



Chapter 2

The Southern Levant During the Last Glacial and Zooarchaeological Evidence for the Effects of Climate-Forcing on Hominin Population Dynamics

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Abstract Climate forcing has been suggested as a possible explanation for dispersal/extinction of hominins in the Southern Levant during the Middle Paleolithic (MP). Evidence from fauna has produced ambiguous results, suggesting that inter-site variation in Last Glacial faunas reflect spatial differences within the region. This study presents a multivariate approach to test the effect of climate change on mammalian communities during the Last Glacial in the Levant and analyzes the distribution of micro and macromammals from the site in the Levant spanning Marine Isotope Stage (MIS) 6-2 using non-metric multidimensional scaling (NMMDS). Results indicate that inter-site differences in faunal composition of Middle Paleolithic sites in the Levant do not reflect an abrupt climate change but are consistent with a spatial environmental mosaic within the Levant. This suggests that although hominin taxa show evidence of turnover during the Late Pleistocene in the Levant, we need to be more cautious about the role of climate forcing in the process.

Keywords Neanderthal extinction • Faunal response to climate change • Mammal community structure • NMMDS

Introduction

The past years have seen a growing interest in the role of climate in European Neanderthal population dynamics (Gamble et al. 2004; Stewart 2005; Finlayson et al. 2006; Finlayson and Carrion 2007; Tzedakis et al. 2007). Several hypotheses have been suggested for the extinction of the Neanderthals in Europe. Primarily, it has been suggested that

modern humans outcompeted the Neanderthals when they arrived in the Europe around 40–45 ka (Bar-Yosef 2000; Kuhn et al. 2004; Mellars 2004, 2006). In contrast, it has been suggested that an increase in climatic fluctuations during the Last Glacial may have led to a fragmentation of Neanderthal habitats, leading to a decrease in the effective population size and finally to their extinction (Finlayson 2004; Finlayson et al. 2006; Finlayson and Carrion 2007). While this hypothesis has gained traction based on a wide range of paleoecological evidence in Europe, which points to an increase in amplitude, frequency and variability of climate change towards the end of the Last Glacial (Guiot et al. 1993; Gamble et al. 2004; Miracle et al. 2009), the paleoecological situation in the Southern Levant is more complex and suggests that a “one answer fits all” solution may not be applicable to the question of the effect of climate on large hominins in general and the Neanderthals in particular.

The Southern Levant is located in mid-latitudes and has a more temperate climate than Europe and more moderate climatic fluctuations (Enzel et al. 2008). It therefore provides us with a unique opportunity to study the possible effect of climate change during the Last Glacial on the Levantine Neanderthal population and their extinction from the region around 45 ka. Within this context it is of interest to test how environmental and climatic changes played out in this local arena in relation to the Levantine populations of Neanderthals.

Tchernov (1992) raised the hypothesis of the relationship between climate change and hominin taxa in the Levant. He suggested that faunal turnover of rodent taxa between MIS 5 and 4 and between MIS 4 and 3 was concurrent with observed shifts in hominin species. The shift between Anatomically Modern Humans (AMH) and Neanderthals (Valladas et al. 1987, 1999; Schwarcz et al. 1989; Valladas and Joron 1989; Solecki and Solecki 1993; Rink et al. 2003) coincided with a shift from a Saharo-Arabian rodent community to that dominated by a more Euro-Siberian rodent community. This shift is dated to the MIS 5/4 transition. The shift between Neanderthals and modern humans (Millard

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2008) coincided with a shift from a Euro-Siberian rodent community back to a Saharo-Arabian one, dated to the MIS 4/3 transition. This hypothesis was based on faunal data from two main sites: Qafzeh, dated to 100–90 ka, and Kebara, dated to ca. 65 ka. However, these two sites are located in two distinct regions in the Southern Levant, Qafzeh being further east than Kebara, which is located in Mount Carmel on the Coast. In contrast to this hypothesis, Jelinek suggested that the observed differences between the micromammal communities might result from the east-west differences in precipitation and an ecotone gradient in vegetation and microhabitat climate rather than temporal differences (Jelinek 1982).

Since the original development of these hypotheses, Shea (2008) proposed that the human population turnover in the Southern Levant was climatically driven. This was based on a wide array of paleoclimate proxies such as speleothem isotope data, ocean foraminifera, and pollen cores, which pointed to a paleoecological pattern of aridification throughout MIS 4, culminating in a cold and dry period known as the Heinrich 5 (H5) event. This temporal paleoclimatic pattern was interpreted as a regional decrease in environmental productivity, which led to the demise of the local Levantine Neanderthals similar to the model proposed for Europe (Shea 2008).

The aim of this paper is to reevaluate the evidence for an environmental shift, which occurred between Marine Oxygen Isotope Stage (MIS) 4 and 3 and which may have contributed to the extinction of the Levantine Neanderthals. This analysis will use data derived from Southern Levantine assemblages of small and large mammals dated to the Last Glacial. It is hypothesized that if the regional environmental mosaic is the driving force that controls the variance in fauna among sites during the Last Glacial, it will reveal a spatial patterning according to geographic provenance related to rainfall and/or annual temperature (Danin and Orshan 1990). On the other hand, if global climate change is the trigger for the change in faunal communities in the Southern Levant, we will see a greater similarity among sites of similar age than of similar region.

The Levant

The Levant is a unique biogeographic entity within Southwestern Asia. It lies at the crossroads of Africa and Eurasia and has more lush environments when compared to the alternative dispersal corridor on the southern fringes of the Arabian Peninsula (Thomas 1985; Tchernov 1988). The southern path through the margins of the Arabian Peninsula could be crossed at the Bab el-Mandeb straits during low sea level stands, and along the area that receives the summer

Indian Ocean monsoon to be followed by a passageway through the Hormuz straits into the southern coast of Iran; a northern path could have been taken via the Nile river and the Sinai Peninsula.

The East Mediterranean region is located between the more temperate European climatic zone in the north and the hyper arid regions of the Saharo-Arabian desert belt in the south (Frumkin and Stein 2004). Southwestern Asia includes fauna from three biogeographic provinces: Palaearctic, Oriental and Ethiopian in different proportions depending on the environmental condition in each phytogeographic region (Harrison and Bates 1991). Many animal taxa are similar over two or more provinces, giving the entire Near East a coherent faunal community (Harrison and Bates 1991). Two main regions can be observed: the first includes the Mesic Mediterranean, Pontic and Iranian plateau provinces with Palaearctic taxa, and the second includes the Xeric Mediterranean and Arabian provinces with Ethiopian elements.

Methods

Data from herbivores from two groups of taxa differing in size, namely medium-sized herbivores and micromammals, were analyzed. Micromammals include taxa smaller than one kilogram (kg) (e.g., Andrews 1990). Confining the analysis to taxa of a similar size range (in the broad sense), and a community of trophically similar and sympatric species (Hubbell 2001), reduces the effect of sampling of rare species (such as primates and carnivores) as well as collection bias of smaller and larger taxa. The use of individual abundance data, i.e., Number of Identified Specimens or NISP, is particularly problematic in fossil analyses as it is mostly driven by taphonomic rather than paleoenvironmental factors (Behrensmeyer et al. 2000).

Only data for presence absence was used to maintain high ecological fidelity. Using relative abundance (i.e., those for which we could observe a change in the relative abundance of a species which can be related to climatic change) rests on our ability to remove one or more taphonomic biases, which may erroneously produce the appearance of change where one may not have existed. For example, given two assemblages, if one was accumulated by carnivores and the other not, the selectivity of prey by carnivores may increase the proportion of specific species in the fossil (death) assemblage compared to an assemblage accumulated by other factors. This would create the impression that an increase in species proportion had occurred between strata, when in actuality it did not.

Analysis of taphonomic factors and live-death comparisons has shown that presence-absence preserves the strongest fidelity between the living community and the death

assemblage, followed by rank abundance (Kidwell and Flessa 1995, 1996; Roy et al. 1996; Behrensmeyer et al. 2000; Rogers and Kidwell 2000; Kidwell 2001, 2002, 2008; Kidwell et al. 2001; Kidwell and Holland 2002; Zohar et al. 2008; Tomasovych and Kidwell 2009; Terry 2010; Belmaker and Hovers 2011). Evidence for the fidelity of relative abundance for vertebrates such as micromammals (Terry 2010) is usually limited to recent death accumulation with time and space averaging of up to several hundreds rather than thousands of years.

Macromammal and micromammal data from archeological sites were retrieved from the literature. The macromammal sites, date and the reference from which they were retrieved are presented in Table 2.1 and the micromammal sites, date and the reference from which they were retrieved are presented in Table 2.2. Location of sites mentioned in the text are shown in Fig. 2.1a (Middle Paleolithic) and b (Upper Paleolithic). The strength of meta-analysis, such as this, which relies on data retrieved from the literature, is in the ability to amass large dataset, which provides robust statistical results. However, when using published literature, the difficulty is in controlling for similar data acquisition. Since method of excavation highly affects both species richness and abundance, we can expect fauna richness to differ among sites with different collection protocols. Total number of NISP from the sites ranged from 2 to over 8000 for macromammals and from 79 to over 28,000 for the micromammals.

In order to correct for sites that were under-sampled, only sites with five or more species recovered at the site were included. A minimum of five species per site was chosen as a cut off number as it was the median number of species per site in the assemblages. This procedure was adopted to avoid the problem of under-sampling due either to small sample size or to high selectivity, both of which would not represent the environment adequately. While it is possible that some sites with low number of species were not entirely representative of the environment, the main premise of this study was similarity or dissimilarity among site that was achieved by maintaining similar sampling strategies among sites while maintaining a large enough sample size sites over all.

Macromammal species used in the analysis included *Hippopotamus amphibius*, *Coelodonta antiquitatis*, *Bos primigenius*, *Cervus elaphus*, *Dama mesopotamica*, *Capreolus capreolus*, *Sus scrofa*, *Alcelaphus buselaphus*, *Equus asinus*, *Equus* cf. *mauritanicus*, *E. hemionus* and *E. hydruntinus*. Other species were identified at the genus level due to similarities between congeneric taxa; identification to the species level was not always possible when two species may be present at the same site. These included *Ovis/Capra/Ibex*, *Gazella* sp., *Equus* sp., and *Camelus* sp. Micromammal taxa included in this study were: *Suncus etruscus*, *Suncus murinus*, *Crocidura russula*, *Crocidura leucodon*, *Talpa chthonia* (= *T. davidiana*), *Sciurus anomalus*, *Myomimus*

qafzensis, *Myomimus roachi* (= *Myomimus personatus*), *Allocricetulus magnus*, *Mesocricetus auratus*, *Cricetulus migratorius*, *Gerbillus dasyurus*, *Meriones tristrami*, *Spalax ehrenbergi*, *Ellobius fuscocapillus*, *Microtus guentheri*, *Arvicanthus ectos*, *Mastomys batei*, *Mus macedonicus*, *Apodemus mystacinus*, *Apodemus sylvaticus*, *Apodemus flavicollis*, *Arvicola terrestris*, *Acomys cahirinus*, *Rattus rattus*. Several taxa were only analyzed at the genus level due to several sympatric congeners and included: *Dryomys* sp., *Psammomys* sp., *Eliomys* sp., *Allactaga* sp., and *Jaculus* sp.

Data were derived from sites spanning MIS 6-2 throughout Southern Levant. Data were analyzed by two different independent variables. The first was *environment* and the second was *period*. Five environmental categories were chosen based on precipitation level (Danin and Orshan 1990) and are presented in Table 2.3.

In order to assign the variable *Period* to sites, I relied on cultural period attribution derived from the literature. The chronology of the Middle and Upper Paleolithic of the Levant has been based on the succession of the Levantine Mousterian lithic assemblages based on the three phase model proposed by Copeland and modeled after the three major phased in Tabun Cave: Tabun D, C and B. Subsequently named Early Middle Mousterian, Middle Middle Mousterian and Later Middle Mousterian (see Shea 2003 for details). Radiometric dates using ^{14}C , TL, ESR and U series that were applied to sites were able to confirm the basic model. These three stages also corresponded to MIS 7-6, MIS 4 and MIS 4/3 respectively (Wallace and Shea 2006 and references therein). Since many sites with faunal remains were assigned to the different lithic traditions but were not radiometrically dated, we used these traditions as markers of chronology, albeit relative, because it allowed a larger subset of sites and has been proven to span the geographic range of the southern Levant in this paper (Bar-Yosef 1992). Table 2.4 presents the list of cultural entities used and the estimate absolute dates assigned to them. Since we wanted to include several younger sites from the Upper Paleolithic, we continued with the scheme as well for the younger sites.

To analyze the data, non-metric multidimensional scaling (NMMDS) was used, which is a non-parametric version of principal coordinates analysis (PCA). PCA is used on parametric variables only, while NMMDS is based on a similarity/distance matrix, thus non-parametric. It attempts to approximate the ranks of the dissimilarities between sites based on species occurrences. NMMDS creates a configuration of points whose inter-point distances approximate a monotonic transformation of the original dissimilarities. The algorithm then attempts to place the data points in a two- or three-dimensional coordinate system such that the ranked differences are preserved. For example, if the original distance between points three and eight is the tenth largest of all distances between any two points, points three and eight will be

Table 2.1 List of sites used in macromammal analysis

#	Site	Culture	Environment	Reference for fauna
1	Ein Difla	Tabun D	Arid	Lindley and Clark (1987) in Shea (2003)
2	Bezez Cave B	Tabun D	Hyper Mesic Mediterranean	Garrard (1982) in Shea (2003)
3	Hayonim E > 405 bd	Tabun D	Mesic Mediterranean	Stiner and Tchernov (1998) in Shea (2003)
4	Tabun D	Tabun D	Mesic Mediterranean	Bar-Yosef (1989) in Shea (2003)
5	Rosh Ein Mor	Tabun D	Semi Arid	Tchernov (1986) in Shea (2003)
6	Ksar Akil 18-10	Tabun C	Hyper Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
7	Naamé	Tabun C	Hyper Mesic Mediterranean	Fleisch (1970) in Shea (2003)
8	Ras el Kelb A-O	Tabun C	Hyper Mesic Mediterranean	Garrard (1982) in Shea (2003)
9	Tabun C	Tabun C	Mesic Mediterranean	Bar-Yosef (1989) in Shea (2003)
10	Hayonim E < 405 bd	Tabun C	Mesic Mediterranean	Stiner and Tchernov (1998) in Shea (2003)
11	Qafzeh V–XV	Tabun C	Xeric Mediterranean	Rabinovich and Tchernov (1995) in Shea (2003)
12	Qafzeh XVI–XXIV	Tabun C	Xeric Mediterranean	Rabinovich and Tchernov (1995) in Shea (2003)
13	Dederiyeh 11	Tabun C-B	Semi Arid	Griggo (1998) in Shea (2003)
14	Dederiyeh 3	Tabun C-B	Semi Arid	Griggo (1998) in Shea (2003)
15	Douara III	Tabun B	Arid	Payne (1983) in Shea (2003)
16	Douara IV	Tabun B	Arid	Payne (1983) in Shea (2003)
17	Amud B	Tabun B	Mesic Mediterranean	Rabinovich and Hovers (2004)
18	Skhul B	Tabun B	Mesic Mediterranean	Bar-Yosef (1989) in Shea (2003)
19	Tabun B	Tabun B	Mesic Mediterranean	Bar-Yosef (1989) in Shea (2003)
20	Kebara F	Tabun B	Mesic Mediterranean	Davis (1982) in Shea (2003)
21	Umm el Tlel V2βa	Tabun B	Semi Arid	Griggo (1998) in Shea (2003)
22	Umm el Tlel VIIa	Tabun B	Semi Arid	Griggo (1998) in Shea (2003)
23	Umm el Tlel VI3 b'1	Tabun B	Semi Arid	Griggo (1998) in Shea (2003)
24	Far'ah II L.1	Tabun B	Semi Arid	Gilead and Grigson (1984) in Shea (2003)
25	Far'ah II L.2	Tabun B	Semi Arid	Gilead and Grigson (1984) in Shea (2003)
26	Abu Noshra I	MP-UP transition	Arid	Phillips (1988) in Rabinovich (2003)
27	Abu Noshra II	MP-UP transition	Arid	Phillips (1988) in Rabinovich (2003)
28	Abu Halka IVd	MP-UP transition	Hyper Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
29	Antelias	MP-UP transition	Hyper Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
30	Abu Halka IVf	MP-UP transition	Hyper Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
31	Abu Halka IVe	MP-UP transition	Hyper Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
32	Ksar Akil 6-9	MP-UP transition	Hyper Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
33	Abu Halka IVc	MP-UP transition	Hyper Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
34	Ain Aqev (D31)	MP-UP transition	Semi Arid	Tchernov (1976) in Rabinovich (2003)
35	Shukbah D	MP-UP transition	Xeric Mediterranean	Garrod and Bate (1942) in Shea (2003)
36	El Wad E	Early Ahmarian	Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
37	Kebara III	Early Ahmarian	Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
38	Emireh	Early Ahmarian	Mesic Mediterranean	Bate (1927) in Rabinovich (2003)
39	El Wad F	Early Ahmarian	Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
40	Erq el Ahmar B	Early Ahmarian	Semi Arid	Vaufrey (1951) in Rabinovich (2003)
41	Erq el Ahmar C	Early Ahmarian	Semi Arid	Vaufrey (1951) in Rabinovich (2003)
42	Erq el Ahmar D	Early Ahmarian	Semi Arid	Vaufrey (1951) in Rabinovich (2003)
43	Erq el Ahmar E	Early Ahmarian	Semi Arid	Vaufrey (1951) in Rabinovich (2003)
44	Erq el Ahmar F	Early Ahmarian	Semi Arid	Vaufrey (1951) in Rabinovich (2003)
45	Qafzeh	Early Ahmarian	Xeric Mediterranean	Rabinovich (1998) in Rabinovich (2003)
46	Hayonim D3	Levantine Aurignacian	Mesic Mediterranean	Rabinovich 1998 in Rabinovich (2003)
47	Hayonim D1/2	Levantine Aurignacian	Mesic Mediterranean	Rabinovich (1998) in Rabinovich (2003)
48	Rakefet B-G 18-23 XVI	Levantine Aurignacian	Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
49	Rakefet B-G 18-23 XV	Levantine Aurignacian	Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
50	Hayonim D4	Levantine Aurignacian	Mesic Mediterranean	Rabinovich (1998) in Rabinovich (2003)
51	Sefunim 9-11	Levantine Aurignacian	Mesic Mediterranean	Tchernov (1984) in Rabinovich (2003)
52	Rakefet B-G 18-23 XIV	Levantine Aurignacian	Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)

(continued)

Table 2.1 (continued)

#	Site	Culture	Environment	Reference for fauna
53	El Wad D	Levantine Aurignacian	Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
54	Yabrud II	Levantine Aurignacian	Semi Arid	Lehmann (1970) in Rabinovich (2003)
55	El Quesir D	Levantine Aurignacian	Semi Arid	Perrot (1955) in Rabinovich (2003)
56	El Quesir C	Levantine Aurignacian	Semi Arid	Perrot (1955) in Rabinovich (2003)
57	El Wad C	Atlitian	Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
58	Nahal Ein Gev I	Atlitian	Xeric Mediterranean	Davis (1982) in Rabinovich (2003)
59	Tor Hamar G	Nebekian	Arid	Klein (1995) in Rabinovich (2003)
60	Uwaynid 14	Nebekian	Arid	Garrard et al. (1988) in Rabinovich (2003)
61	Tor Hamar F	Nebekian	Arid	Klein (1995) in Rabinovich (2003)
62	Uwaynid 18	Nebekian	Arid	Garrard et al. (1988) in Rabinovich (2003)
63	Jilat 9	Nebekian	Arid	Garrard et al. (1988) in Rabinovich (2003)
64	Yabrud III	Nebekian	Semi Arid	Lehmann (1970) in Rabinovich (2003)
65	Fazael X	UP-Early Epipaleolithic	Arid	Davis (1982) in Rabinovich (2003)
66	Fazael XI	UP-Early Epipaleolithic	Arid	Davis (1982) in Rabinovich (2003)
67	Masraq e-Naj	UP-Early Epipaleolithic	Arid	Perrot (1955) in Rabinovich (2003)
68	El-Bezez A	UP-Early Epipaleolithic	Arid	Garrard (1980) in Rabinovich (2003)
69	WHS 784	UP-Early Epipaleolithic	Arid	Clark et al. (2000) in Rabinovich (2003)
70	Fazael IX	UP-Early Epipaleolithic	Arid	Davis (1982) in Rabinovich (2003)
71	WHS 618	UP-Early Epipaleolithic	Arid	Clark et al. (2000) in Rabinovich (2003)
72	Ksar Akil 25-19	UP-Early Epipaleolithic	Hyper Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
73	Ksar Akil 9-6	UP-Early Epipaleolithic	Hyper Mesic Mediterranean	Garrard (1980) in Rabinovich (2003)
74	Ohalo II	UP-Early Epipaleolithic	Xeric Mediterranean	Rabinovich (1998) in Rabinovich (2003)

Table 2.2 List of sites used in micromammal analysis

#	Site	Culture	Environment	References
1	Hayonim (Lower E)	Tabun D	Mesic Mediterranean	Tchernov (1998)
2	Tabun D	Tabun D	Mesic Mediterranean	Tchernov (1994)
3	Hayonim (Upper E)	Tabun C	Mesic Mediterranean	Tchernov (1994)
4	Tabun C	Tabun C	Mesic Mediterranean	Tchernov (1994)
5	Qafzeh (XVII–XXIII)	Tabun C	Xeric Mediterranean	Tchernov (1998)
6	Tabun B	Tabun B	Mesic Mediterranean	Tchernov (1994)
7	Kebara VI–XII	Tabun B	Mesic Mediterranean	Tchernov (1998)
8	Geula	Tabun B	Mesic Mediterranean	Heller (1970)
9	Amud	Tabun B	Mesic Mediterranean	Belmaker and Hovers (2011)
10	Qafzeh 2-9	UP	Xeric Mediterranean	Tchernov (1994)
11	Douara	Tabun B	Arid	Payne (1983)
12	Ksar Akil XXXIII–XXVIA	Tabun B	Hyper Mesic Mediterranean	Kersten (1992)
13	Kebara UP	UP	Mesic Mediterranean	Tchernov (1994)
14	Rakefet UP	UP	Mesic Mediterranean	Tchernov in Ronen (1984)
15	Rakefet Natufian	Natufian	Mesic Mediterranean	Nadel et al. (2008)
16	El Wad Natufian	Natufian	Mesic Mediterranean	Weissbrod et al. (2005)
17	Sefunim	UP	Mesic Mediterranean	Tchernov in Ronen (1984)
18	Ohalo II	UP	Xeric Mediterranean	Belmaker et al. (2001)

placed such that their Euclidean distance in the 2D plane or 3D space is still the tenth largest. It is important to note that NMMDS does not take absolute distances into account. Thus, large inter-point distances correspond to large dissimilarities, and small inter-point distances to small dissimilarities.

The degree of correspondence between the distance among the points implied by the NMMDS map and the raw data matrix is measured by the Kruskal statistics of *stress*. Stress is

a measure of how well the solution recreates the dissimilarities. Smaller values indicate a better fit and are defined as

$$\sqrt{\frac{\sum_{i,j} (d_{ij} - x_{ij})^2}{\sum_{i,j} d_{ij}^2}}$$

where d_{ij} is the association between i and j as measured by the similarity index and x_{ij} is the associations between i and j as predicted using distances on the Shepard's plot (i.e., by the regression). A stress value between 0.1 and

Table 2.3 Environmental categories and corresponding climatic parameters (After Danin and Orshan 1990)

Environment category	Mean annual precipitation (mm)	Lang's rain factor ^a	Emberger pluviothermic quotient ^b
Arid	<50	<7	<10
Semi-arid	50–300	13–9	40–10
Xeric Mediterranean	300–540	28–15	90–40
Mesic Mediterranean	540–780	29–37	122–90
Hyper Mesic Mediterranean	780–1200	>61	>141

^aLang's rain factor is calculated as $L = \frac{P}{T}$ where P is the mean annual precipitation and T is the mean annual temperature

^bEmberger's pluviothermic quotient is calculated as $E = \frac{P \times 100}{(T_{mx} + T_{mn}) + (T_{mx} - T_{mn})}$ where P is the mean annual precipitation and T_{mx} is the average mean temperature of the warmest month and T_{mn} is the average mean temperature of the coldest month

Table 2.4 Culture categories

Time period	MIS	Culture	Absolute dates ka
Early Middle Paleolithic	MIS 6	Tabun D	250–130
Middle Middle Paleolithic	MIS 5	Tabun C	128–75
		Tabun C-B	
Late Middle Paleolithic	MIS 4/early MIS 3	Tabun B	75–47/45
Early Upper Paleolithic	MIS 3	MP-UP transition (Emiran)	47/45–40/38
	MIS 3	Levantine Aurignacian	36–38
	MIS 3	Early Ahmarian	38–25
Late Upper Paleolithic	MIS 3	Atlitian	25–20
	MIS 3	Nebekian	22–20
	MIS 2	UP-Early Epipaleolithic	20–15
Holocene	MIS 1	Natufian	12.5–10.2

0.15 is considered “good” and below 0.1 “excellent”. Any value above 0.15 is considered unacceptable.

Different indices were used for the different groups of taxa (macromammals and micromammals) following Hausdorf and Hennig (2003). For micromammals the Kulczynski similarity index for binary data was used; this index is more appropriate for taxa that have home ranges of unequal sizes as it would be expected from smaller mammals that may have endemic populations. The index for similarity between sites

j and k is calculated as $d_{jk} = \frac{\frac{M}{M+N_j} + \frac{M}{M+N_k}}{M+N}$, where M is the number of matches between site j and k and N_j is the number of species unique to site j and N_k is the number of species unique to site K .

For macromammals the Jaccard similarity index was used; this index is more appropriate for taxa that have home ranges of unequal size. The index is for similarity between sites j and k and is calculated as $d_{jk} = \frac{M}{M+N}$ where M is the number of matches between site j and k and N is the number of species unique to either site j or k .

Differences in the NMMDS scores between habitat and periods were analyzed using two-way ANOVA and post hoc Bonferroni corrections for multiple comparisons.

To visualize the results in a form that more closely resembles a PCA result, a PCA on the raw NMMDS results (as these are distributed normally) was applied. Doing so assured that the axes were uncorrelated with one another and therefore allowed for a more robust interpretation.

Statistical analyses used the statistical programs PAST 2.2, SPSS 18.0 and Aable for the Mac.

Results

Macromammals

Results from the NMMDS for the *environment* variable indicate that good representation was obtained (Kruskal's stress = 0.1486). Axes 1, 2 and 3 of the NMMDS account for 93.36% of the variance ($R^2 = 0.429, 0.2445$ and 0.2662 respectively; since NMMDS axis numbers are arbitrary, the percent of variance represented by the R^2 does not decrease with the increasing axis number).

NMMDS scores on Axis 1 (42.9% of the variance) and Axis 2 (24.45% of the variance) were significantly different between *period* categories ($F_{9,67} = 3.065, P = 0.005$ and $F_{9,73} = 3.516, P = 0.001$), while differences in scores between *period* categories on Axis 3, which accounts for 26.62% of the variance, were not significant ($F_{9,73} = 2.5, P = 0.016$). NMMDS scores on Axis 1 (42.9% of the variance) and Axis 2 (24.45% of the variance) were highly significantly different between *environment* categories ($F_{5,73} = 11.4643, P < 0.001$ and $F_{5,73} = 12.2599, P < 0.001$), while differences in scores between *period* categories on Axis 3, which accounts for 26.62% of the variance were not significant ($F_{5,73} = 1.015,$

$P = 0.416$). The effect of *period*environment* was not significant for Axis 1 (P value = 0.033) and 3 (P value = 0.936), but was significant for Axis 2 (P value < 0.001).

Bonferroni post hoc analysis for the variable *period* along the first axis shows that two of the pair-wise comparisons were significant: Tabun B vs. the Levantine Aurignacian (P value < 0.001) and Tabun B vs. the UP-Early Epipaleolithic transition (P value < 0.001). Along the second axis, pair-wise comparisons were significant: Tabun B vs. Nebekian (P value < 0.001) Tabun C vs. Nebekian (P value < 0.001), Tabun D vs. Nebekian (P value < 0.001) and Levantine Aurignacian vs. Nebekian (P value < 0.001). Since the Nebekian is limited to the arid regions of South Jordan, the significant difference between sites in the mesic Mediterranean, throughout the Last Glacial, and a specific time period with a local and limited geographic distribution is evident in the significant correlation along this axis between *period* and *environment*.

These results can be visualized in scatter plots. Figure 2.2 presents the NMMDS PCA for the sites when they were coded for *environment*.

Axis 1 explains the difference between all the Mediterranean habitats (hyper mesic, mesic and xeric Mediterranean and the arid ones (semi-arid and arid), while Axis 2 is less clear. However, it appears to explain the difference between the arid habitat and those with some rainfall. All the habitats that score above 0.0, including the hyper Mediterranean, mesic Mediterranean, and the semi-arid habitat have rainfall amounts of above 150 mm (mm) annually. A score below 0.0 includes arid habitats (albeit with some sites from semi-arid environments) and indicates little to no rainfall.

Figure 2.3 presents the NMMDS PCA for the sites when they were coded for *period*.

It shows that Tabun B sites have lower values than other sites along the first axis and that Nebekian sites have lower values along the second axis.

Since the previous tests included a wide range of habitats ranging from mesic Mediterranean to arid, one could argue that the faunal communities' differences among them are much greater than any changes we may expect in any given region, despite significant climate changes. Thus, in order to test if temporal climate changes had an impact on the local faunal community, a subset of the data confined only to the Mediterranean sites was retested. The Mediterranean sites (mesic and xeric) were chosen because they include the majority of Neanderthal sites in the region and allow for the testing of these hypotheses with an ample sample size.

Results for this test indicated there was no clear clustering among the sites that could be observed, and the Kruskal stress fell higher than the cutoff level of 0.15 (and even the very conservative value of 0.30), suggesting that there was too much noise in the dataset. In sum, results from the macromammals support the hypothesis that ecotones and mosaic habitat rather than a temporal shift accounts for the variance in large mammal distribution across sites in the Last Glacial of the Southern Levant.

Micromammals

Results from the NMMDS indicate that an excellent representation was obtained (Kruskal stress = 0.099). Axes 1, 2 and 3 of the NMMDS account for 100% of the variance ($R^2 = 0.48, 0.28$ and 0.32 respectively). NMMDS scores on Axes 1 and 2 were not significantly different between *period* categories ($F_{4,17} = 0.34, P > 0.5$ and $F_{4,17} = 0.40, P > 0.5$). However, differences in scores between periods on Axis 3, which accounts for 32% of the variance, were highly significant ($F_{4,17} = 7.414, P = 0.002$). Bonferroni post hoc analysis indicates that four of the pair-wise comparisons were significant: Tabun D vs. the Natufian (P value < 0.001), Tabun C vs. the Natufian (P value = 0.002), Tabun B vs. the Natufian (P value < 0.001) and the UP vs. the Natufian (P value = 0.003).

These results can be visualized in scatter plots. Figure 2.4 presents the NMMDS PCA for Axes 1 and 2 when the sites were coded for *period*. Along the first and second axes, there is no distinction according to time periods, similar to the results obtained for macromammals; however, along the third axis (Fig. 2.4b), there is a gradient that positively correlates with time. The earliest sites, i.e., MIS 6, have very negative values, all MIS 5-3 have near neutral values and MIS 2 sites have positive values. While there is a significant correlation with time, it is worth noting that there is no correlation among the sites spanning the MIS 4-3), which represent the time frame during which Neanderthals dispersed into the region and disappeared from it.

NMMDS scores on Axes 1 (48% of the variance) and 2 (28% of the variance) were significantly different between *environment* categories ($F_{4,17} = 6.82, P = 0.005$ and $F_{4,17} = 10.3, P \leq 0.001$), while, differences in scores between *period* categories on Axis 3 were not significant ($F_{4,17} = 0.015, P \geq 0.5$). Bonferroni post hoc analysis for the first axis indicates that only one of the pair-wise comparisons was significant: mesic vs. xeric Mediterranean



Fig. 2.1a Location of Middle Paleolithic sites mentioned in the text. 1. Ein Difla, 2. Bezez Cave B, 3. Hayonim (E > 405; E < 405), 4. Tabun (D, C, B), 5. Rosh Ein Mor, 6. Ksar Akil (18-10), 7. Naamé, 8. Ras el Kalb A-O, 9. Qafzeh (V–XV; XVI–XXIV), 10. Dedariyeh (11; 3), 11. Douara (III; IV), 12. Amud B, 13. Skhul B, 14. Kebara F, 15. Umm el Tlel (V0Ba; V11a; V13b'1), 16. Far'ah II (L.1; L.0)

(P value < 0.001), while four pair-wise comparison were significant for Axis 2: mesic Mediterranean vs. arid (P value = 0.005), mesic Mediterranean vs. hyper mesic Mediterranean (P value < 0.001), xeric Mediterranean vs. hyper mesic Mediterranean (P value = 0.004) and arid vs. hyper mesic Mediterranean (P value = 0.005).

These results can be visualized in the scatter plots. Figure 2.5 presents the NMMDS PCA when the sites were coded for *environment*. Axis 1 explains the difference between the Mediterranean habitats (mesic and xeric Mediterranean); however, since this does not appear to distinguish between the hyper mesic Mediterranean region and arid region, it does not

appear to be related to rainfall. However, this may be related to vegetation cover, with sites from more open habitats, i.e., xeric and arid Mediterranean having more positive values, and sites with more closed habitats, i.e., mesic and hyper mesic Mediterranean, having negative values.

Axis 2 distinguishes a gradient along rainfall. Sites with the most precipitation have the most negative values, sites with intermediate rainfall, both mesic Mediterranean and xeric Mediterranean have neutral values, and arid sites have positive values. Along this axis, the difference in precipitation between the mesic (ca. 780–540 mm) and xeric (540–300 mm) Mediterranean cannot be distinguished.



Fig. 2.1b Location of Upper Paleolithic sites mentioned in the text: 1. Abu Noshra (I; II), 2. Abu Halka (IVc; IVd; IVe; IVf), 3. Antelias, 4. Ksar Akil (06-09; 05-19; 9-6), 5. Ain Aqev (D31), 6. Shukbah D, 7. El Wad (D; E; F), 8. Kebara III, 9. Emirah, 10. Erq el Ahmar (B; C; D; E; F), 11. Qafzeh, 12. Hayonim (D3; D1/0), 13. Rakefet, 14. Sefunim, 15. Yabrud (II), 16. El Quesir (C; D), 17. Tor Hamar (F; G), 18. Uwaynid 18, 19. Jilat 9, 20. Nahal Ein Gev I, 21. Fazael (X; XI; IX), 22. Masraq e-Naj, 23. El Bezez A, 24. WHS 784, 25. WHS 618, 26. Ohalo II

In sum, the results from the micromammal database support the hypothesis that the distribution in mosaic habitats, rather than a temporal shift in environment, accounts for the variance in community distribution across sites in the Last Glacial of the Southern Levant. While there is evidence for a temporal shift in the micromammal community, it does not span the MIS 4-3 transition.

Discussion and Conclusions

Shifts in the community structure of macromammals and micromammals in the Southern Levant indicate two different patterns. On the one hand, there is a clear pattern that emerges, which reflects the local mosaic of habitats. The majority of the variance in both large and small mammals

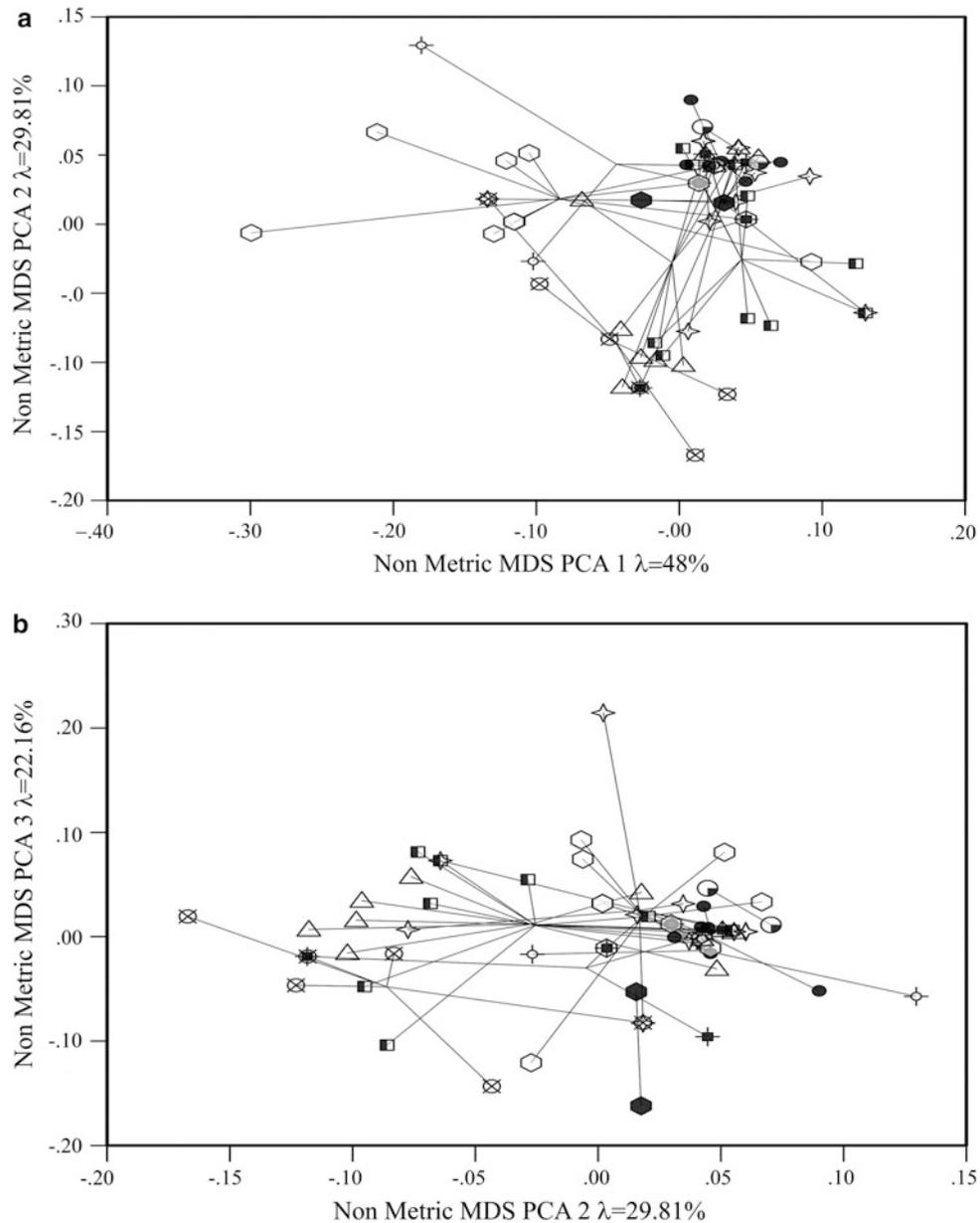


Fig. 2.2 Results of the NMMDS for macromammals with sites scored on the *environment* variable. **a** Scattergram for axis 1 and 2; **b** Scattergram for axis 2 and 3. Legend: ▲ Hyper Mesic Mediterranean, ◻ Mesic Mediterranean, ◇ Xeric Mediterranean, ★ Semi arid, ■ Arid

over time can be explained by spatial variation. In addition, there is a smaller percent of the variance that can be explained by temporal variation. However, in both cases, the temporal difference is only observed between the very early sites (MIS 6 and 5) and those from the Late Pleistocene and MIS 2. There is no significant difference between MIS 4 and MIS 3 or between the MP and the MP-UP transition as expected from the hypothesis of climatic forcing. Thus, this difference cannot be used as an indicator for solely a temporal climate change.

The pattern that emerges from this study is a temporal shift in the mammalian community that occurred after the Levantine Aurignacian or towards the UP-Early Epipaleolithic transition, but not prior to that time. There is no unequivocal evidence which supports a climate temporal change and that cannot be related to the environmental ecotonal mosaic structure of the Southern Levant. Furthermore, none that can be assigned specifically to the MIS 4-3 transition and the H5 event and that may be associated with the demise of the Neanderthal population in the region as suggested by Shea (2008).

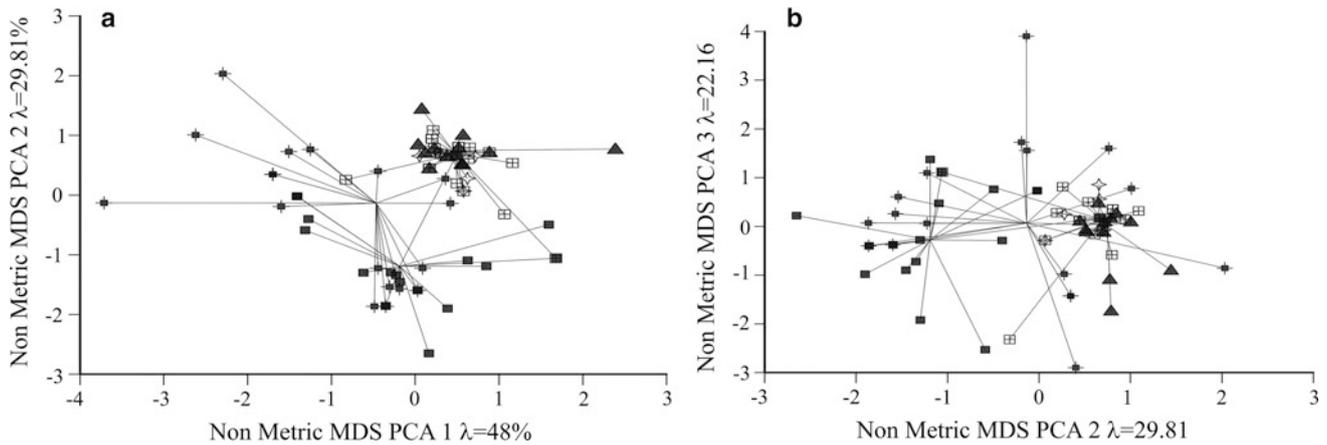


Fig. 2.3 Results of the NMMDS for macromammals with sites scored on the *period* variable. **a** Scattergram for axis 1 and 2; **b** Scattergram for axis 2 and 3. Legend: \diamond Tabun D, \bullet Tabun C, \bullet Tabun C-B, \circ Tabun B, \blacksquare MP-UP transition, \triangle Early Ahmarian, \diamond Levantine Aurignacian, \odot Atlitian, \boxtimes Nebekian, \blacksquare UP-Early Epipaleolithic

However, the lack of change in community structure among mammals stands in contrast to evidence derived from other paleoclimatic proxies obtained from the region. Stable isotope data derived from speleothems in Levantine caves for the late Middle Paleolithic have suggested a shift in climate throughout the Last Glacial. Climate change recorded in the isotopic record from Peq'iin Cave (Bar-Matthews and Ayalon 2003) is interpreted to represent changes in rainfall that indicate a shift from a wet to a dry habitat as well as a decrease in environmental productivity throughout MIS 4. This pattern is confirmed by other proxies, such as stable isotope data from foraminifera in East Mediterranean sediment cores (Bar-Matthews and Ayalon 2003) and increased pollen from steppe desert taxa in marine sediment cores in the Eastern Mediterranean (Almogi-Labin et al. 2004). This has indicated a period of overall lower ecological productivity during MIS 4 and leading up to the Heinrich event at 50–45 ka. Analysis of pollen core 95–09 in the Eastern Mediterranean, dating from 75.5–56.3 ka, indicates a low proportion (up to 7%) of arboreal pollen along the entire sequence. Deciduous oak is more prevalent in the lower part of the core, which is supportive of a dry Last Glacial in general and of a decline in regional productivity throughout the MIS 4 in particular (Langgut 2007).

How can these seemingly contradictory data sets be reconciled? The relationship between climate, the biotic environment, and humans is a complex one. In order to fully understand how climate affected human population dynamics, we need to understand the relationship between climate–plants–animals and humans. Within this paradigm, I suggest applying a hierarchical model following Rahel (1990), which describes the tiered response of plants and animals to climate change (Fig. 2.6).

This model looks at the relationship between the amplitude (which could comprised of frequency, intensity and/or the variance) of climate change against the level of biological response in a mammalian community. In low amplitude climate change, there is often no change in the biological community. This is called stasis, persistence or stability. In higher amplitudes of climate change, there is only a small level of change. This is manifested in the change in the diets of herbivores from browse to graze as their proportions change in the environment. In even higher amplitudes of climate change, there is a more noticeable change in relative abundance. This is often the result of a change in the distribution of the population across the region. This may be due to a decrease in local resources, which can no longer sustain the population at its former levels. At higher amplitudes of climate change, there is a change in presence-absence of species, i.e., some species become locally extinct and new species appear where they did not occur before; however, the overall community structure does not change. Only at the highest amplitude of climate change do we have an overall shift in biome structure, which corresponds to a total shift in species composition, community structure, and niche composition.

The response to tiered levels of climate change differs depending on the trophic level and the size of the organism. Specifically, herbivores are more sensitive to climate change than carnivores, and smaller taxa are more sensitive to lower amplitudes of climate change than larger taxa are.

If we interpret the results of this paper in light of the hierarchical model, we can observe that this is indeed the case in the Last Glacial in the Southern Levant. We have evidence for changes in precipitation i.e., climate and also for a shift in plant remains for this time period, as is

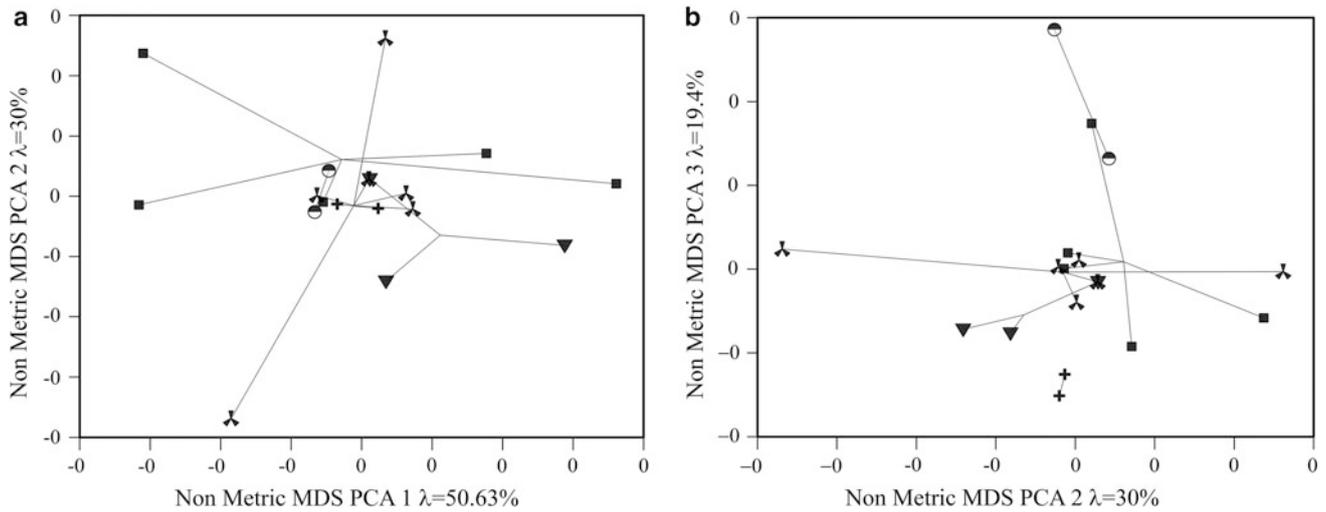


Fig. 2.4 Results of the NMMDS for micromammals with sites scored on the *period* variable. **a.** Scattergram for Axis 1 and 2; **b.** Scattergram for Axis 2 and 3. Legend: + Tabun D, ▼ Tabun C, ♣ Tabun B, ■ Upper Paleolithic, ● Natufian

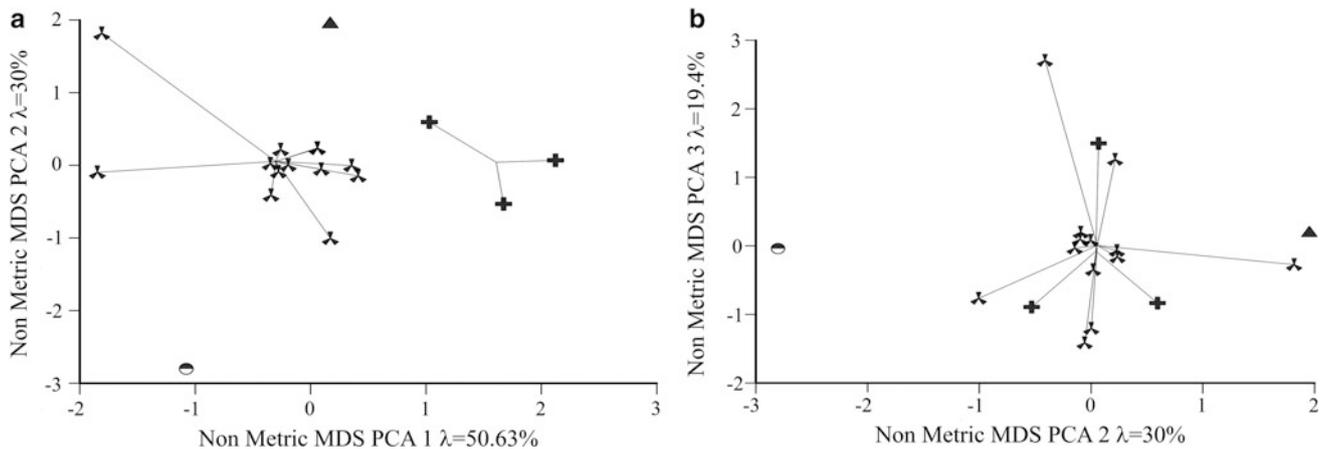


Fig. 2.5 Results of the NMMDS for micromammals with sites scored on the *environment* variable. **a.** Scattergram for axis 1 and 2; **b.** Scattergram for axis 2 and 3. Legend: ● Hyper Mesic Mediterranean, ♣ Mesic Mediterranean, + Xeric Mediterranean, ▲ Arid

demonstrated by the pollen (Bar-Matthews and Ayalon 2003; Bar-Matthews et al. 2003; Langgut 2007).

Other evidence for climate change comes from stable isotope data derived from ungulate teeth. Stable oxygen and carbon analyses of ungulate teeth from the sites of Amud, Qafzeh and Skhul have indicated a difference in climate at the three sites. The ungulates from Amud indicate a cooler and wetter climate than today, which differs from the climate in Qafzeh, which is dryer and warmer. While these two findings can be consistent with either hypothesis presented in this paper, it is interesting to note that the data from Skhul indicate a C_3 environment compared to the C_4 environment in Qafzeh, which is what would be expected from the regional mosaic hypothesis (Hallin 2004).

The question that is relevant for hominin population dynamics is not whether we can detect evidence for climate change, but whether the amplitude of this was large enough to evoke a shift in the large and small mammal communities. Therefore the question is not if we can observe climate change but if we can observe an *effective* climate change i.e., one that has an appreciable effect on hominins.

This paper has shown that there is no shift in community structure in either large or small mammals between MIS 4 and 3. Only at around 30 ka did climate change in a large enough degree to shift the presence-absence of taxa in the region. Can we track changes in mammalian community structure at lower levels of climate change, i.e., relative abundance and/or a shift in diet? Either of these would

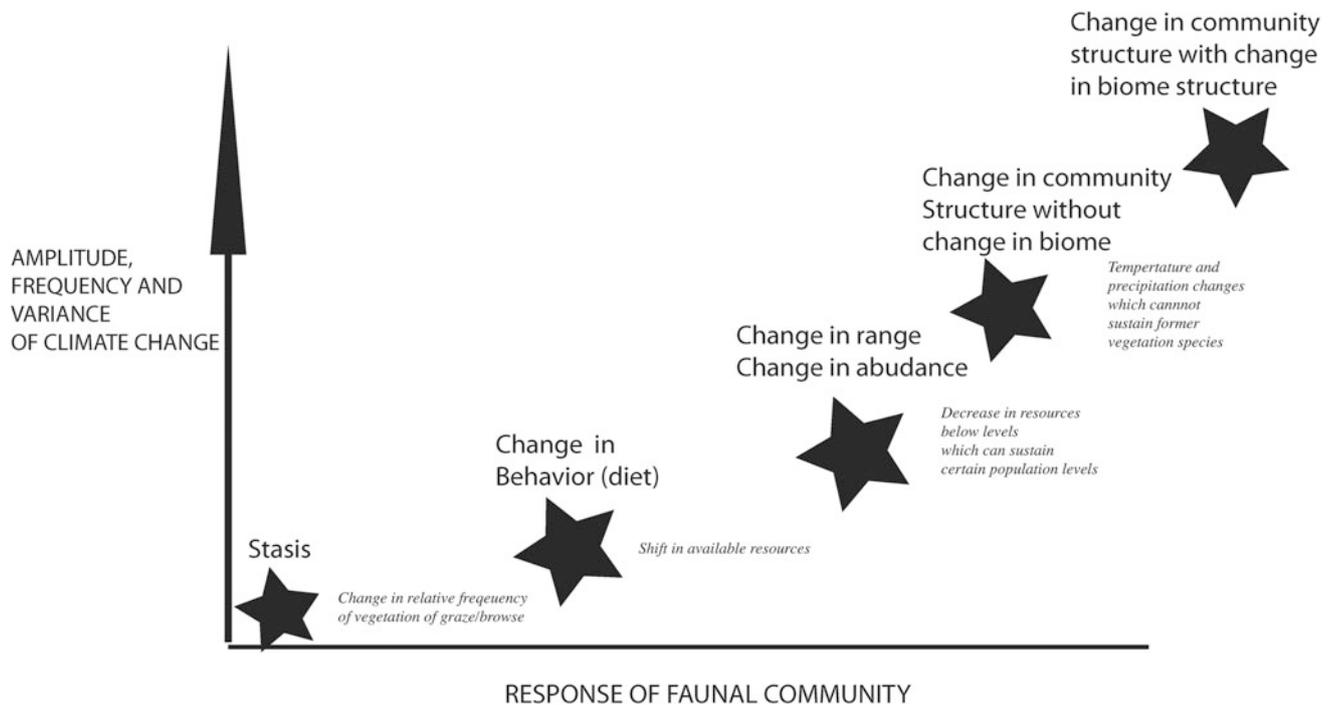


Fig. 2.6 Schematic model describing the relationship between amplitude of climatic change and response of mammalian community

suggest a climate change of lesser amplitude, which may have affected hominins as well.

Mesowear analysis measures the abrasion of upper molars on selenodont ungulates and has been shown to be a reliable proxy for diet in both extant and extinct species, specifically in distinguishing the degree of browse vs. graze in the diet (e.g., Fortelius and Solounias 2000; Franz-Odenaal et al. 2003; Kaiser and Solounias 2003; Kaiser and Franz-Odenaal 2004; Muhlbachler and Solounias 2006; Rivals and Sempredon 2006). Mesowear is a function of dental wear over ca. the last 6 months of an individual's lifetime and is independent of the effects of seasonality, migration patterns or stochastic effects, such as the effects of the individual's last meal, which is common in other paleodietary methods (e.g., Sempredon et al. 2004). Mesowear measures two variables, occlusal relief and occlusal shape, on the paracone of upper M1/M2 of selenodont ungulates. Occlusal relief has two variables: high and low, which are dependent on the height of the cusps above the valley between them. Occlusal shape has three variables: sharp, round and blunt. It has been shown that Southern Levantine ungulates did not shift their diet from browse to graze between MIS 6-3 (Belmaker 2008). That a shift did occur in ungulate diet and could be observed only around 35 ka, which post-dates the disappearance of Neanderthals in the region and the appearance of *Homo sapiens* in the Southern Levant and also is consistent with the pattern of an

increase in aridity, which can be observed in the changes in community structure (Fig. 2.7).

Paleodietary studies of small rodents have been difficult to obtain because of the animals' small size, although current analysis currently is being undertaken using various methods, including microwear texture analysis (Belmaker and Ungar 2010). Observing the next levels of changes, those that occur along with a shift in relative abundance of individuals, are highly susceptible to bias induced by taphonomic changes in the fossil record (Kowalewski et al. 2003; Tomasovych and Kidwell 2009; Terry 2010). This is particularly true for Levantine micromammal assemblages, which are dominated by *Microtus guentheri*, at times comprising up to 90% of the assemblages (Belmaker and Hovers 2011).

Given this situation, we may conclude that results observed from relative abundance analyses may be inconclusive due to any known or unknown taphonomic biases. We have shown that the macromammals do not shift their diet over the time period in question (Fig. 2.7). Therefore, based on the proposed hierarchical model, we would not expect any change in relative abundance, as it would be inconceivable to have a climate change of a high enough amplitude to cause a shift in relative abundance, but not a change in diet. While this expectation is not testable, due to the aforementioned taphonomic biases, the relative proportions of the two most common ungulates, Fallow deer

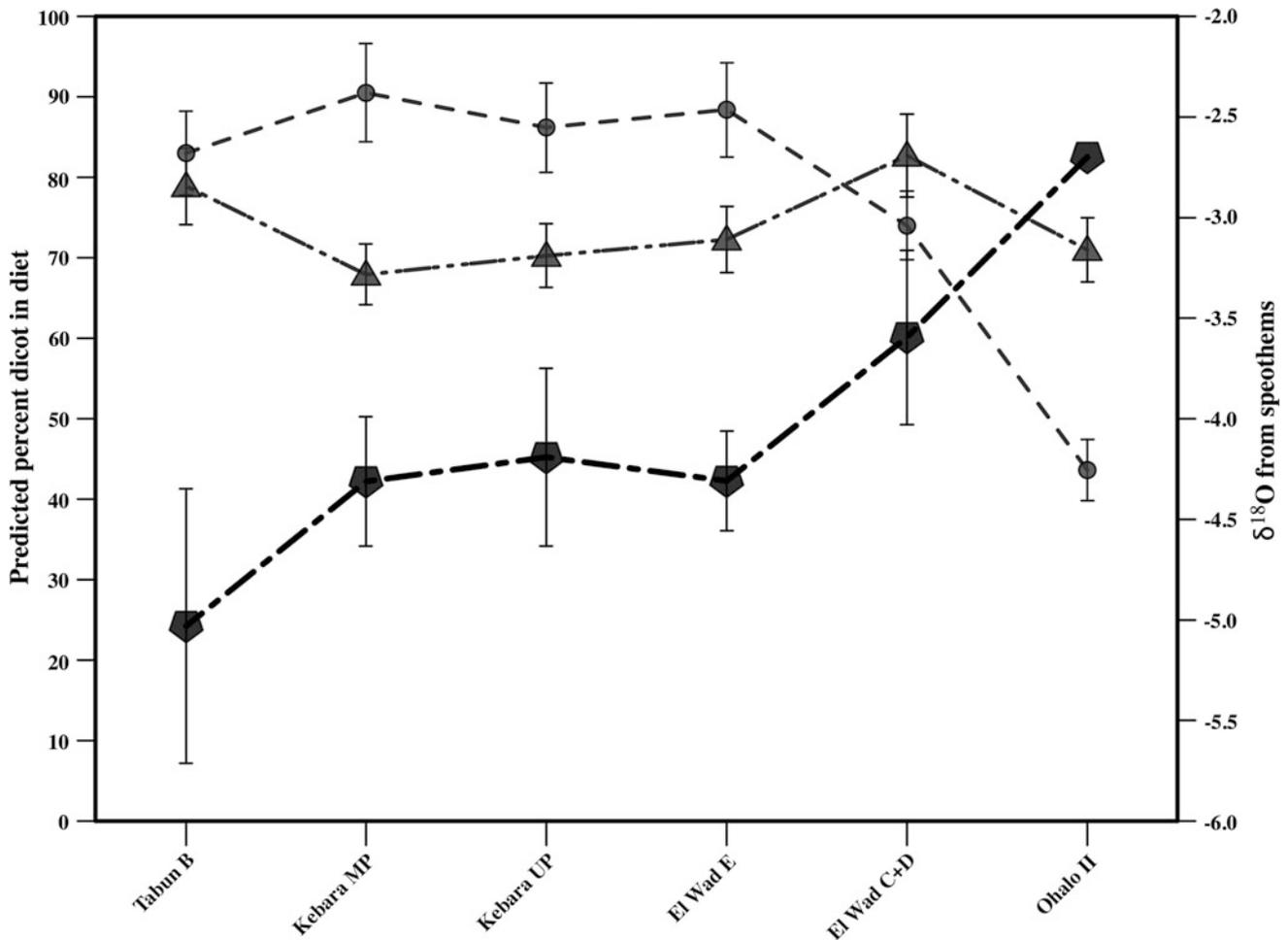


Fig. 2.7 Mesowear result of two ungulate taxa for selected Southern Levantine sites compared to stable isotope from speleothems. Mesowear results presented as percent dicot in diet calculated from prediction regression equations as with 95% confidence intervals (Belmaker 2008). Legend: —●— Fallow deer (*Dama mesopotamica*), - -▲- - Mountain gazelle (*Gazella gazella*), $\delta^{18}\text{O}$ —◆— Data from Bar Matthews et al. (2003)

(*Dama mesopotamica*) and Mountain gazelle (*Gazella gazella*), from Levantine archaeological assemblages from MIS 6 through MIS 2 were compared. The ratio between the two taxa indicates a non-linear change through time and does not indicate a clear change around 45 ka, which would have been expected from the climate forcing hypothesis (Shea 2008). Based on the data observed from this study suggesting a faunal change ca. 35 ka and supported by the mesowear study (Fig. 2.7), the assemblages were divided into two main groups: pre and post 35 ka. Sites that predate 35 ka have a mean of 30% fallow deer with a range of 11–77%, while sites that post-date 35 ka have mean of 16% with a range of 4–54%. This difference supports the results that suggest that a marked climatic shift occurred ca. 35 ka and post-dated the Neanderthal extinction in the region.

Climate also affects morphology of taxa and can be used as a proxy for climate change. Ecogeographic rules such as Bergman and Allen's rule suggest that individual from

different latitudes differ in their proportion. The application of the rules has also been used to track climate change through time (Cussans 2017; Davis 1981). However, studies that have focused on the size of Middle Pleistocene ungulates in the Southern Levant (Davis 1981) have not found changes in size of ungulates that may correspond to a large change in climate.

Thus, despite clear evidence for a climatic shift between MIS 4 and 3, there is no evidence for response to climate change from the lowest tier of response from large mammals (diet), no evidence for change in relative abundance of large mammals (medium tier of response to climate change) and no evidence for change from the highest tier of response from both micromammal and macromammals (presence-absence).

What are the implications for hominin population dynamics in the region and specifically for Neanderthal local extinction? Shea (2001, 2003, 2008) posits that the

extinction of the Levantine Neanderthals was due to decreased productivity throughout the MIS 4 and the climatic crisis that occurred during the Heinrich 5 (H5) event of 50–45 kyr. The assertion that climate forcing was responsible for Neanderthal extinction in the region is based on the underlying hypotheses that the climatic change was severe enough to cause depletion in either plant or animal resources. More specifically, climate change during the H5, or during the MIS 4 leading up to it, was so severe as to cause a noticeable decrease in resources available for Neanderthals. Neanderthals subsisted on a hunter-gatherer diet (Speth 1987, 2004, 2006; Lev 1993; Albert et al. 2000; Speth and Tchernov 2001; Rabinovich and Hovers 2004; Lev et al. 2005). We can hypothesize what affect an environmental decrease in productivity, resulting from less rainfall in the Southern Levant, would have on the Neanderthal diet. A decrease in productivity would have resulted in a decrease in the productivity of oak and other fruit bearing trees, which would have resulted in less fruits and nuts for gathering. In addition, a shift in the total ratio of trees to open grassland, favoring an increase in grassland, may have resulted in fewer trees used for bedding and fire. Moreover, the decrease in browse would have led to a dietary shift in ungulates from predominantly browse to graze and the decrease in food availability would lead to a decrease in the fecundity of fallow deer and gazelles available for hunting.

However, when climate change is severe enough to evoke an extinction of ecosystem, we often see the extinction of complete ecosystems, trophic levels and/or body sizes. This can be observed in the study presented in this volume, which discusses the extinction in the Quaternary of Northern South America and presents the differential extinction of larger mammals and the elimination of several Quaternary habitats due to climate change (Ferrusquia et al. 2017). The situation in Northern South America described by Ferrusquia et al. (2017) differs from that which we present in this paper. Specifically, in Northern South America, the climatic fluctuation in the Pleistocene led to extensive changes in species composition (i.e., presence-absence) and changes in the geographic distribution of species. In contrast, in the Southern Levant, as presented in this paper, the only species to become locally extinct at the H5 were the Neanderthals. Since Neanderthals were at the top of the trophic level, if climate change contributed to their extinction, we expect to see evidence of change in the population dynamics of taxa in trophic levels below that of Neanderthals. These would include both large and smaller herbivores.

This paper suggests that there is no change in the species composition in both large and small herbivore fauna throughout the time span of Neanderthal presence in the Levant and shortly after Neanderthal extinction in the Levant. While the climate fluctuations in Northern South

America were severe enough or of sufficient amplitude to evoke a shift in mammalian species composition, the amplitude of climate shift in the Southern Levant was of not as severe as to lead to a total shift in species composition in the ungulate and small mammal communities. Thus, a major climate shift did not occur between MIS 4 and 3 (contra Shea 2003, 2008). As suggested by the hierarchy model (Rahel 1990), lower amplitude climate shifts may affect the diet of herbivores. However, we have shown in the mesowear study that the ungulates did not shift their diet. This further supports the hypothesis that there is little evidence for the presence of climate change during the H5.

Shea (2008) has suggested that the extinction of the Neanderthals was a result of a decrease in productivity resulting from a climate change during the H5 event. It may be argued, that a prolonged decrease in productivity would not have led to a shift in community composition nor shift in diet, but a smaller population in the region, both in species, size of population and size of individuals. An interesting study by Speth and Clark (2006) points to the fact that the hunted herbivores in Kebara Cave decrease between 75 and 45 ka from large *Aurochs*, *Cervus* and *Dama* to the smaller sized *Gazelle* and further more to the smaller sized juvenile gazelle.

This archaeological pattern may be produced by several phenomena. It may be the results in a decrease in prey abundance due to a decrease in local productivity or an increase in human abundance and better hunting efficiency. Given the evidence presented here which do not support a high amplitude climate change in the Levant during the H5, it appears more prudent to attribute this phenomena to local over-hunting by Neanderthals populations, perhaps due to an increase in local Neanderthal population. Furthermore, this pattern of a decrease in size of prey throughout MIS 4/3 has not been repeated in other Neanderthals sites in the Levant (e.g., Amud see Rabinovich and Hovers 2004).

Neanderthals and other Middle Paleolithic hominins are large mammals, and it stands to reason that they were affected primarily by large amplitudes of climate change and not by smaller fluctuations, which may have occurred during this time period. Thus, even if climate changes did occur during the MIS 4 and the H5 in the Levant, they were of such small amplitude as to not have a noticeable effect on the mammalian community. Since hominins were highly adaptive, these small amplitude climate changes would probably not have such an effect on their population as to lead to their complete extinction in the Southern Levant. While there is a clear record of climate change throughout MIS 4 in the Southern Levant present in speleothems, pollen spectra and other climatic proxies there is little evidence of an *effective climate* change during the time period, which may have contributed to the local extinction of Neanderthals in the Southern Levant.

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