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Niche exploitation profiles predict the palaeoclimate of tropical mammal communities

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A B S T R A C T

There are multiple ways in which fossil mammal communities can be used to reconstruct palaeoenvironments, but their relationship to paleoclimate conditions is less clear. In this study, we used a database of mammal species present at 167 modern localities across the tropical zone to construct niche profiles in which each taxon is assigned to a locomotor and diet behaviour category. Cluster analysis identifies significantly different groups of localities on the basis of these profiles, driven by their relative proportion of terrestrial herbivores, terrestrial animalivores, arboreal frugivores, and terrestrial frugivores. These groups are shown to vary according to climate, particularly to aspects of precipitation. We added three Plio-Pleistocene fossil localities to our analytical model to reconstruct their palaeoclimates based on their niche exploitation profiles: Esquina Blanca (Uquía Formation), Argentina, Laetoli, Tanzania, and Thum (Tham) Wimam Nakim (Snake Cave), Thailand. In accordance with independent studies, we show Esquina Blanca to have had a low rainfall and seasonal climate and Laetoli a moderately low rainfall climate. Thum Wimam Nakim falls in a moderate rainfall, moderate temperature climate cluster, but is likely to be a non-analog community.

1. Introduction

There is a long-established history of the use of niche exploitation profiles in distinguishing habitat types at both global and continental scales in extant and fossil mammal communities (Fleming, 1973; Andrews et al., 1979; Reed, 1998; Andrews and Humphrey, 1999; Mendoza et al., 2005; Louys et al., 2011; Lintulaakso and Kovarovic, 2016). Using niche profiles rather than taxonomic presence/absence data has a distinct advantage for palaeoecologists working with the fossil record where taxonomic identification is often stymied by the fragmented state of an assemblage or uncertainty surrounding classification. Niche profiles consider the ecological behaviours of the individual taxa present, relying on adaptive morphologies to indicate the array of trophic and spatial niches exploited by the entire community which, in turn, point to the type of environment that supported the community. This work implicitly focuses on the physical characteristics of habitats, such as the amount of vegetation cover.

It has been much more challenging to associate mammal communities with climate, although palaeoecologists have long sought to do so and, at present, it is increasingly imperative that we develop a picture of mammalian responses to past climate change so that we can accurately predict the future distribution of animals and their adaptive habitats in light of human-mediated climate change. Many attempts to associate mammal communities and climate rely on taxonomic composition, sometimes of just one part of the community (e.g. Hernández and Peláez-Campomanes, 2003, 2005; Linchamps et al., 2023). By contrast, a non-taxonomic ecometric approach averages mammalian functional traits across parts of communities and explicitly links their average trait values to climate (see Vermillion et al., 2018). Ecometric analyses often focus on one aspect of the climate such as precipitation, or a single geographic area (Kay and Madden, 1997; Fortelius et al., 2002; Eronen et al., 2010a, 2010b; Fortelius et al., 2016; Rowan et al., 2016; Žliobaitė et al., 2016), although some work demonstrates that an ecometric approach can predict both vegetation cover and precipitation on a global scale (Short and Lawing, 2021). Both taxonomic composition-based methods and ecometrics have their merits, but species identification can confound the former and the latter leaves out important parts of the community that provide valuable environmental and climatic information.

In this study, we circumvent the shortcomings of the methods noted above by determining if community niche exploitation profiles - which do not require species identifications, but do allow the entire community

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to be assessed - can be linked to climate factors and then use this to predict palaeoclimate at three fossil localities. We use Hierarchical Cluster Analysis (HCA) to identify distinct groups of modern mammal communities using locomotion and dietary niche profiles. We then apply ANOVA and SIMPER to determine if these “faunal clusters” are defined by significant differences in climate and, if so, which niche exploitation groups are responsible for the differences. Our analysis is based on a large dataset ($n = 167$) of localities in the tropical zone of Africa, Asia, and the Americas, thus considering patterns of mammal community diversity and climate on a global scale. We consider 21 bioclimatic variables and elevation and determine which of these are associated with the faunal clusters. Secondly, we use the faunal cluster distinctions to predict the climatic conditions of three Plio-Pleistocene fossil localities that differ in age, location, and community characteristics: Esquina Blanca (Uquía Formation), Argentina, Laetoli, Tanzania and Thum Wimam Nakin, Thailand. These sites have well-studied independent palaeoenvironmental and palaeoclimate proxies (detailed below) in order to verify our reconstructions.

2. Methods

2.1. Modern localities and mammal species lists

We compiled 167 modern mammal species lists (following the taxonomic nomenclature of Wilson and Reeder, 2005) excluding Chiroptera, Sirenia, Cetacea, and species weighing less than 1 kg. We include only localities with twenty or more species which is consistent with similar work (cf. Andrews et al., 1979; Reed, 1998; Mendoza et al., 2004; Louys et al., 2011) and higher than the threshold of 12 taxa that has been previously identified as a minimum requirement for distinguishing between mixed and open or open versus closed habitats (Louys et al., 2009). Localities are restricted to the tropical zone (i.e., between 23° 30′ N and 23° 30′ S) of Africa ($n = 72$), Asia ($n = 49$) and the Americas ($n = 46$) (Fig. 1). Coordinates for each locality are from the World Database on Protected Areas (IUCN, UNEP, 2009).

Species lists for each modern locality are derived primarily from Badgley et al. (2001), Van Dam et al. (2001), Damuth et al. (2002) and additional published literature; many lists have been included in previous mammal community studies (e.g., Andrews et al., 1979; Reed, 1998, 2008; Andrews and Humphrey, 1999; Louys, 2007; Lintulaakso and Kovarovic, 2016). Supporting Information Dataset S1 lists the localities, their coordinates, and their species list references. Supporting Information Dataset S2 summarises the taxa present at each locality.

2.2. Niche exploitation variables

Each species was assigned to a locomotor and dietary category that describes their broad niche preferences (Badgley et al., 2001; Van Dam et al., 2001; Damuth et al., 2002; Jones et al., 2009; Liow et al., 2008, 2009; Lintulaakso, 2013). The locomotor categories include arboreal (A), arboreal–terrestrial (AT), subterranean (S), subterranean–terrestrial (ST), terrestrial (T) and terrestrial–aquatic (TA) (Table 1) (Miljutin, 2009; Lintulaakso and Kovarovic, 2016). These categories reflect the habitat substrate to which the animal is best adapted. Dietary categories reflect food resource exploitation and include animalivore (A), frugivore (F) and herbivore (H) (Table 1) (Miljutin, 2009; Lintulaakso and Kovarovic, 2016). These locomotor and diet categories were combined for each species and there are a total of 17 unique niche exploitation groups (Table 1). Individual species classifications are found in

Table 1
Combined locomotor and diet niche exploitation categories.

Combined category	Abbreviation
Arboreal-Animalivore	A-A
Arboreal-Frugivore	A-F
Abroeal-Herbivore	A-H
Arboreal-Terrestrial-Animalivore	AT-A
Arboreal-Terrestrial-Frugivore	AT-F
Arboreal-Terrestrial-Herbivore	AT-H
Subterranean-Frugivore	S-F
Subterranean-Herbivore	S-H
Subterranean-Terrestrial-Animalivore	ST-A
Subterranean-Terrestrial-Frugivore	ST-F
Subterranean-Terrestrial-Herbivore	ST-H
Terrestrial-Animalivore	T-A
Terrestrial-Frugivore	T-F
Terrestrial-Herbivore	T-H
Terrestrial-Aquatic-Animalivore	TA-A
Terrestrial-Aquatic-Frugivore	TA-F
Terrestrial-Aquatic-Herbivore	TA-H

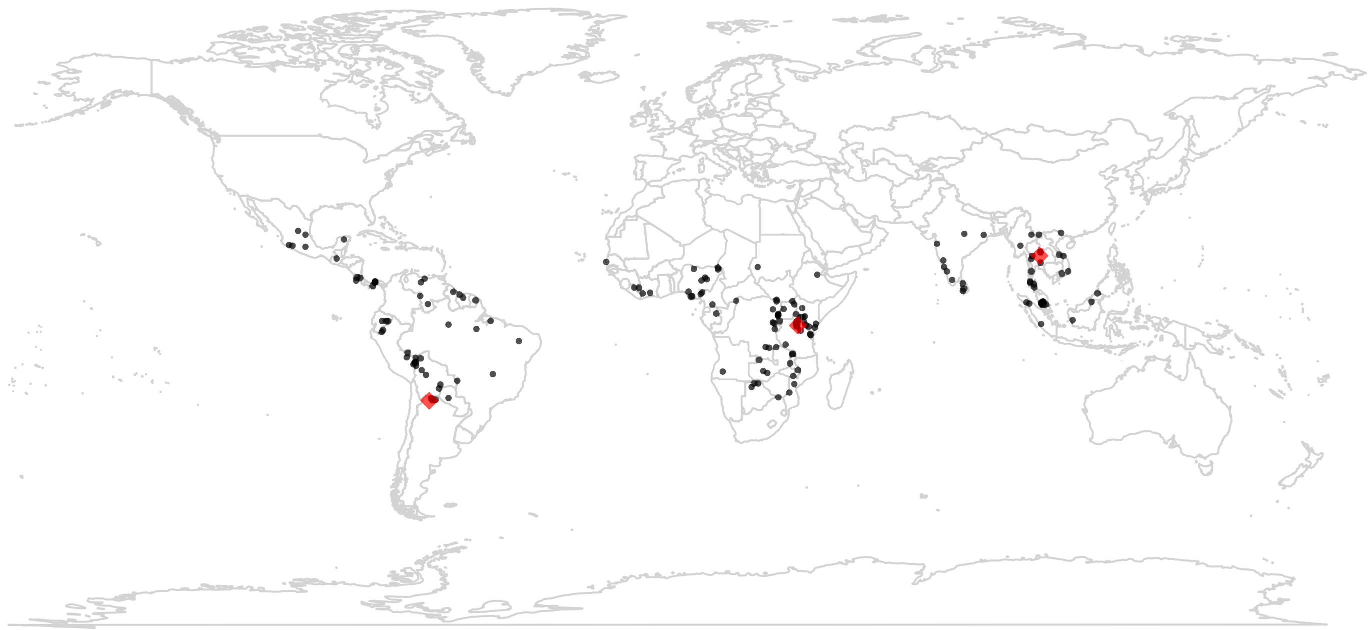

Fig. 1. Map of the 167 tropical localities included in this study. Three fossil localities are denoted by a grey diamond: Esquina Balance (Uquía Formation) in South America, Laetoli in Africa, and Thum Wimam Nakim in Asia.

Supporting Information Dataset S2.

2.3. *Climate variables*

We used 21 bioclimatic variables (Table 2); 19 variables are from WorldClim (available at http://www.worldclim.org/bioclim; see Hijmans et al., 2005) which represent climatic trends that occur on an annual and seasonal cycle (e.g., mean annual temperature, mean temperature of the warmest quarter). The remaining two variables represent the limits imposed on plant growth by temperature and water availability: temperature limiting factor considers the number of growing days over the year as influenced by average minimum monthly temperatures and water limiting factor is a ratio of precipitation to potential evapotranspiration (PET) (Nemani et al., 2003).

Using geographical coordinates (Supporting Information Dataset S1), we positioned our 167 localities in a 10 min (~340 km^2) global grid system and associated each locality with the average climate values of its grid cell. In addition to these climate variables, we included the elevation of each locality (Hijmans et al., 2005).

2.4. *Palaeontological localities*

The three fossil communities that we used as test cases include Esquina Blanca (Uquía Formation), Argentina, Laetoli, Tanzania and Thum (Tham) Wimam Nakin (Snake Cave), Thailand (denoted by diamonds in Fig. 1). Each fossil species was assigned to one of the combined niche exploitation categories. Their body mass, locomotor, and dietary preferences came from the NOW Database (http://www.helsinki.fi/science/now/), Paleobiology Database (https://paleobiodb.org/#/), and MammalBase (http://www.mammalbase.net/) but this information was frequently supplemented with additional literature to confirm the assignments; occasionally sources pertaining to the fossil species' close living relatives, or genus and family, if extant, were consulted. All classifications and sources are listed in Supporting Information Dataset S3.

Table 2

Bioclimatic variables and elevation.

Code	Variable definitions	Source
BIO1	Annual Mean Temperature	WorldClim
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	WorldClim
BIO3	Isothermality (BIO2/BIO7) (* 100)	WorldClim
BIO4	Temperature Seasonality (standard deviation *100)	WorldClim
BIO5	Max Temperature of Warmest Month	WorldClim
BIO6	Min Temperature of Coldest Month	WorldClim
BIO7	Temperature Annual Range (BIO5-BIO6)	WorldClim
BIO8	Mean Temperature of Wettest Quarter	WorldClim
BIO9	Mean Temperature of Driest Quarter	WorldClim
BIO10	Mean Temperature of Warmest Quarter	WorldClim
BIO11	Mean Temperature of Coldest Quarter	WorldClim
BIO12	Annual Precipitation	WorldClim
BIO13	Precipitation of Wettest Month	WorldClim
BIO14	Precipitation of Driest Month	WorldClim
BIO15	Precipitation Seasonality (Coefficient of Variation)	WorldClim
BIO16	Precipitation of Wettest Quarter	WorldClim
BIO17	Precipitation of Driest Quarter	WorldClim
BIO18	Precipitation of Warmest Quarter	WorldClim
BIO19	Precipitation of Coldest Quarter	WorldClim
TEMPLIM	Temperature Limiting Factor	Nemani et al., 2003
H2OLIM	Water Limiting Factor	Nemani et al., 2003
ELEV	Elevation	WorldClim

Bioclimatic data available at: http://www.worldclim.org/bioclim. The Temperature Limiting Factor and Water Limiting Factor variables are calculated as in Nemani et al., 2003.

2.4.1. *Esquina Blanca (Uquía Formation), Argentina*

Esquina Blanca is situated just north of the Tropic of Capricorn in the Quebrada de Humahuaca, an intermontane valley in the Eastern Cordillera of the Andes Mountains in northwest Argentina. It is one of three major Uquían outcrops and the type area for the Uquía Formation. It records vertebrate fauna during the Great American Biotic Interchange (GABI) at what was likely a moderate elevation around 1400-1700 m, and possibly even lower (Reguero et al., 2007); today it is found at a much higher elevation of approximately 2800 m. The mammalian community considered here is derived from the Middle Unit of these Middle-Late Pliocene deposits (Supporting Information Dataset S3a). The assemblage is assigned to the Vorohuean–Sanandresian sub-ages of the Marplatan South America Land Mammal Age (SALMA) (Reguero et al., 2007). The Middle Unit begins near the "Dacitic Tuff" dated to 3.54 Ma (Marshall et al., 1982) and is capped by the ~2.5 Ma U1 Tuff (Walther et al., 1998).

The Uquía area is of significance to our understanding of the biogeography of mammals during the GABI. The record of vertebrates here demonstrates that northwest Argentina was home to a distinct fauna in the second half of the interchange which included extinct sloth families, an extinct Order of ungulates (Litopterna), and a variety of large armadillo-like glyptodonts, among other groups no longer extant (Simpson, 1980; Reguero et al., 2007; Ortiz et al., 2012; Domingo et al., 2020). Previous interpretations of the Uquían macromammals suggest a more humid and seasonal climate than today (Reguero et al., 2007). A study of the micromammal vertebrate community from the nearby Uqíuan locality, San Roque, records a possible turnover event in the region linked to increasing aridity (Ortiz et al., 2012).

The Esquina Blanca faunal list is from Reguero et al. (2007), to which Felinae *indet.* was added (Ercoli et al., 2019). We included only three of the six glyptodont taxa named in Reguero et al. (2007), as more recent studies suggest that six is too high as a richness value for this group (Zurita et al., 2014; Zurita et al., 2016; Cuadrelli et al., 2020), so we were conservative with our estimate of the likely taxa present (further details in Supporting Information Dataset S3a). It is almost certain that there are still several unidentified or unrecovered taxa at Esquina Blanca, as the >1 kg species list is comprised of only 18 taxa. However, this is higher than the 12 taxa minimum requirement (Louys et al., 2009).

2.4.2. *Laetoli, Tanzania*

Laetoli, Tanzania is located in the southern part of the African Rift Valley in the modern-day Serengeti ecosystem. This site records Early Pliocene to recent sediments and is well-sampled across fossil localities covering a surface area of approximately 1000km^2 (Harrison and Kweka, 2011). Here we focus our analysis on the mammalian fauna of the Upper Laetolil Beds, dated 3.85–3.63 Ma (Deino, 2011).

Laetoli is unusual compared to most East African Rift sites from the same time period because sediments were not accumulated in a fluvial or lacustrine context, although there is evidence of a significant wet season drainage system (Ditchfield and Harrison, 2011). Deposits are primarily aeolian and volcanic, likely stemming from the extinct Satiman volcano to the east (Mollel et al., 2011), with several distinct tuffs yielding accurate dates that have contributed to a well-defined stratigraphy (Hay, 1987; Deino, 2011).

A rich mammalian fauna of 69 taxa >1 kg is known from the Upper Laetolil Beds, including the holotype and approximately 30 other specimens of the hominin species *Australopithecus afarensis* (Harrison, 2011a, 2011b) (Supporting Information Dataset S3b). The fauna is known for being dominated by large herbivores and although primates (including hominins) are present, they are rare (Su and Harrison, 2008; Harrison, 2011a, 2011b). A multitude of palaeoenvironmental studies (see Su and Harrison, 2015 and references therein) have yielded a variety of interpretations that converge on the view that Laetoli was a mosaic environment featuring open and closed woodlands, bush and shrublands and occasional grasslands. At present, it is more arid and open than it was during the Pliocene (Kingston, 2011; Rossouw and Scott, 2011; Tattersfield, 2011).

2.4.3. Thum Wimam Nakin, Thailand

Thum (or Tham) Wimam Nakin, also known as Snake Cave, is situated in the mountainous northeastern part of Thailand in a flood plain on the side of a hill, approximately 10 m above the surrounding plain (Chaimanee, 1998). It is a late Middle Pleistocene cave locality deposited during the Saalian Glaciation, dated to 169 Ka (Esposito et al., 2002).

Multiple chambers within the cave have yielded a well-documented fauna of over 30 taxa >1 kg (Tougard et al., 1998; Louys, 2007; Suraprasit et al., 2021) (Supporting Information Dataset S3c). Both the micro- and macromammal assemblages are diverse and reasonably well preserved, but of particular importance is the discovery of a well-worn fourth premolar assigned to *Homo* sp. (Tougard et al., 1998), which represents the best and oldest fossil human remains in the country. It is important in documenting the presence of *Homo* in this part of Southeast Asia where large-bodied non-human primates such as *Pongo* and the extinct *Gigantopithecus* are much better-known (Bocherens et al., 2017).

Faunal analyses have suggested the presence of mixed habitats and forests that were more open than in the present day and, although likely to have been humid, it was also more temperate relative to the present (Tougard and Montuire, 2006; Louys and Meijaard, 2010). This interpretation is supported by an isotopic study which found that closed forest and open vegetation were available, but many of the species consumed a significantly higher proportion of open C4 vegetation than they do today (Pushkina et al., 2010). The site samples a time when mammals migrated across the mainland during the Saalian Glaciation when conditions were even more open and arid than interglacial periods, and mammals from the Indochinese and Sundaic ecoregions shifted their ranges (Tougard, 2001; Suraprasit et al., 2019). The Thum Wimam Nakin assemblage, although comprised entirely of extant taxa, is therefore likely to record a community “in transition” with an unusual association of fauna.

Our faunal list of 32 taxa is from Louys (2007), with three new species identified by Suraprasit et al. (2021) including *Panthera* cf. *tigris, Meles* cf. *leucurus* and *Naemorhedus goral* (Supporting Information Dataset S3c).

2.5. Analysis

We created a community composition matrix of the raw data in which the localities are rows, the species traits are columns, and the number of species within each group comprise the cell values. We transformed these values using the formula $\log2(x) + 1$ for $x > 0$, where x is the number of species (Anderson et al., 2006; *decostand* in R package vegan (Oksanen et al., 2007)). After this transformation, a Bray–Curtis distance matrix was calculated (Bray and Curtis, 1957; Legendre and Legendre, 1998). We performed hierarchical cluster analyses (HCA) with the transformed community composition data using the Ward method (Ward, 1963). The resulting tree was first cut into two clusters ($k = 2$), and we continued to cut the tree into a pre-defined number of clusters up to $k = 10$. We refer to the resulting clusters as “faunal clusters”.

The next step determined if the faunal clusters differ in their climate values independent of the niche exploitation profiles which defined them in the HCA. After each cut, omnibus ANOVA tested for significant differences among the means of each of the climatic variables and elevation across any of the clusters. If significant differences were found, a *t*-test was performed to test the pairwise comparisons between the cluster climate means. This identified the specific climate variables that are significantly different between all the clusters. Summary statistics of the climatic variables were also generated for these faunal clusters.

Finally, we used SIMPER (similarity percentage) to determine the relative contribution of each of the 17 niche exploitation groups to the dissimilarity between faunas (Clarke, 1993). If a specific variable consistently contributes to both the within-group similarity and between group dissimilarity, it is considered a good discriminator.

The same analytical procedure described above was performed three times with the separate addition of each of the fossil localities. This allowed us to identify which of the clusters each site belongs to, and whether or not the inclusion of the fossil community changed the original clustering.

All analyses were conducted in R version 3.5.3, using R-packages *stats* and *vegan* (Oksanen et al., 2007; R Development Core Team, 2005).

3. Results

Here we report results from the analyses where $k = 3$ and $k = 4$. Results of $k = 2$ can be found in Supporting Information (Tables S1a-d) and are not described in the main text. The modern localities that make up each cluster resulting from the HCAs can be found in Supporting Information Tables 2a-d. The complete SIMPER results are reported in Supporting Information Tables 3a-d.

3.1. Modern faunal clusters

Significant differences are present among faunal clusters when the HCA tree is divided into three or four clusters, but no greater number. Table 3 shows the bioclimatic variables that are significantly different among clusters when $k = 3$ and $k = 4$. Table 4 summarises how the faunal clusters differ by their number of localities (n), average value for each significantly different climate variable, and the average number of species in each niche exploitation group identified by SIMPER as a significant contributor to cluster differences, of which there were four (see below). Note that specific faunal clusters will henceforth be abbreviated by FC.

3.1.1. Climate and elevation

When the HCA tree is cut into three clusters, there are three statistically significant climatic differences between these faunas related to precipitation: annual precipitation (BIO12), precipitation of the wettest quarter (BIO16) and precipitation of the warmest quarter (BIO18) (Table 3). FC1 has the lowest mean annual precipitation, whereas FC2 is the wettest, with FC3 in the middle of these extremes (Table 4). The

Table 3
Pairwise faunal cluster t-test results.

Variable	k = 3	k = 4
BIO1	0.271	0.519
BIO2	0.903	0.900
BIO3	0.973	0.972
BIO4	0.771	0.768
BIO5	0.663	1.000
BIO6	0.388	0.385
BIO7	0.753	1.000
BIO8	0.248	0.954
BIO9	0.416	0.413
BIO10	0.837	0.716
BIO11	0.267	0.265
BIO12	**< 0.001**	**< 0.001**
BIO13	0.091	0.847
BIO14	0.073	0.485
BIO15	0.709	1.000
BIO16	**0.015**	0.897
BIO17	0.140	0.364
BIO18	**0.011**	0.085
BIO19	0.282	0.371
H2OLIM	0.257	0.252
TEMPLIM	1.000	1.000
ELEV	0.158	0.252

Significant *p*-values are in bold.
Climate variable definitions in Table 2.

Table 4
Bioclimatic variable values and average number of species in niche exploitation groups by faunal cluster.

Variable	Faunal Cluster 1					Faunal Cluster 2					Faunal Cluster 3					Faunal Cluster 4				
	climate values				species	climate values				species	climate values				species	climate values				species
k=3	n=74					n=37					n=56									
	min	ave	max	SD		min	ave	max	SD		min	ave	max	SD						
BIO12	304	1057	4221	678	11.9 T-H	1137	2431	3524	691	1.4 T-H	515	1952	3269	631	6.3 T-H					
BIO16	148	577	3293	450	8.2 T-A	523	967	1445	241	6.0 T-A	346	785	1337	238	4.2 T-A					
BIO18	32	283	1101	173	1.6 A-F	156	536	1266	244	6.5 A-F	134	434	844	167	7.1 A-F					
					3.3 T-F					4.8 T-F					4.8 T-F					
k=4	n=45					n=29					n=37					n=56				
	min	ave	max	SD		min	ave	max	SD		min	ave	max	SD		min	ave	max	SD	
BIO12	304	832	1554	309	15.7 T-H	590	1407	4221	917	5.9 T-H	1137	2432	3524	691	1.4 T-H	515	1952	3269	632	6.3 T-H
					9.2 T-A					6.8 T-A					6.0 T-A					4.2 T-A
					1.2 A-F					2.2 A-F					6.5 A-F					7.1 A-F
					3.5 T-F					3.0 T-F					4.8 T-F					4.8 T-F

All climate variables that differed significantly between the clusters are shown. Climate values are in mm. BIO12 = annual precipitation, BIO16 = precipitation of the wettest quarter, BIO18 = precipitation of the warmest quarter. Only the four niche exploitation groups that were identified by SIMPER as being the most important in creating the observed pattern of the average overall Bray-Curtis dissimilarity between the faunal clusters are shown: terrestrial herbivores (T-H), terrestrial animalivores (T-A), arboreal frugivores (A-F) and terrestrial frugivores (T-F). The average number of species in each group in the cluster is shown; for example 11.9 T-H indicates that there are an average of 11.9 terrestrial-herbivores at the localities in Faunal Cluster 1 when k = 3. n = the number of localities in each cluster.

same trend across the clusters is observed in the mean precipitation of both the warmest and wettest quarters, such that FC1 has the least amount of rainfall, FC2 has the highest, and FC3 falls in the middle.

Cutting the HCA tree further into four clusters yields only one significant climate difference between them: annual precipitation (BIO12) (Table 3). This analysis divides the cluster with the least amount of precipitation (FC1) from the k = 3 analysis into two new clusters which represent the driest (FC1) and second driest (FC2) of the four (Table 4).

3.1.2. *Niche exploitation groups*

SIMPER results show that there are four niche exploitation groups that are the most important in creating the observed pattern of the average overall Bray-Curtis dissimilarity between the faunal clusters (Supporting Information Table S3a). Terrestrial herbivores, terrestrial animalivores, arboreal frugivores, and terrestrial frugivores cumulatively contribute between 54 and 73 % of the differences between them.

When k = 3, the cluster with the least amount of precipitation, FC1, has the highest average number of terrestrial herbivores and terrestrial animalivores, and the lowest mean number of arboreal frugivores and terrestrial frugivores. FC2, the highest rainfall cluster, has the lowest mean number of terrestrial herbivores. With moderate rainfall, FC3 has the highest mean number of arboreal frugivores and terrestrial frugivores, but the lowest mean number of terrestrial animalivores (Table 4).

Similar to the pattern observed when k = 3, when k = 4 the driest (FC1) and wettest (FC3) cluster are contrasted by having the greatest and lowest mean number of terrestrial herbivores, respectively. The second highest rainfall cluster, FC4, has the greatest average number of arboreal frugivores and terrestrial frugivores combined (11.9), although only marginally higher than FC3, the wettest cluster (11.3). However, these two high rainfall clusters have more frugivorous taxa than the two drier clusters with average combined totals of only 4.7 (FC1) and 5.2 (FC2) frugivores (Table 4).

3.2. *Fossil localities*

When our analytical procedure was conducted with the addition of Uquía or Laetoli there were significant differences with three and four faunal clusters, but when Thum Wimam Nakin is included there were only significant differences when k = 3 and the original clustering

Table 5
Pairwise faunal cluster t-test results from analyses including fossil localities.

Variable	Uquía Formation		Laetoli		TWN
	k = 3	k = 4	k = 3	k = 4	k = 3
BIO1	0.271	0.519	0.271	0.519	0.078
BIO2	0.903	0.900	0.903	0.900	0.382
BIO3	0.973	0.972	0.973	0.972	0.323
BIO4	0.771	0.768	0.771	0.768	0.648
BIO5	0.663	1.000	0.663	1.000	1.000
BIO6	0.388	0.385	0.388	0.385	0.087
BIO7	0.753	1.000	0.753	1.000	0.195
BIO8	0.248	0.954	0.248	0.954	0.162
BIO9	0.416	0.413	0.416	0.413	0.243
BIO10	0.837	0.716	0.837	0.716	0.254
BIO11	0.267	0.265	0.267	0.265	0.109
BIO12	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**0.002**
BIO13	0.091	0.847	0.091	0.847	0.548
BIO14	0.074	0.485	0.074	0.485	**0.014**
BIO15	0.709	1.000	0.709	1.000	**0.029**
BIO16	**0.015**	0.897	**0.015**	0.897	0.127
BIO17	0.140	0.364	0.140	0.364	**0.026**
BIO18	**0.011**	0.085	**0.011**	0.085	**0.001**
BIO19	0.282	0.371	0.282	0.371	0.156
H2OLIM	0.257	0.252	0.257	0.252	**0.016**
TEMPLIM	1.000	1.000	1.000	1.000	0.563
ELEV	0.158	0.282	0.158	0.282	**0.004**

Significant p-values are in bold. TWN = Thum Wimam Nakin. Climate variable definitions in Table 2.

changed (Table 5; k = 2 results are in Supporting Information Tables S1b-d). Table 6 presents the total number of localities (n) in each faunal cluster, as well as the average of every significantly different climate variable and the average number of species in the four most important niche exploitation groups identified by SIMPER (Supporting Information Tables S3b-d).

3.2.1. *Esquina Blanca (Uquía Formation) and Laetoli*

When k = 3 or k = 4 and either the Uquía or Laetoli fauna are added to the analysis, the results are the same as those reported above. Neither the cluster composition (Supporting Information Tables S2a-c) or the bioclimatic variables differing significantly among clusters has changed (Table 5) and therefore the average climate values are also unchanged (Table 6). The addition of the fossil locality fauna may have had a very minor impact on the average number of species in some of the niche exploitation groups in their cluster (for example, there are 3.3 terrestrial frugivores in FC1 when k = 3, but the addition of the Laetoli fauna increases this to 3.4).

When the localities are divided into three clusters, both sites belong to FC1, the driest cluster with the lowest mean annual precipitation (1057 mm/year), and the least amount of rainfall in the wettest and warmest quarters (Table 6). However, when k = 4, the Uquía Formation fauna remains in the driest cluster (832 mm/year), but Laetoli is in the second driest, FC2 (1407 mm/year).

3.2.2. *Thum Wimam Nakin*

The inclusion of Thum Wimam Nakin changed the composition of the original clustering of the modern localities (Supporting Information Table S2d) and the combination of bioclimatic variables that differed significantly among the clusters. When k = 3, a total of seven variables differed including both annual precipitation (BIO12) and the precipitation of the warmest quarter (BIO18) which are significant in the previous analyses (Table 5). Additionally, precipitation of the driest month and quarter (BIO14 and BIO17, respectively), precipitation seasonality (BIO15), elevation (ELEV) and the water limiting factor (H20LIM) are significantly different. No bioclimatic variables were significant when k = 4.

When k = 3, FC1 falls in the middle of the values for each variable where FC2 has the highest average rainfall of any period and the lowest average elevation and FC3 is the driest of any period with the highest average elevation (Table 6). Thum Wimam Nakin is in FC1, which is also the largest cluster with 96 modern localities.

Both FC1 and FC2 have similar average numbers of arboreal and terrestrial frugivores (9.5 and 10.2, respectively) compared to the relatively small average in FC3 localities (2.6). However, FC1 is distinguished from FC2 by its higher number of terrestrial herbivores, although the highest average is in FC3, which also has the greatest number of terrestrial animalivores.

4. Discussion

4.1. *Modern faunal clusters and climate*

Our analysis reveals some clear climatic patterns in the faunal clustering. When there are two clusters (Supporting Information Tables S1a, S1b, S3a) they differ in the majority of the variables such that there is a colder, drier, more seasonal and higher elevation cluster compared to a warmer, wetter, less seasonal and lower elevation cluster. The well-established general relationship between high rainfall and high plant primary productivity (Rosenzweig, 1968; Walter, 1971; Gentry, 1988; Sala et al., 1988; Kay et al., 1997; Nemani et al., 2003) is evident in our results; the “wet” cluster is characterised by a large number of frugivores, whereas the “dry” cluster cannot support them in high numbers. It is known that in areas of high rainfall, vegetation is more diverse and complex and, additionally, these areas have limited cool or dry seasons so that fruiting trees are available throughout the year, thus providing an abundant food source for a large frugivore community.

Temperature is no longer significant when the localities are split into three or four clusters, although it is implicitly important in terms of the amount of rainfall during the warmest quarter of the year (BIO18), which is one of the three significant climate variables when k = 3. It has previously been noted that rainfall has a greater effect on variation in mammal communities than temperature (Andrews and O’Brien, 2000), which our results support. The aforementioned direct relationship between high rainfall and a high number of frugivores is more clearly evident in our results if the average numbers of species in the four most meaningful niche exploitation variable groups are converted to proportions (Fig. 2a and b). If only the raw numbers are considered (Table 4), the highest average number of both arboreal and terrestrial frugivores is associated with a cluster with only moderate rainfall, but proportionally they are still greatest in the highest rainfall clusters (Fig. 2a and b; FC2 when k = 3 and FC3 when k = 4). An additional distinguishing feature of the wettest clusters is the low average number and relative proportion of terrestrial herbivores. The driest cluster is characterised by the highest number of both terrestrial herbivores and terrestrial animalivores when k = 3. This pattern remains when four clusters are identified, demonstrating that low average rainfall across the year and rainfall that occurs seasonally results in the types of vegetation suitable for terrestrial browsers and grazers (Olff et al., 2002; Hopcraft et al., 2010) and, in turn, the terrestrial predator guild. Conversely, these vegetation types are unsuitable for a large number of arboreal species, particularly arboreal frugivores. The driest of the four clusters, in fact, has the smallest proportion of these species (Fig. 2b). It appears that at average annual rainfall values below approximately 1950 mm/yr, the number of frugivores is limited. Where k = 4 (Fig. 2b), FC2 is defined by an average annual precipitation value of 1407 mm/yr and approximately 12 % of the mammal community are arboreal frugivores. FC3 and FC4, however, have annual precipitation values of 1957 mm/year or greater, and the proportion of arboreal frugivores in their communities is approximately 32–35 %. In light of this, it is interesting to note that at very high levels of annual rainfall in the realm of 2000–2500 mm/yr and above, plant productivity does not continue to increase on a global scale (Kay et al., 1997) and species richness declines (Olff et al., 2002).

4.2. *Climate reconstructions*

The three localities subjected to climate reconstructions were specifically chosen as test cases because their well-sampled fauna provide robust datasets for this community-based method and given their differences in location and age, they provide an opportunity to explore how well the method performs in different circumstances. Confidence in a climate reconstruction stems partly from the degree to which the inclusion of the fossil fauna changes the overall clustering pattern observed in the analysis restricted to the modern localities. The faunal clustering is not affected by either the Uquía Formation or Laetoli (see Table 6). They are taxonomically distinct from extant communities, being comprised of a large number of extinct species (see Supporting Information Dataset S3a and b). This is particularly the case for the Uquía Formation which includes, for example, the pre-GABI endemic and extinct family Glyptodontidae representing nearly a third of the mammals. That such taxonomically unique fauna have not impacted the clustering speaks to the utility of this “taxon-free” methodology.

The Uquía Formation consistently clusters with the driest localities suggesting that it had a low average annual rainfall; its cluster average when k = 4 is 832 mm/yr. The k = 3 analysis also indicates that it had low rainfall during both the warmest and wettest quarters of the year. Reguero et al. (2007) concluded that the area was more humid than it is now, with some evidence to support seasonal patterns in rainfall. Today Esquina Blanca receives only an average of 220 mm/yr (based on our grid cell average values computed from the WorldClim dataset). Our results indicate that in the past it was a relatively dry and likely seasonal

Table 6

Bioclimatic variable values and average number of species in niche exploitation groups by faunal cluster (with fossil localities).

Variable			Faunal Cluster 1					Faunal Cluster 2					Faunal Cluster 3					Faunal Cluster 4			
	fossil #		climate values			species		climate values			species		climate values			species		climate values			species
UQUÍA FORMATION																					
k = 3		***n* = 75***					**n = 37**					**n = 56**									
		min	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**						
BIO12	12 T-H	304	1057	4221	678	11.9 T-H	1137	2431	3524	691	1.4 T-H	515	1952	3269	632	6.3 T-H					
BIO16	1 T-A	148	577	3293	450	8.1 T-A	523	967	1445	241	6.0 T-A	346	785	1337	238	4.2 T-A					
BIO18	0 A-F	32	283	1101	173	1.6 A-F	156	536	1266	244	6.5 A-F	134	434	844	167	7.1 A-F					
	0 T-F					3.2 T-F					4.8 T-F					4.8 T-F					
k = 4		**n = 46***					**n = 29**					**n = 37**					**n = 56**				
		min	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**	
BIO12	12 T-H	304	832	1554	309	15.6 T-H	590	1407	4221	917	5.9 T-H	1137	2431	3524	691	1.4 T-H	515	1952	3269	632	6.3 T-H
	1 T-A					9.0 T-A					6.8 T-A					6.0 T-A					4.2 T-A
	0 A-F					1.2 A-F					2.2 A-F					6.5 A-F					7.1 A-F
	0 T-F					3.4 T-F					3.0 T-F					4.8 T-F					4.8 T-F
LAETOLI																					
k = 3		**n = 75***					**n = 37**					**n = 56**									
		min	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**						
BIO12	31 T-H	304	1057	4221	678	12.1 T-H	1137	2431	3524	691	1.4 T-H	515	1952	3269	632	6.3 T-H					
BIO16	18 T-A	148	577	3293	450	8.4 T-A	523	967	1445	241	6.0 T-A	346	785	1337	238	4.2 T-A					
BIO18	0 A-F	32	283	1101	173	1.6 A-F	156	536	1266	244	6.5 A-F	134	434	844	167	7.1 A-F					
	12 T-F					3.4 T-F					4.8 T-F					4.8 T-F					
k = 4		**n = 45**					***n* = 30***					**n = 37**					**n = 56**				
		min	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**	
BIO12	31 T-H	304	832	1554	309	15.7 T-H	590	1407	4221	917	6.8 T-H	1137	2431	3524	691	1.4 T-H	515	1952	3269	632	6.3 T-H
	18 T-A					9.2 T-A					7.1 T-A					6.0 T-A					4.2 T-A
	0 A-F					1.2 A-F					2.1 A-F					6.5 A-F					7.1 A-F
	12 T-F					3.5 T-F					3.3 T-F					4.8 T-F					4.8 T-F
THUM WIMAM NAKIN																					
k = 3		***n* = 97***					**n = 46**					***n* = 25**									
		min	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**		**min**	**ave**	**max**	**SD**						
BIO12	14 T-H	515	1696	4221	761	8.6 T-H	590	2121	3524	895	1.5 T-H	304	685	1378	268	15.8 T-H					
BIO14	1 T-A	0	40	228	48	5.6 T-A	1	61	207	55	6.2 T-A	0	6	61	12	9.8 T-A					
BIO15	5 A-F	13	70	162	34	5.2 A-F	11	58	104	21	5.5 A-F	31	95	171	32	0.1 A-F					
BIO17	3 T-F	0	149	791	158	4.3 T-F	9	69	677	172	4.7 T-F	0	27	235	48	2.5 T-F					
BIO18		83	383	1101	190		107	501	1266	237		32	211	386	104						
H2OLIM		0.0	22.5	69.0	19.3		0.0	14.5	51.9	15.3		0.0	47.8	73.5	18.1						
ELEV		18	648	1862	524		12	391	2379	419		283	1102	2179	491						

All climate variables that differed significantly between the clusters are shown. Biolcimatic variable codes as in Table 2. Only the four niche exploitation groups that were identified by SIMPER as being the most important in creating the observed pattern of the average overall Bray-Curtis dissimilarity between the faunal clusters are shown: terrestrial herbivores (T-H), terrestrial animalivores (T-A), arboreal frugivores (A-F) and terrestrial frugivores (T-F). The average number of species in each group in the cluster is shown; for example, in the Uquía Formation analysis, 11.9 T-H indicates that there are an average of 11.9 terrestrial-herbivores at the localities in Faunal Cluster 1 when k = 3.

The fossil fauna belongs to the cluster denoted with a *.

n = the number of localities in each cluster.

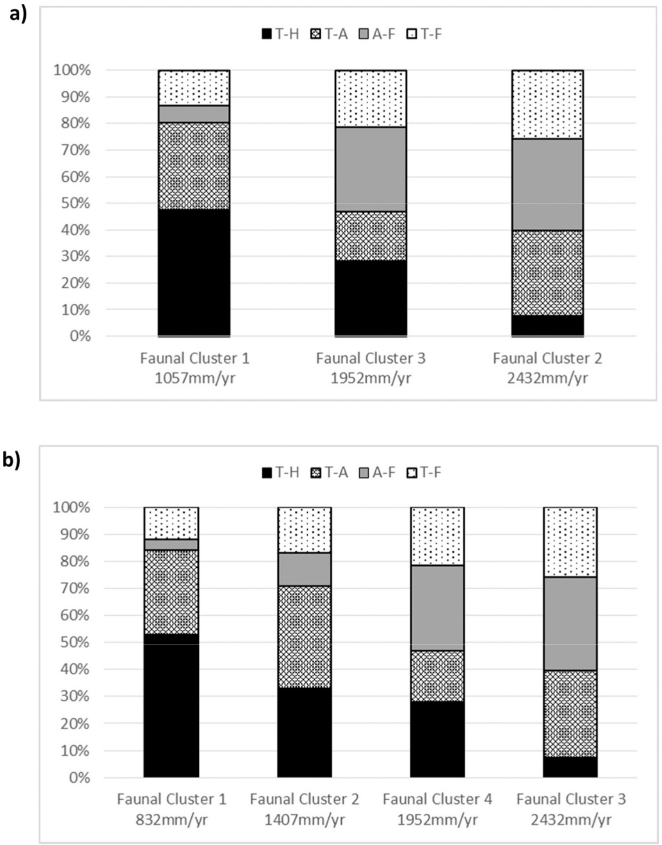

Fig. 2. Proportions of species in four niche exploitation variable groups in (a) three and (b) four clusters of modern localities. The faunal clusters are ordered right to left according to their average annual rainfall. The four niche exploitation groups are: terrestrial herbivores (T-H), terrestrial animalivores (T-A), arboreal frugivores (A-F) and terrestrial frugivores (T-F).

climate, and that it may have received more annual rainfall than at present, but the results do not necessarily indicate greater humidity. Reguero et al.'s (2007) climate interpretations were derived largely from the presence of ecologically-sensitive morphologies observed in the fossil community including the relatively brachydont dentition of the camelids (although the Uquía camels are known from the Upper and not the Middle Unit, which was the focus of our analysis). Their specific conclusion of humidity was based on the presence of a crocodilian tooth, as crocodiles today are observed in mostly humid tropical and subtropical environments. However, in climate analyses the presence of these ectotherms is linked to temperature but not to rainfall or other factors, although their richness does tend to decrease in arid areas (Markwick, 1998; Mannion et al., 2015). The presence of a crocodilian thus indicates the availability of freshwater, which is not at odds with hydrogeological reconstructions of the Quebrada de Humahuaca as a braided river system (Galli et al., 2021). Nor is it at odds with inferences drawn from studies of the small mammals and volcanic ash isotopes which suggest this time period was characterised by increasing aridity as Andean uplift continued (Ortiz et al., 2012; Pingel et al., 2014). Note that although extant crocodiles are not found at high elevations and indeed are only present today in the Andean foothills, Esquina Blanca was likely 1000+ metres lower than its current 2800 m elevation. At lower elevations, temperatures are less likely to dip below the crocodilian threshold of 14.4 °C for mean annual temperature (Markwick, 1998).

Although the Uquía fauna consistently clusters with the driest localities and bears the hallmark high number of terrestrial herbivores characteristic of dry climate fauna, it's important to note that it is unusual in lacking terrestrial animalivores, as well as terrestrial or arboreal frugivores. Pre-GABI South American faunas are well known for endemic families and other characteristics, such as a lack of meso- and hypocarnivores (Simpson, 1980; Croft, 2006; Croft et al., 2018; Domingo et al., 2020). Some of these characteristics are evident at Uquía; for example, two of the three animalivores present are semi-subterranean armadillos (the other is an unidentified Felinae). There are also no strictly arboreal taxa (although a handful of species that are partly arboreal and partly terrestrial) and there is only one frugivore present in *Erethizon* (Supporting Information Dataset S3a) (note that although its taxonomic identification is contested, the dietary classification would not change if it was reclassified as *Coendou* as suggested by Sussman (2011)). The clustering of Uquía here is a function of its high number of terrestrial herbivores in relation to the other three most meaningful niche exploitation groups and, to a lesser extent, the two semi-subterranean taxa (Table S3b).

Like Uquía, Laetoli does not change the clustering of the modern localities, is characterised by a large proportion of terrestrial herbivores and few arboreal taxa, and is nested in the driest, coolest and most seasonal faunal cluster when k = 2 and k = 3, (Supporting Information Table S1d, Table 6). However, when k = 4, Laetoli is situated in the second driest cluster where the average annual rainfall is 1407 mm/yr. Today the Serengeti ecosystem is quite arid with a highly seasonal, low rainfall regime known for its unpredictability (Norton-Griffiths et al., 1975). Laetoli is located in the southern part of the Serengeti in an area with greater topographic relief and a more variable rainfall regime than the plains. According to the Tanzania Natural Resources Information Centre's (TANRIC) land-cover map it receives approximately 700–900 mm of rainfall a year (Andrews et al., 2011), which encompasses the value of 799 mm/yr that we calculate for its grid cell. Earlier studies of the geology, gastropods, and flora concluded that the Pliocene conditions were more humid than modern times (Hay, 1987; Bonnefille and Riollet, 1987; Verdcourt, 1987); a shift towards open and drier conditions is not noted until the younger Upper Ndolanya Bed sequence (Kingston, 2011; Kovarovic and Andrews, 2011; Rossouw and Scott, 2011; Su, 2011; Tattersfield, 2011). Our analysis accords with suggestions that the area was wetter in the past, but our annual rainfall estimate based on the cluster average is higher than the 650–1000 mm/yr range suggested by Verdcourt's (1987) analysis of gastropods.

Thum Wimam Nakin is represented by the youngest fauna with only extant species (Supporting Information Dataset S3c), so the community is modern from a taxonomic perspective. Despite this, it changes the overall clustering patterns reported in all of the other analyses. Firstly, there are no significantly different climate variables between the clusters when k = 4. Secondly, the composition of each faunal cluster and the significant bioclimatic variables among the clusters are different. The site falls in a large cluster of generally moderate precipitation values where annual rainfall averages 1696 mm, but the average and maximum rainfall values during the driest quarter of the year are the highest of any cluster (149 mm and 791 mm, respectively) (Table 6). This characteristic did not emerge as significant in the other analyses, but would infer that the faunal communities in the cluster are presented with vegetation resources that change seasonally, but are not restricted by a more extreme lack of rainfall at any time of the year.

General inferences can be made about this locality despite the changes it introduces to the clustering. The results reported here do not contradict previous work, particularly an earlier estimate of 1614 mm annual rainfall based on murine species richness (Tougard and Montuire, 2006). This and the cluster average (1696 mm) from our analysis are similar, and certainly higher than the approximately 1130 mm/yr the area receives today, which is characterised by a tropical forest (Pushkina et al., 2010). Other studies have also shown that the area was humid, but much wetter and cooler in the past (Chaimanee, 1998; Tougard and Montuire, 2006). Further, there were probably more extensive areas of open forest, which are indicated by the isotopic signatures from across the palaeocommunity, including primates, ungulates, rodents, and carnivores, point towards a much greater amount of C4 consumption than the modern mammalian community (Pushkina et al., 2010). The presence of open forest is not at loggerheads with the number of frugivorous species ($n = 8$) at the site either; these species would easily survive in areas with the amount of woody vegetation that is present in areas of moderate precipitation, such as that predicted for Thum Wimam Nakin.

4.3. Non-analog fauna

The impact of including Thum Wimam Nakin on the clustering raises the issue of non-analog fauna and the challenge of using such fauna to infer ecological or climate conditions in the past. Although the Ward's linkage method used in the HCA, which minimises variance within each cluster, is less susceptible to outliers than other linkage methods, it is not immune (Milligan, 1980; Cheng and Milligan, 1996) and an extreme outlier will, in fact, form a singleton cluster. The addition of Thum Wimam Nakin has not had such an extreme effect, but it has changed the boundaries of the resultant clusters. The analysis cannot specifically identify the site as a non-analog fauna, but its impact on the clustering indicates that it does not share the same characteristics as the modern comparative sites.

While much has been written about non-analog fauna, flora and habitats (e.g. Coope, 1987; Graham and Grimm, 1990; Alroy, 1999; Stafford Jr. et al., 1999; Graham, 2005; Soligo and Andrews, 2005; Williams and Jackson, 2007; Faith et al., 2019; Catena and Croft, 2020), there is no consensus on the exact parameters of such non-analogous communities, although definitions broadly coalesce around how the constituent species occupy niches in a structure that is different from any community structure today, or by extension that the community occupied a habitat in the past that has no modern comparison. Could Thum Wimam Nakin represent a non-analogous community, but one that is, geologically-speaking, quite modern? There are other examples of relatively recent non-analog Asian habitats, such as the mammoth steppe which was present in high latitudes across Eurasia and North America during the Mid to Late Pleistocene (see Guthrie, 2001; Zimov et al., 2012). However, the Pleistocene fossil record of this area of Asia samples terrestrial migrating mammals that entered the region during glacial periods; northern fauna, such as the goral, moved southward as an open savanna corridor expanded into Thailand (Tougard, 2001; Louys et al., 2007; Suraprasit et al., 2019; Suraprasit et al., 2023). An exchange of taxa between the Indochinese and Sundaic ecoregions also became possible with exposed land bridges when the sea level was low, although migration was restricted to some degree by the persistence of rainforest refugia in peninsular Thailand which acted as a barrier for some taxa (Suraprasit et al., 2019; Suraprasit et al., 2023).

As noted, all of Thum Wimam Nakin's fauna are extant. However, these extant species are clearly found at the site in an unusual association. Many of Thum Wimam Nakin's taxa are also regionally extinct in Thailand, such as *Pongo* and *Ailuropoda* (Louys et al., 2007). Others such as *Felis tigris* are generally absent from sites of the same age in Thailand, yet are known from this assemblage (Suraprasit et al., 2021). We could therefore argue that Thum Wimam Nakin is a non-analog fauna, but the explanation hinges on the fact that this region of Asia was the site of two regionally distinct communities mixing during migrations between the mainland and southeastern Asia during glacial periods (Tougard, 2001). We note that the two rhinoceros species present, *Rhinoceros unicornis* and *Rhinoceros sundaicus,* represent the Indochinese and Sundaic ecoregions, respectively. It can be assumed that the forest mosaic habitats of the time period, which included more open savanna-like areas to some degree, were capable of supporting their different dietary behaviours (*R. unicornis* is largely a grazer whilst *R. sondaicus* is a browser), and indeed the atypical association of herbivorous fauna and predators that existed at the time. Thus, the mixing of two regionally distinct fauna here creates the superficial appearance of a single non-analog community representing a habitat unknown today.

A large global sample of extant communities such as ours is effective at mediating against some of the problems caused by studying what might be regionally non-analogous palaeocommunities. Although it seems intuitive that if one wishes to understand the past of a locality in a particular biogeographical region, that other communities from that region have a greater likelihood of being more informative, this does not allow for the possibility that a palaeocommunity more closely resembles an extant one that is geographically distant. Communities evolve over time; there is good evidence, for example, that African mammal communities attained their modern structure only in the past 700,000 years (Faith et al., 2019). Using a global comparative dataset captures a greater level of diversity in mammal niche exploitation patterns than would be evident in a geographically restricted study. The importance of this has also been demonstrated for South American Miocene sites which share structural similarities with modern Asian faunas (Catena and Croft, 2020).

5. Conclusion

This study has shown that, on a global scale, tropical mammal community niche exploitation profiles can be used to define clusters of modern localities that share similar climate characteristics, particularly in relation to rainfall variables. In turn, palaeocommunity profiles can be used to predict past climate conditions, demonstrated by analyses of the Uquía Formation, Laetoli and Thum Wimam Nakin, although the latter site demonstrates how issues of historical contingency matter in the interpretation. This work builds on both mammal community and ecometric research that has focussed on specific morphologies and ecological diversity as it relates to differences in physical habitat types (Fleming, 1973; Andrews et al., 1979; Reed, 1998; Andrews and Humphrey, 1999; Mendoza et al., 2005; Louys et al., 2011; Lintulaakso and Kovarovic, 2016) or individual climate parameters (Kay and Madden, 1997; Fortelius et al., 2002; Eronen et al., 2010a, 2010b; Fortelius et al., 2016; Rowan et al., 2016; Žliobaitė et al., 2016).

CRediT authorship contribution statement

Kris Kovarovic: Methodology, Investigation, Funding acquisition, Data curation, Conceptualization, Writing – original draft. **Kari Lintulaakso:** Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2025.112860.

Data availability

All data used in this research are available in supplementary files.

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