more prevalent when we are looking at niche partitioning between the anthracothere species (Figure 7A). Nevertheless, we wanted to investigate possible interesting patterns of niche partitioning and directional competition potential detectable to open new directions for future research. Given the severe problems with sample size in *S. pondaungensis* discussed in the previous section, we cannot discuss its niche overlap in comparison with the other species. It is apparent that there is a lot of niche overlap between the anthracothere species, leading to more diffuse competition than niche partitioning in this context (Figure 7). The Pondaung habitat must have provided sufficient area to fulfil the ecological requirements of the anthracotheres and sustain all of the species sampled in this study.

When we generalize the results formed based on the comparison *Anthracotherium* and *Anthracokeryx* in the previous section we propose the following hypothesis: Species with higher body mass have a competition advantage; hence, we expect them to have a higher percentage of shared niche space with the smaller species (Figure 7B). *Anthracokeryx tenuis*, the smallest of these anthracotheres, follows this prediction in every instance and always shares a smaller percentage of its niche area than the bigger species with which it is compared. For the other species this relationship is not as simple. *Anthracotherium pangan* is the largest anthracothere from Pondaung. However, the second largest *A. crassum* shares more of its core niche with it than vice versa. This might be because *A. crassum* also has a much narrower core ecological niche than *A. pangan*. This fact would be consistent with the latter having more generalist ecological requirements than the former. *Anthracokeryx birmanicum* mostly fulfils the expectations based on our hypothesis. The shared niche space between it and *A. pangan* however, are the same. They only share around 5% of their ecological core niches with one another. Given this small overlap area, distinct ecological requirements of these two anthracothere species probably led to a reduced competition potential where the body mass advantage of *A. pangan* was irrelevant.

To sum up, we could further prove the existence of a proto-monsoon already in the Eocene even at the low paleolatitude of 5°N

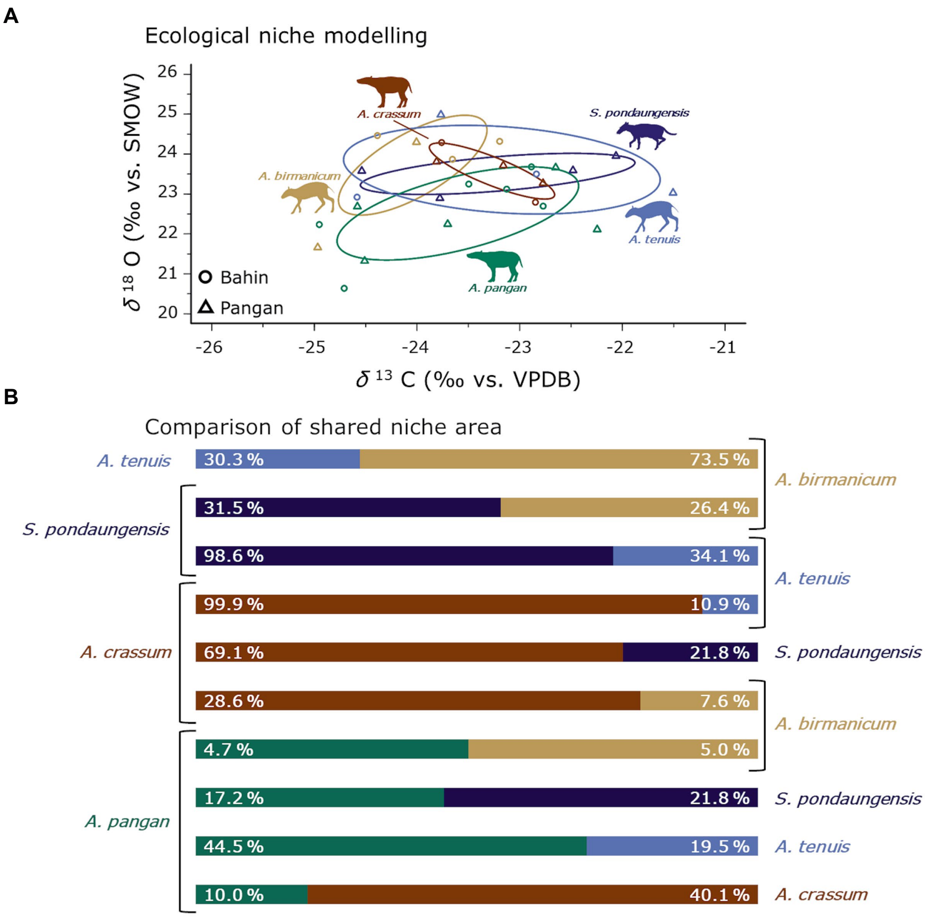

FIGURE 7
Ecological niche modelling of the anthracotheres from Bahin/Pangan per species **(A)**. Ellipses represent the core ecological niches. In **(B)** the results of the shared niche area (A_A—A_B, and A_B—A_A) between each taxonomic group are visualized. Silhouettes are from Phylopic under CC BY 3.0 license (*Anthracotherium* by Zimices, *Anthracokeryx* by Nobu Tamura and vectorised by T. Michael Keelsey, and *Siamotherium* is Public Domain).

of the equator. The $\delta^{13}C$ and $\delta^{18}O$ values also showed significant differences in both overall humidity and vegetation structure between the Bahin/Pangan and Mogaung areas. Although our results are consistent with the hypothesis that favor a spatial pattern of the vegetation structure, temporal differences cannot be ruled out and require more detailed investigation of the dating and stratigraphic relationship of the different fossil localities of the Pondaung Fm. Although the Mogaung area was more humid and more densely forested than the other two, the organization of the mammal fauna was not different, which is consistent with ecological flexibility of this Middle Eocene greenhouse mammal fauna. A high degree of niche overlap was observed on genus and species level resolution for the anthracotheres. Interestingly, there is no evidence for semi-aquatic adaptations in any of the taxonomic groups, when we test for significant offsets in $\delta^{18}O$ values and a reduction of their variability. This means that at the same time when ancestral whales were already returning to aquatic life, anthracotheres that are ancestral to hippos still were fully terrestrial even though the paleo river channel associated with the Pondaung Fm. would have offered enough suitable habitats for this lifestyle. That the primate fossil record from the Pondaung Fm. also does not show any significant differences in the occurrences of the different taxa is also consistent with this and also indicates ecological flexibility in this taxonomic group. Therefore, the Pondaung Fm. represents diverse microhabitats that were used by a dynamically organized mammal fauna. This environment proved to be conducive for the diversification and radiation of many taxonomic groups such as primates, anthracotheres and rodents.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

SH, OC, and HB contributed to conception and design of the study and worked together with SD on data analysis. SH and SS performed the sampling, sample preparation and SH did the statistical analysis and wrote the first draft of the manuscript. OC, YC, JJ, CS, and AS were essential for fieldwork during which the fossil specimens were collected. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1110331/full#supplementary-material

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