



# Hominin reactions to herbivore distribution in the Lower Palaeolithic of the Southern Levant



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## ARTICLE INFO

### Article history:

Received 30 May 2013

Received in revised form

7 April 2014

Accepted 12 April 2014

Available online 20 May 2014

### Keywords:

Lower Palaeolithic

Large herbivores

Seasonal movements

Hominin site locations

Edaphic potential

## ABSTRACT

We explore the relationship between the edaphic potential of soils and the mineral properties of the underlying geology as a means of mapping the differential productivity of different areas of the Pleistocene landscape for large herbivores. These factors strongly control the health of grazing animals irrespective of the particular types of vegetation growing on them, but they have generally been neglected in palaeoanthropological studies in favour of a more general emphasis on water and vegetation, which provide an incomplete picture. Taking the Carmel–Galilee–Golan region as an example, we show how an understanding of edaphic potential provides insight into how animals might have exploited the environment. In order to simplify the analysis, we concentrate on the Lower Palaeolithic period and the very large animals that dominate the archaeofaunal assemblages of this period. Topography and the ability of soils to retain water also contribute to the differential productivity and accessibility of different regions and to patterns of seasonal movements of the animals, which are essential to ensure a supply of healthy fodder throughout the year, especially for large animals such as elephants, which require substantial regions of good grazing and browsing. Other animals migrating in groups have similar needs. The complex topography of the Southern Levant with frequent sudden and severe changes in gradient, and a wide variety of landforms including rocky outcrops, cliffs, gorges, and ridges, places major limits on these patterns of seasonal movements. We develop methods of mapping these variables, based on the geology and our substantial field experience, in order to create a framework of landscape variation that can be compared with the locations and contents of archaeological sites to suggest ways in which early hominins used the variable features of the landscape to target animal prey, and extend the analysis to the consideration of smaller mammals that were exploited more intensively after the disappearance of the elephants. We consider some of the ways in which this regional-scale approach can be further tested and refined, and advocate the development of such studies as an essential contribution to understanding the wider pattern of hominin dispersal.

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## 1. Introduction

The Southern Levant offers many points of interest in the study of early hominins. It lies on one of the major routes for the Pleistocene dispersal of hominin and mammalian species between Africa and Eurasia. It is bounded by physical barriers of desert, coast and mountains, which were sensitive to Pleistocene climatic and sea level change, and imposed significant constraints on the entry

and exit of human and mammalian populations, sometimes being more open to movement from the south and at other times from the north. The area is tectonically active, which results in the creation and rejuvenation of complex landscape features that have been shown to be particularly favourable for hominin occupation. It is also relatively rich in Palaeolithic remains and has been extensively studied, so that there is a database of observations on which synthetic research can draw (Bar-Yosef, 1995; Tchernov, 1999; Turner, 1999; Goren-Inbar et al., 2000; O'Regan et al., 2005; King and Bailey, 2006; Shea, 2008; Belmaker, 2010; Fleagle et al., 2010; Issar, 2010; Bailey et al., 2011; Bar-Yosef and Belmaker, 2011; Winder et al., 2012). All of this makes the region an interesting

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regional 'laboratory' for the examination of the various factors that may have promoted or constrained hominin occupation and dispersal.

The pattern and causes of hominin dispersal have been the focus of intense, recent interest. Discussion typically focuses on dispersal as a macro-scale phenomenon, and on global or continental-scale constraints or opportunities imposed by large-scale variations in climate, vegetation, fauna, and changes in the cognitive, technological and social abilities of different hominin taxa (e.g., Mithen and Reed, 2002; Holmes, 2007; Maslin and Christensen, 2007; Potts, 2007; Agustí et al., 2009; Carto et al., 2009; Bailey and King, 2011; deMenocal, 2011; Leroy et al., 2011; Martínez-Navarro and Rabinovich, 2011; Abbate and Sagri, 2012; Bar-Yosef and Belfer-Cohen, 2013; Dennell, 2013). The effect of interactions between hominins and other mammals in this process was a particular interest of Alan Turner (Turner, 1992, 1999; Turner and O'Regan, 2007), and we follow that interest here, but with a different focus. Here, we take a 'bottom-up' approach, focussing on the structure of the physical environment at a local-to-regional scale, and a simplified sub-set of variables which we believe to be of key importance in mapping the geographical dimension of the relationship between people, animals and the physical landscape. Given that large-scale dispersal is the long-term outcome of small-scale, incremental movements involving expansion of small groups into adjacent terrain, we regard a small-scale regional approach of the type explored here as a necessary contribution to understanding the wider processes of dispersal.

Our principal aim is to illustrate a new approach to reconstructing the biotic potential of the physical landscape in relation to patterns of hominin settlement and mobility. We emphasise variables of geology, topography, tectonic geomorphology, large mammals considered as food resources, and edaphic potential, and take the Southern Levant as an example region. More specifically, we aim to develop proxy measures that can be used to map the variable attractiveness of different areas within a regional landscape for concentrating herd animals of importance in hominin subsistence and for channelling their seasonal movements. We concentrate on the large herbivores, and particularly the elephants, because they were clearly a dominant presence in the faunal community of the region over a long period, and their bones are well represented in archaeological sites as prey items and major sources of food (see in particular Goren-Inbar et al., 1994; Horowitz, 2002; Horowitz and Monchot, 2002; Bello et al., 2009; Ben-Dor et al., 2011). We do not imply that other food resources were ignored or unimportant, such as smaller mammals, plants and aquatic foods, which are in evidence in the region from an early period (Goren-Inbar et al., 2002). Nor do we discount the potential interactions between plants and animals as members of wider ecological communities, although we do not pursue them here in the interests of highlighting other variables that we believe have been overlooked in previous work. Rather our aim is to create maps of physical landscape features as an independent framework, against which the locations and contents of archaeological sites can be compared. The resulting inferences about animal and human distributions are put forward here as models, intended to provide new perspectives, and ultimately to open up new hypotheses and stimulate new observations that can aid in refining the initial models and integrating other sources of information. Our time range is from 1.4 Ma to 250 ka – from the earliest evidence of hominin settlement to the final disappearance of the elephant fauna – broadly coterminous with the Lower Palaeolithic and the Early and Middle Pleistocene.

We rely on the creation of maps derived from satellite imagery combined with extensive field observation as visual and empirical sources of data that complement interpretations in the text and

provide the means for independently evaluating them. These involve a comparable degree of analysis, have the same status and should be treated in the same way as tables of anatomical or geochemical measurements. We further use these maps to examine the spatial relationship between landscape features and archaeological site locations, especially those containing faunal remains of the large herbivores, and use that relationship to make inferences about the interactions between hominins and large herbivores, and the extent to which variations in the physical landscape may have controlled the distribution and seasonal movements of the animals and their accessibility to hominin exploitation. Our approach develops ideas and methods first proposed in the 1980s (Sturdy and Webley 1988; Sturdy et al., 1997), with the major difference that in a digital age we are able to produce maps much more rapidly, accurately and extensively by exploiting and manipulating satellite imagery than would be possible by printed maps and field observation alone.

It is axiomatic that proxy measures should be invariant in such a way that they can be extrapolated with some confidence through deep time and across the vagaries of Pleistocene fluctuations in landscapes, climate and vegetation, or should vary in ways that can be directly measured, hence our emphasis on geological substrates and physical topography. Of course, even these can change, especially on Pleistocene time scales and in a tectonically active region. However, recent developments in tectonic geomorphology and the geodynamic theory of landscape evolution have greatly improved the ability to identify and assess such changes (King and Bailey, 2006; Bailey et al., 2011; Devès et al., 2011; Reynolds et al., 2011).

We place particular emphasis on 'edaphics', by which we mean the capacity of the geological or sedimentary substrate and the soils that form on it to provide the mineral nutrients essential for animal growth and health. We distinguish this from 'fertility', which is the capacity of the soil to support vegetation. In our maps we concentrate on edaphic variables, because of their importance in determining patterns of animal grazing, because they are relatively unchanging in the face of changes in climate and vegetation, and because they can be mapped at a variety of spatial scales appropriate to our objectives. The fertility of soils, in contrast, especially as judged by the amount of vegetation growing on them, is not only a poor guide to their potential to support herbivores, it is also sensitive to variations in climate and vegetation that are increasingly difficult to measure as one goes further back in time except at a spatio-temporal resolution that is either too coarse for our mapping purposes or too localised. Long Pleistocene sequences from lakes, speleothems and deep-sea cores are available for this region (e.g. Horowitz, 1989b; Tzedakis, 1994; Cheddadi and Rossignol-Strick, 1995; Bar-Matthews and Ayalon, 2001; Almog-Labin, 2011; Rohling et al., 2013), but these are notoriously insensitive to micro-environmental variation at the scale we are interested in, while records with more localised catchments (e.g. Weinstein, 1976) are patchy, and cannot be generalised to larger areas or longer time spans. Reconciling these different types of palaeoenvironmental records is a major challenge in Pleistocene landscape studies, rarely attempted (for an exception and an exposition of the problems involved, see Bailey, 1997, and chapters therein), and one that we do not pursue here in the interests of focussing on other variables. This is an important point because some of the animals we examine have varied in their emphasis on browsing or grazing, and some herbivores such as elephants and cervids are capable of adapting to these different modes of feeding, depending on the particular climatic and vegetational conditions prevailing at different times and places. The edaphic constraints explored in the following apply regardless of whether the animals were grazers or browsers, and we refer loosely to the vegetation to which animals were adapted as 'fodder'. We do not ignore climate

or vegetational change but incorporate it only when adequate information is present, and when relevant to the main line of our argument with its emphasis on spatial mapping and modelling. Nor do we assume that elephants, or hominins, were continuously present throughout our period, only that when present they would have been subject to the physical and spatial constraints that we explore.

For archaeological distributions and their faunal contents we rely of necessity on the sites reported in the literature with all the uncertainties that attach to sampling bias, dating, inter-site correlation and the status of sites that are most likely time-averaged palimpsests of many different activities and durations (Bailey, 2007, 2008; Fanning et al., 2009). We do not make any preliminary assumptions about the functions of the sites we know about or whether they were linked together as part of a contemporaneous system of resource exploitation, but we do assume that, when used, their contents must reflect to a large degree conditions in the surrounding environment.

We first define the region of study and its boundaries, and structure the discussion that follows with (1) detail on the methods and assumptions used to construct maps, (2) reconstruction of relevant changes in the physical characteristics of the region, (3) mapping of the key variables, (4) models of the distributions and seasonal movements of the large herbivores, particularly the elephants, in relation to these variables, and (5) analysis of the locations of archaeological and faunal material in relation to these models.

## 2. The study region

### 2.1. Definition

We take as our larger region of study an area bounded by natural barriers, to the North the mountains of Hermon, Lebanon and Anti-Lebanon extending into Syria, to the East a desert margin, to the West the Mediterranean coastline, and to the South the central Jordan and Samarian highlands and the Dead Sea (Fig. 1). Within this larger region we pay particular attention to a central area comprising the Carmel and Galilee regions, the Golan Heights and the edge of the Jordanian plateau, where the topography is suitable for the largest herbivores such as elephants (Fig. 2).

The dominant structural feature is the Jordan Valley, extending from the Red Sea and the Wadi Arabah in the South, via the Dead Sea and Lake Kinneret to the Beqaa Valley in the North. This valley is often referred to as the 'Rift' valley, or the Dead Sea Valley, although the term 'rift' is not an accurate mechanical description (Devès et al., 2011). In this paper we will refer to it as the Jordan valley. Properly speaking, this is an active transform fault, with ongoing strike-slip motion on a north–south axis, within a steeply downwarped valley (Matmon et al., 1999, 2000a,b; Devès et al., 2011; Le Beon et al., 2012). However, although the valley is narrower, the resulting topography is not unlike that of a true rift, with down-cut valleys, internal drainage, and flanks comprising incised, hilly terrain punctuated by volcanic activity.

### 2.2. Permeability of boundaries

The boundaries of the larger region would have posed significant barriers to contact with adjacent regions, especially for larger herbivores such as elephants, though these barriers would have been variously moderated or amplified by climatic and tectonic change. In the north, the only points of access through the mountain barrier are along the coast and between the Hula and Beqaa Valleys (Fig. 1). The former would always have been restricted, even at lowered sea level, because the coastal plain is narrow and steeply

shelving (Elias et al., 2007), while the latter would have been periodically closed by ongoing tectonic and volcanic activity (Daeron et al., 2007).

To the East, the desert imposes a barrier, but periods of increased rainfall would have moved the desert margin, opening up extensive grazing territory and pathways eastwards, while periods of increased aridity would have closed down that option. To the east, desert limits animal abundance – a limit that moves east and west as rainfall increases and decreases in different periods, but is normally (not always) present somewhere throughout the ~1 million years of the Lower Palaeolithic (note Cordova et al., 2013).

That dispersal was possible, either northwards via the Beqaa valley or to the northeast around the desert margin, is demonstrated by the Palaeolithic sites in the Al-Kawm (El Kowm) basin in Syria, north of the area shown in Fig. 1 (Hennig and Hours, 1982; Le Tensorer and Hours, 1989; Le Tensorer et al., 2007). However, contact northwards and eastwards would always have been constrained by tectonic and climatic factors.

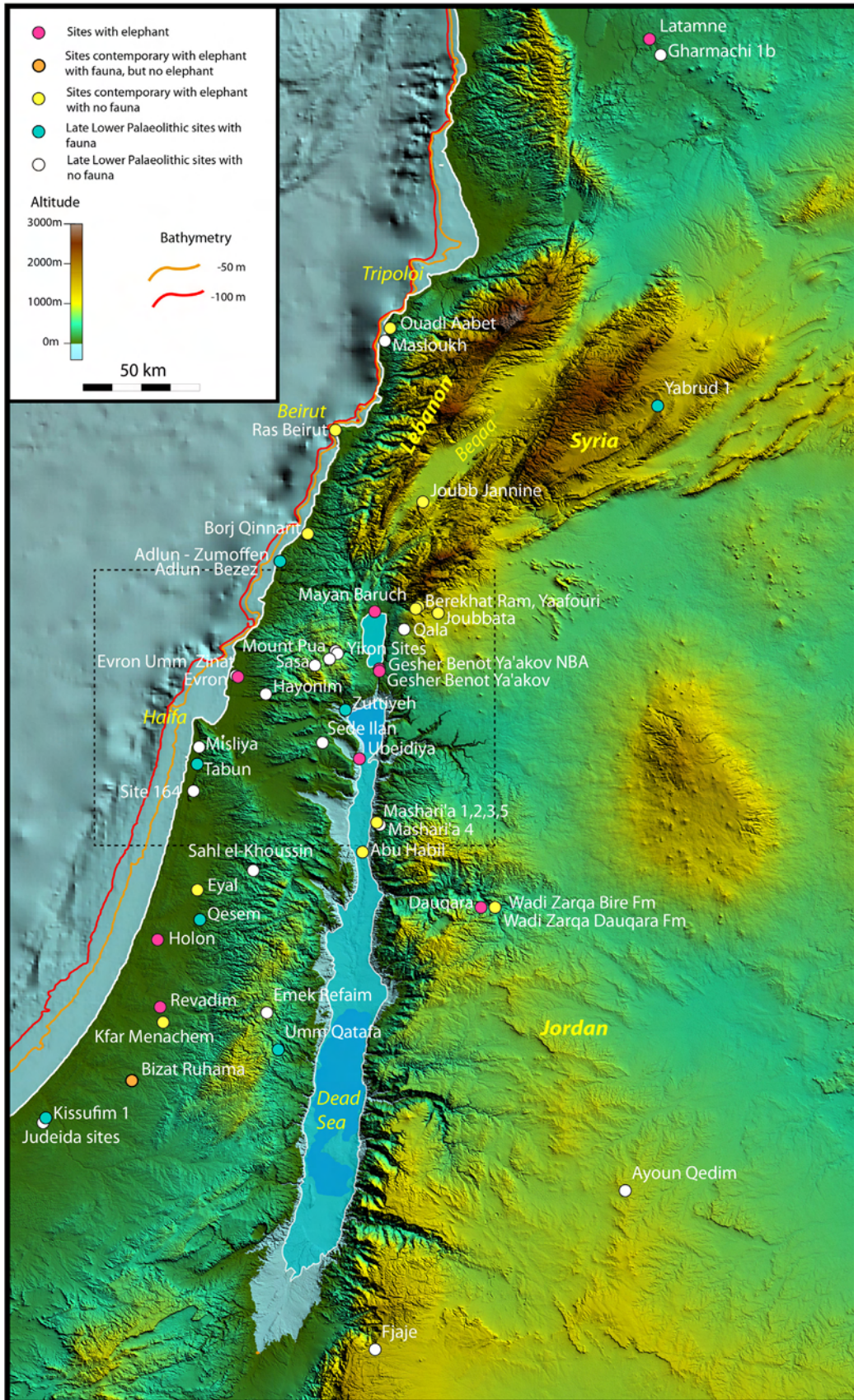
Boundaries to the South are more open, and completely open to the West along the coastal plain, which widens to the South. More variable is the current Dead Sea area. At times of increased rainfall, the rise in water level would have filled a much more extensive area with a palaeolake, referred to as Lake Lisan (Horowitz, 1987, 1989a; Issar and Zohar, 2007). Earlier lakes filled the same valley and have been referred to as Lake Amora and Lake Samra (Stein, 2001; Walman et al., 2009; Torfstein et al., 2009). Here we refer to all of these lakes as Lake Amora, although we also show the known highest level of Lake Lisan in our maps. The potential attractions of this lake region are moderated by the fact that as lake levels rise, so the lake margins increasingly abut against topographical barriers imposed by old shorelines, terraces and steep, impassable valley flanks. Conversely, at lower lake stands, improved access is offset by increased water salinity and increasingly barren surroundings as today. We conclude that the Dead Sea Valley would only rarely have provided an attractive environment during our period.

## 3. Methods and materials

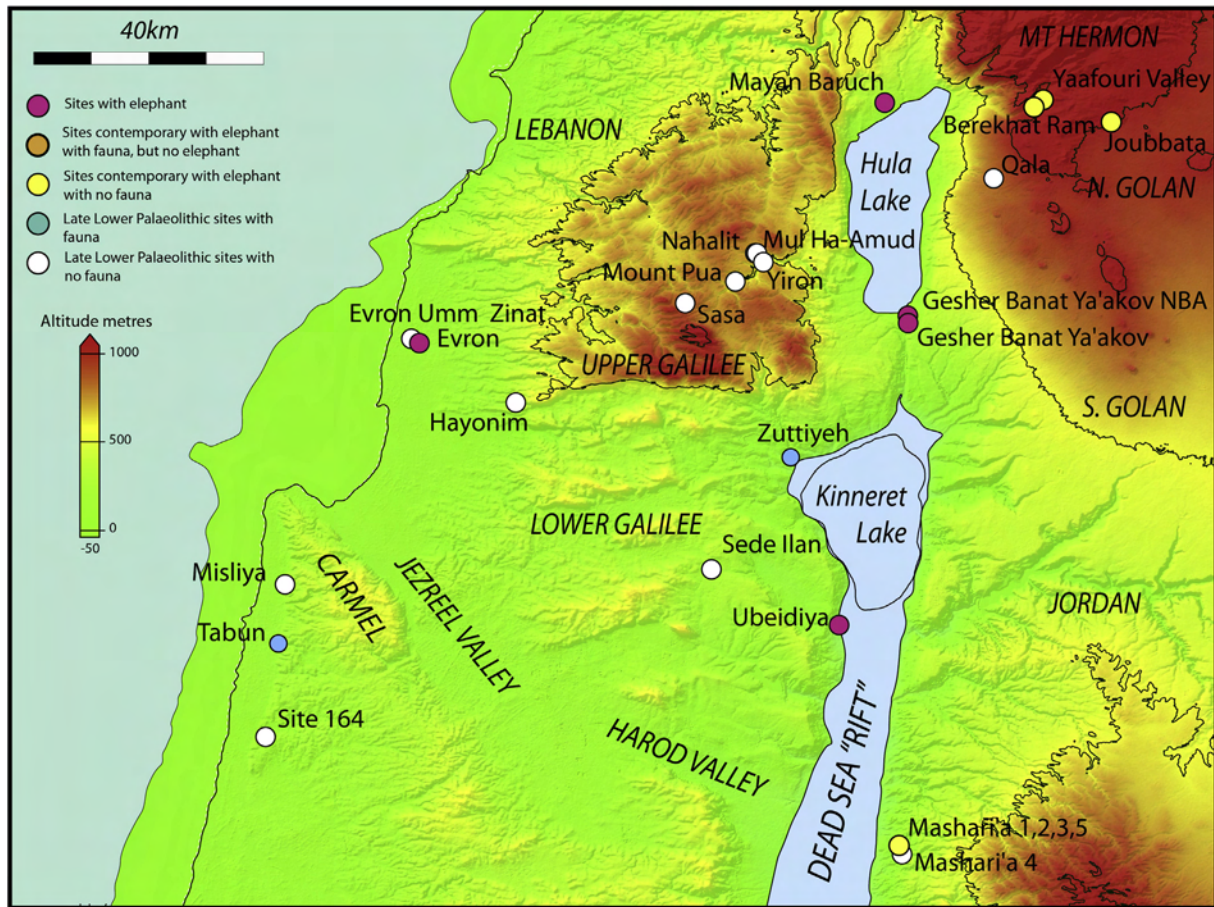
In constructing our maps, we pay particular attention to variations in the edaphic potential of different areas and topographic roughness. We also map a number of additional variables of particular relevance to the habitats and behaviour of the large herbivores. We define here these variables and the methods we use to measure and map them.

### 3.1. Edaphics

Edaphic potential is the ability of the regolith (i.e. soils and subsoils) to supply, by plant take-up, the nutrients necessary for herbivore growth and health. For all herbivores, the edaphic factors are critical to the growth of young animals and the health of all the animals. The availability of soluble phosphates is especially critical, as without adequate supplies the animals cannot grow bones. We stress that simple phosphorus or phosphate levels in soils and subsoils are not, on their own, guides to the edaphic quality of the soils. Tricalcium di-orthophosphate, the main constituent of animal bones, is only soluble in ionised acidic water, and its release into soils in a form which can be taken up by plants is therefore normally very slow. So for high edaphic quality in relation to phosphates, not only is an adequate source of the minerals required, but the conditions must be such that the minerals can actually be taken up by the fodder which the herbivores eat (Schillhorn van Veen and Loeffler, 1990; Henkin et al., 1995; Corah, 1996). The critical season is usually spring–early summer when plants concentrate more of these nutrients.



**Fig. 1.** Significant Lower Palaeolithic sites in the Southern Levant, plotted on to a relief map. The Late Lower Palaeolithic sites probably postdate the extinction of elephants in the region. The sea levels shown are the present-day, -50 m (orange contour) and -100 m (red contour). The current Dead Sea is shown in dark blue and Lake Lisan is shown at its maximum extent in light blue. This can be taken to approximate high levels of Lake Amora. Changing lake levels illustrate the sensitivity to climate changes. Note that the coastal plain becomes very narrow for all sea levels in what is now Lebanon restricting access to the north. Briefly sea level could have been a few metres higher than at present. A black dashed line indicates the region shown in later figures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** The Carmel, Galilee and Golan region showing significant Lower Palaeolithic sites. The current coastline (dashed) and the coastline at  $-50$  m are shown. Lake Lisan is shown at its maximum extent. This can be taken to approximate high levels of Lake Amora. The current Lake Kinneret is outlined. The Jordan Valley is not technically a Rift, but has many features typical of the Red Sea and East African Rifts (Devès et al., 2011). Site colours as in Fig. 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Even where the regolith provides abundant sources of the main minerals and nutrients in a form which can be taken up by plants, specific nutrients may be missing, for example trace elements such as selenium and cobalt, while copper, sodium and potassium are also essential (Burrows et al., 1979; Corah, 1996; Kadim et al., 2003; Formigoni et al., 2011), and animals may need to make occasional movements to places which supply them. Nowadays, fodder supplement and fertiliser providers can handle this requirement without the need to move domestic animals.

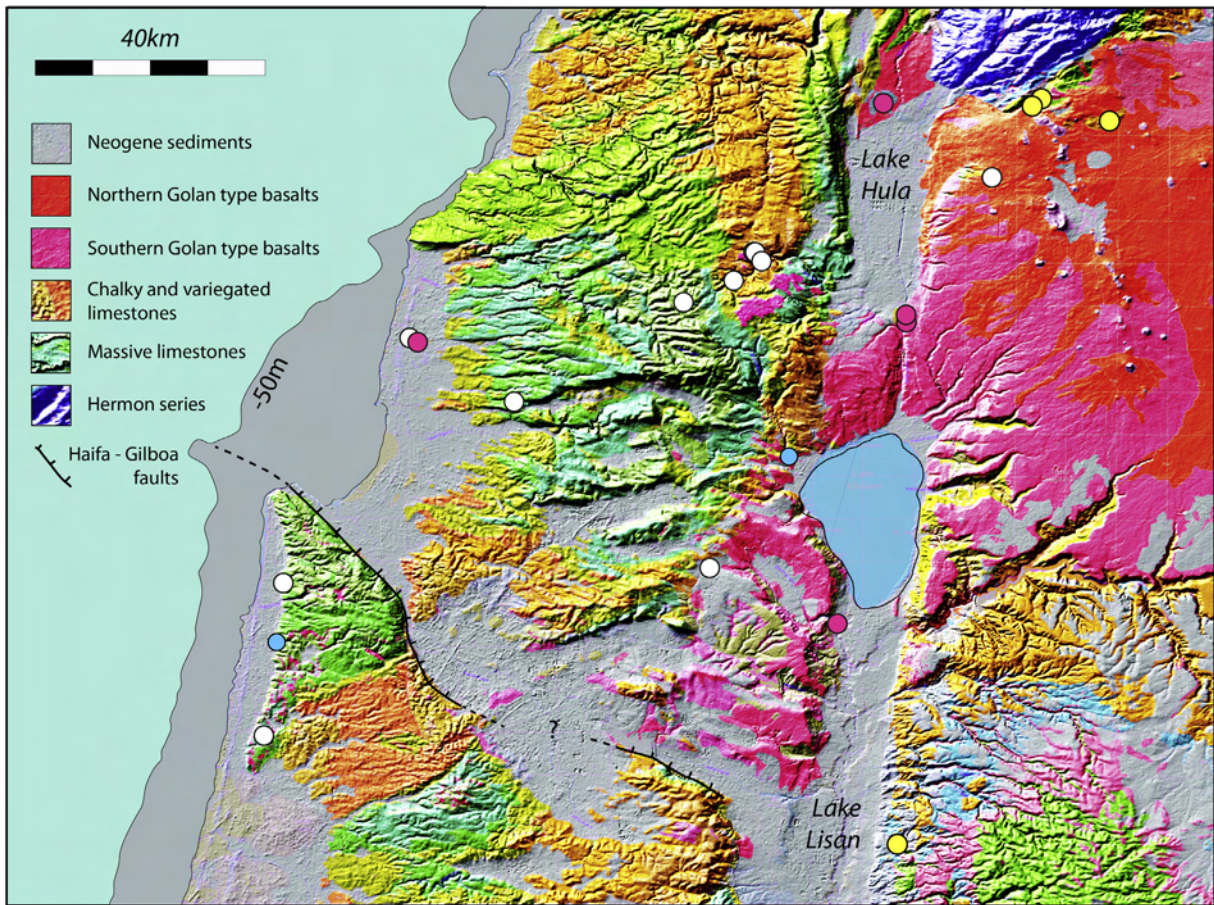
As emphasised earlier, we distinguish edaphic potential from fertility. A given regolith might support abundant vegetation, but this may be of poor quality when viewed as a food source for herbivores. Over wide areas of the Mediterranean, for example, until the recent substantial fall in grazing pressures resulting from changes in human economics, the edaphically poorer areas often carried more abundant vegetation, while the edaphically richer areas were bitten down hard, reflecting their differential attractiveness to herbivores (Sturdy and Webley, 1988; Sturdy et al., 1997).

Palaeosols are rare or absent, and in their absence we use the bedrock geology as our primary guide. The geology is dominated by Mesozoic limestones, marls and chalk, and Tertiary and Quaternary basalts, interspersed with Quaternary sediments derived from local rocks (Fig. 3). The simple geology and the fact that soils are generally thin increase our confidence in relying on the bedrock as a guide to the likely character of the overlying soils.

### 3.2. Topographic roughness

We also pay particular attention to variations in topographic roughness, defined as irregularities in surface morphology (Bailey et al., 2011, 4–5), because these are a powerful influence on the distribution and movements of large herbivores, and on the possibilities for tactical access to and manipulation of animal prey by hominin predators. Roughness can occur at different scales. For this region, we use slope angles derived from DEMs as a measure of large scale roughness, i.e. steep slopes or cliffs that can act as barriers to animal movement. We also look at smaller-scale surface roughness associated with limestone and basalt, both of which are widely distributed, and which can also modify animal behaviour in more subtle, but significant ways. Examples are ‘angry karst’ on limestone (known as ‘ljuti krs’ in Serbo-Croat – a well-known hazard to shepherds of the region), which may appear completely smooth at the 10 m scale, but at close quarters reveals a surface heavily dissected into sharp-pointed ridges alternating with deep fissures. In the European context, only goats (*Capra*) and chamois (*Rupicapra*) can cross these surfaces easily (Miracle and Sturdy, 1991).

Lava flows can also produce small-scale roughness, because slow-moving lava formed at low temperatures, the usual type found in our region, produces a very sharp, jagged, clinker surface when fresh, not unlike angry karst, and may maintain this condition for thousands of years in dry climates. Over time,



**Fig. 3.** Simplified geological map of the Carmel, Galilee and Golan regions, plotted on a relief map. Only the Haifa and Gilboa faults are shown. It is the modest, but ongoing motion on these faults that maintains marshy conditions in the Jezreel and Harod valleys. The morphology of the region is dominated by faulting that has occurred over the last 5 Myr and longer. More information is provided by references in the text. Site colours as in Figs. 1 and 2. The map is modified from the Geological Map of Israel, 1:200,000, State of Israel, Ministry of National Infrastructures, Geological Survey of Israel, Jerusalem 1998. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and especially with a combination of warmth and wetness, the surface can become smoother and rich soils accumulate in hollows, although degrading surfaces can remain rough and blocky. Larger mammals such as bovids, giraffe and elephants cannot cross such surfaces easily (Ripple et al., 2001; Weisengruber et al., 2006).

### 3.3. Animal habitats

We tabulate information on the main food animals found in Lower Palaeolithic sites, and classify them according to habitats, size, requirements and restrictions, and seasonal movements. We tabulate these criteria as best we can in relation to the needs of regional scale mapping, but note that the neat columns of the tables do not exactly reflect the reality of the natural gradients which actually occur, although we believe that they correctly indicate orders of magnitude. The relevant variables include a simple habitat classification (Table 1), live weights, food and water requirements (Table 2), and roughness constraints (Table 3). With regard to habitat variation, despite the existence of a substantial literature on modern ecology and behaviour, particularly for the elephants (e.g., McCullagh, 1969; Laws, 1970; Laws et al., 1975; Owen-Smith, 1988, 1999; Christiansen, 2004; Estes, 2012), much of this information should be used with caution both because of palaeoenvironmental differences, and because of evolutionary

change in the main taxa over the span of the Pleistocene (see in particular Maglio and Cooke, 1979; Vrba, 1995; Lister, 2004, 2005; Lister et al., 2013). We therefore concentrate on the following variables: (1) availability of water; (2) availability of soluble phosphate in the fodder vegetation, at least at some times of the year, to allow bone growth in young animals; (3) availability of fodder in the 'dry' late summer–autumn season; (4) availability of seasonal fodder, such as higher-ground grazing, to avoid over-use of feeding grounds required for other seasons; (5) restrictions on use of highland areas in winter, especially those above 900 m; (6) availability of route ways between grazing areas negotiable by large herbivores.

The calories available to predators from the various herbivores clearly vary according to the efficiency with which the predator is available to convert a carcass, the proportions of fat to lean meat (Ben-Dor et al., 2011), and the size of the animal. It is not our purpose here to attempt a detailed analysis, but simply to note the very large difference between the elephants and, say, gazelles or deer. By any measure, a single elephant will represent between 200 and 300 gazelles (*Gazella*), 40 to 60 fallow deer (*Dama*), or 20 to 30 red deer (*Cervus*). This is an important consideration when assessing the relative palaeodietary importance of animals exploited by hominins. It also has a bearing on estimates of hominin group size and the techniques employed to get at the carcasses.

**Table 1**  
Simple classification of the main herbivores by habitat. A simplistic classification is used to illustrate how the main food animals found in Lower Palaeolithic sites relate to these habitats. For sources of information and further discussion, see text.

	Lakesides and river banks	Denser woodland	Open woodland/parkland	Savannah and steppe	Semi-desert	Hilly and rougher terrain
Hippopotamus	x					
Wart hogs	x	x	x			
Pig/boar	x	x	x			
Cattle, bison	x	x	x	x		
Fallow deer		x	x			
Giant deer			x			
Red deer			x			x
Gazelle			x	x		
Goat			x			x
Giraffe			x	x		
Elephant			x	x		
Rhinoceros				x		
Hartebeest				x		
Horse/zebra				x		
Steppe ass					x	
Camelus					x	

The likelihood of seasonal movements to maintain animal health and numbers is another factor that we seek to map. While, as a general rule, the smaller the herbivore, the shorter the seasonal movements, this is by no means a universal relationship. For example, in the Arctic, the smaller caribou/reindeer make much longer movements than the larger musk oxen; and in many transhumant instances, where terrain exercises a significant control, the smaller sheep and goat move farther than the larger cattle. Nevertheless, we suggest that, in the Pleistocene Southern Levant, the larger animals probably made the longer movements.

We also take into consideration broad variations in climate and vegetation, and expect these to have some impact on the overall productivity of the region for supporting animals. However, we do not attempt to pursue these variables in detail, both because of the difficulties of reconstruction noted earlier, and because these changes most likely become relevant at a larger geographical scale in relation to large-scale animal dispersal, which would take us beyond the boundaries of our region, and examination of which we defer in the present exercise.

### 3.4. Methods of mapping

For the construction of the maps, we use ASTER GDEM version 2 (ASTER GDEM is a product of METI and NASA) and Landsat

ETM + pan mosaics. Bailey et al. (2011) summarise the mathematical definition of roughness used by Earth Scientists and its method of application using spatial filtering. We also rely on our own extensive field observations, which we integrate with the satellite imagery and elevation data.

## 4. Changes in the study region

### 4.1. Changes in the physical landscape

The maps and figures in this paper are based on present day data. However, in the last 1.5 Myr the physical landscape has changed in a number of ways as a result of tectonic and volcanic activity and as a consequence of the climate changes discussed above.

#### 4.1.1. Tectonic changes in the Jordan Valley

While the Jordan valley is a highly visible area of tectonic activity, the actual amount of landscape change is likely to have remained small with respect to the scale of our study, especially in northern Israel (Matmon et al., 1999, 2000a,b; 2003). The main movement in our period is that the Eastern side of the rift has moved northwards, relative to the western side, by 5–7 km, a movement of 3–5 mm per year (Le Beon et al., 2012). This horizontal movement has changed locations in the valley and left little

**Table 2**  
Approximate live weights, and dietary preferences and restrictions, for herbivores found in Southern Levant Lower Palaeolithic contexts. Data from Estes (2012), Clark (1983). See also text for further sources of information and discussion.

Animal	Size in kg	Main diet	Diet and water restrictions
Elephant	6–7000	Generalised browse, grasses and herbs	250–300 kg of food per day, 150–200 L of water per day; significant trampling effect
Hippopotamus	1000–2000	River and lake vegetation	Cannot leave water for long
Rhinoceros	1000–1500	Generalised browse, grasses and herbs	Tends to return to predictable local water resource, making it vulnerable to hominin predators
Cattle (aurochs)	600–1000	Grass	Requires predictable water resource
Camelus		Browse	
Giraffe	700–1100	Tree shoots	Up to 3 days between drinking when green browse is available
Giant deer	200–350	Browse	
Horse/zebra	275–300	Mainly grass	Able to process dry grazing more effectively than ruminants
Hartebeest	125–225	Grass	Directly competitive with Bos for forage
Red deer	180–220	Generalised browse, grass and herbs	
Steppe ass		Grass and herbs	
Fallow deer	90–100	Grass and herbs, some browse	
Wart hogs	60–00	Grass and sub-surface roots etc	Requires a daily water source for drinking and wallowing
Pig/boar	100–200	Sub-surface roots etc	Requires a daily water source
Goat	50–100	Anything green; browse greatly preferred to grass.	
Gazelle	18–22	Browsable shoots, grass and herbs	

**Table 3**  
Roughness criteria as applied to the main herbivores in simplified fashion.

Animal	Limits to negotiating slopes	Accessibility of 'angry karst', new lava
Elephant	Moderate slopes only, not rocky terrain	Impenetrable
Hippopotamus	No slopes	Impenetrable
Rhinoceros	Moderate slopes only, not rocky terrain	Impenetrable
Cattle (aurochs)	Moderately steep slopes, not rocky terrain	Impenetrable
Camelus	Moderate slopes only, rocky terrain only if flat	Impenetrable
Giraffe	Gentle slopes only, not rocky terrain	Impenetrable
Giant deer	Moderately steep slopes, not rocky terrain	Impenetrable
Horse/zebra	Moderately steep slopes, not rocky terrain	Impenetrable
Hartebeest	Moderate slopes only, not rocky terrain	Impenetrable
Red deer	Steep slopes and rocky terrain	Impenetrable
Steppe ass	Moderate slopes only, not rocky terrain	Impenetrable
Fallow deer	Moderate slopes only, not rocky terrain	Impenetrable
Wart hogs	Moderate slopes only, not rocky terrain	Impenetrable
Pig/boar	Moderate slopes only, not rocky terrain	Impenetrable
Goat	Steep slopes and rocky terrain	Negotiable
Gazelle	Moderately steep slopes and rocky terrain	Impenetrable

trace, although remnants can be seen in the excavations of 'Ubeidiya. The vertical motion in the last 1.5 Myr has remained small (Matmon et al., 1999, 2000a,b; 2003; and Matmon pers. comm.). At earlier times vertical rates of motion have certainly been higher (Devès et al., 2011). One can reasonably consider however that the landscape components that we see today are the elements which were present throughout our period, although they were not always in exactly the same place, nor did they look the same in purely local (<2 km scale) terms, as the example of 'Ubeidiya, discussed below, shows. At the highly local level, the western side of the 'rift' presents complex faulting, uplift, sinking, and local change, which is effectively impossible to untangle in precise detail (Devès et al., 2011). Attempting to reconstruct the precise landscape at the 1 km scale for a given period of, say, 50 kyrs, within our period is probably pointless, certainly at the present stage of our knowledge. The eastern side presents a similar pattern of small cliffs and steep slopes cut by west-flowing wadis and the Jordanian hinterland is equally difficult of access except in restricted areas.

#### 4.1.2. Lava/basalt flows in the Golan and Eastern Galilee

More important, for the purposes of our study, are the series of lava/basalt flows which have dominated the landscape of the northern end of the Jordan Valley (see Fig. 3). For example, much of the current surface of the Golan region results from basalt flows which are younger than 3 Myr, some younger than 1 Myr (Mor and Steinitz, 1982; Heimann and Steinitz, 1988). These basalt flows have significant effects on our study because of their mineral, trace-element and phosphatic constituents, which, while they are not uniform, typically yield more fertile soils – especially from the point of view of the edaphic needs of herbivores – than the soils derived from Mesozoic limestones, Neogene marls, and Plio-Pleistocene dune-derived sandstones in the western part of our area. This is reflected in the reluctance of the cattle-raising tribe of Reuben to cross the Jordan, mentioned in the biblical accounts of the Israelite 'conquests' of Canaan (Numbers 32: 1 ff, Joshua 1: 12 ff), and the famed size and strength of the 'Bulls of Basan' from the Southern Golan.

The first difficulty here is that we rarely have information about the qualities of the soils from previous land surfaces now buried by later lava flows (but see, for example, Hartman (2011) for a splendid exception in the Gesher Benot Ya'aqov (GBY) area). The Acheulean artefacts at Berekhat Ram were found in a colluvium sandwiched between two dated lava flows (Singer, 1983; Goldberg, 1992), but

except that the colluvium was substantially pedogenically altered after the artefacts were deposited, we know little about the value of the buried soils at that site for animal grazing. We have therefore assumed that the essential characteristics of soils derived from basalts dated from 1 Ma to 500 ka are the same as those of the later basalts in the same area.

The second difficulty is that the sharp, hostile surface of new lava flows cannot be crossed by herbivores, as noted earlier. We currently know little about the detailed distribution in time and space of new lava surfaces over much of the Lower Palaeolithic period, particularly for the Golan Heights, compared to the weathered surfaces available to grazing animals. We can only extrapolate and assume that, although they would be distributed differently, the land surfaces and the origins and chemical constituents of the soils of the Golan would have been broadly similar to those of more recent times.

#### 4.1.3. Tectonic changes: the Carmel–Jezreel area

The Carmel and Jezreel regions are dominated by motion on the NE dipping Haifa or Carmel fault and its extension east to the Gilboa fault. This has predominantly dip-slip motion with uplift to the southwest and subsidence to the northeast. Long-term motion has resulted in the observed topography and the deep sediment of the Jezreel and Harod valleys (Figs. 2 and 3). Although modest, continued motion ensures that these valleys remain well watered and marshy in many places. These conditions make the valleys difficult to cross, but ensure water during dry seasons. On the eastern side of the Carmel, the Lower Palaeolithic inhabitants are likely to have seen a landscape not significantly different from that of today except in the distance to the sea-coast (see below).

#### 4.1.4. Changes of lake levels

For much of our period, the Jordan Valley held much larger lakes than at present, especially in a North–South direction. The interaction of climate and tectonics has resulted in relatively rapid changes in the exact shorelines, but we can make some generalisations for much of the period. The Hula lake was normally of larger extent (Zohar and Biton, 2011), reaching south to Gesher Benot Ya'aqov and the start of the modern upper Jordan gorge, while Lake Kinneret and the Dead Sea (as noted above) were frequently joined into a lake (Lake Amora), which filled the whole of the current central Jordan valley to varying depths. The current conditions are distorted by modern water extraction for human use and present a highly atypical picture of the amount of water normally present.

These larger water bodies meant that animals (and hominins) could rarely cross the Jordan Valley between the present southern end of the Dead Sea and the northern end of Lake Kinneret, although land bridges at the southern end of Lake Kinneret would occasionally have been present. 'Ubeidiya is on the western end of such a bridge. Passage for animals around the northern end of the Hula Lake, and especially along the western margin, would have been similarly restricted.

#### 4.1.5. Sea level changes

For much of our period, sea level was lower than today, interspersed with short-lived higher stands, and we use general sea-level curves in relation to bathymetry as a general guide (Siddall et al., 2003). The additional amounts of land revealed at –50 m and –100 m, though locally significant, are small in relation to the total region under discussion (Fig. 1). On occasions, for periods which are relatively short on the timescale concerned, sea level was higher than the present. These changes are mainly of relevance in expanding or contracting the coastal pathway for movement of large herbivores northwards beyond our region.



#### 4.2. Changes in climate

In charting climate changes associated with the glacial–interglacial cycle, we follow Frumkin et al. (2011), who argue convincingly that between MIS 6 and 2 ‘glacial’ periods coincided with rather cooler, wetter (often considerably wetter) conditions in the Southern Levant, but with little variation in winter and summer temperatures. Detailed climatic data for the periods before MIS 6 are very patchy and rarely well constrained in time, and in their absence we assume that a similar pattern can be extrapolated to earlier periods.

The combination of species present in the vegetation appears to have changed little over the span of the Pleistocene (Belmaker, 2008). Rather, the changes are likely to have been in the relative extent of woodland compared to grass and scrublands in the West and in the extension of steppe vegetation into present desert areas in the East and South. Rainfall is clearly highly important in this region (Frumkin et al., 2011). A relatively small increase in rainfall renders areas of semi-desert to the East of our region (in modern Syria and Jordan), and to the South in the Negev (Vaks et al., 2007), available to herbivores (and hence hominins) for at least some part of the year. It also quickly increases the size of the Jordan Valley lakes (Bookman (Ken-Tor) et al., 2006), so that in the wettest periods ‘Lake Amora’ fills the whole of the modern Dead Sea basin, the Lower Jordan valley and an extended area around the modern Lake Kinneret in one large, elongated lake.

Rainfall is not just important for grazing quantity: it is also critically important to grazing quality. Naveh (1982) shows that variation in annual rainfall makes the difference, for the Galilee region grazing, between a semi-desertic biome and a subhumid woodland-grassland biome, with concomitant increase in productivity with higher rainfall.

#### 4.3. Time trends in animals

A number of long-term changes have taken place in the region, particularly with regard to the morphology of elephants as reflected in the evolution and replacement of elephant taxa (e.g., *Stegodon*, *Mammuthus*, *Palaeoloxodon*; Table 4). The issue of taxonomic nomenclature is not wholly resolved, and we sidestep this in favour of working terms for recognisable animal types like ‘elephants’ and ‘rhinoceros’. Other common food animals, such as *Gazella gazella*, *Cervus elaphus*, *Dama mesopotamica* and *Bos primigenius*, show comparatively little morphological change over the period. There were also a number of pulses of faunal movement into and out of the Levant, variously involving African/European (Africotropical/Palaearctic) faunal assemblages (Tchernov et al., 1994). Certainly there were such pulses when typical African species became frequent or dominant, or when they were effectively absent. By 250 ka, the typical African large herbivores were either rare or locally extinct, including elephants and rhinoceros, the

antelopes (apart from hartebeest), and most of the warthogs. The dominant gazelle throughout the Lower Palaeolithic appears to be related to Asian rather than African species, and Eurasian deer species (*Cervus*, *Dama*) and large bovids (*Bos/Bison*) were always present.

Whether these morphological and evolutionary changes have affected animal habitats in ways relevant to the variables that we concentrate on in our maps is unclear. Size changes might be relevant to food requirements and foraging range, and we have incorporated such factors into our assessment of habitat requirements where possible (Tables 1 and 2), but these are in any case defined quite broadly, and information that might allow us to track time trends in relation to more narrowly defined habitat preferences is not available.

### 5. Mapping of animal distributions and their interpretation

#### 5.1. Relative edaphics in the Carmel–Galilee–Golan area

We use a simplified geological map of the area (Fig. 3) and contrasting edaphic values of the fodder grown on different soils derived from different subsoils and bedrocks (Fig. 4). A ‘broad-brush’ approach is intentionally adopted. After all, a herd of say 10 elephants, each consuming an average of some 200 kg of vegetation a day (Table 2), cannot usefully be related to very local studies (such as a site or a ‘site-catchment’) except in terms of the whole landscape in which they feed. Therefore small-scale variations within broad classifications such as we use here, while interesting, are not directly relevant to this study.

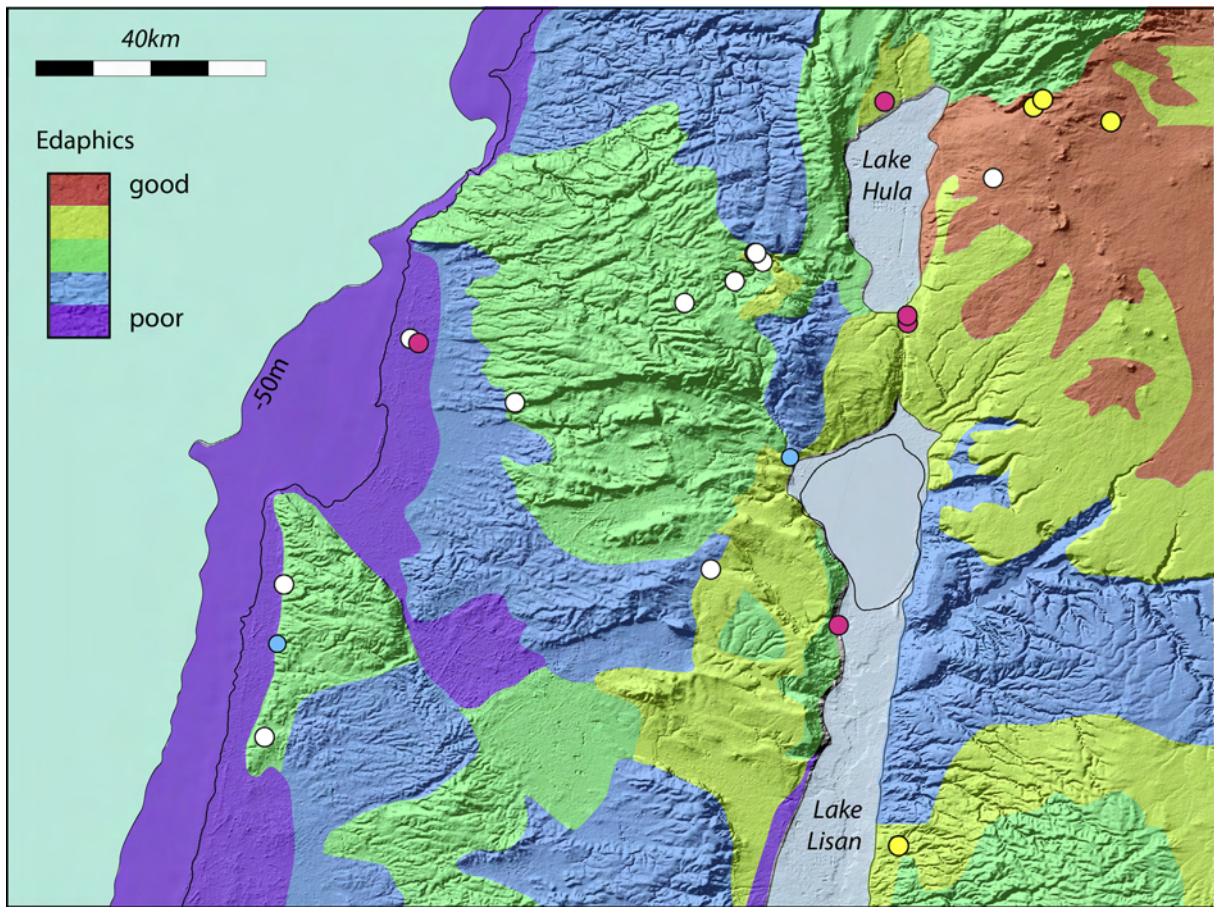
In general terms, the Neogene marls of the western Jezreel valley, and the dune-rocks of the coastal plains, offer the poorest edaphics. The variegated limestones of the Mesozoic–Palaeogene series, although they form deeper soils, tend to lack the minerals which create good grazing, so that although the grazing may be seasonally plentiful it is not of very good quality (Henkin et al., 2007). The finer-grained limestones, mostly from earlier in the Mesozoic sequence, are better in this respect although soils are thin; but the pockets of terra rossa soils typically derived from them are relatively good at providing phosphates in soluble form in certain seasons.

The key areas from the edaphic point of view are the basalt soils. These also vary; the soils of the East Galilee and the Southern Golan, although they may contain plenty of phosphorus, do not contain it in a form which is abundantly available to be taken up by plants, and therefore animals. The vital area is the Northern Golan and the more recent basalt flows. Here the phosphorus elements are up to three times as frequent as in the Southern Golan, and the availability can reach up to 70% (Singer, 1987).

In areas of some relief, the edaphics can reflect the characteristics of upslope rocks as a result of normal weathering and geomorphological processes, as well as of the immediately

**Table 4**  
Simplified summary of large herbivores in the Southern Levant that show significant morphological changes during the Pleistocene. After Tchernov et al. (1994). See text for further discussion and additional sources of information.

Animal type	Species names and period			
	1.4 Ma	1 Ma	0.6 Ma	0.3 Ma
Elephants	<i>Mammuthus meridionalis</i>	<i>Mammuthus trogontherii</i>	<i>Palaeoloxodon antiquus</i>	Almost extinct
Hippopotamus	<i>Hippopotamus behemoth</i>	<i>Hippopotamus cf behemoth</i>	<i>Hippopotamus cf amphibius</i>	<i>amphibius</i>
Rhinoceros	<i>Dicerorhinus etruscus</i>	<i>Dicerorhinus hemitoechus</i>	<i>Dicerorhinus hemitoechus/merckii</i>	<i>Dicerorhinus cf merckii</i> , rare
Horses	<i>Equustabeti</i> , + <i>cf caballus</i>	<i>Equus altidens</i>	<i>Equus cf caballus</i>	<i>Equus caballus</i>
Wart hogs	<i>Kolpochoerus olduvaiensis</i>	<i>Kolpochoerus olduvaiensis</i>	<i>Kolpochoerus evronensis</i>	
Pigs	<i>Sus cf strozzii</i>		<i>Sus cf scrofa</i>	<i>Sus cf scrofa</i>
Giant deer	<i>Praemegaceros verticornis</i>	<i>Praemegaceros verticornis</i>	<i>Praemegaceros verticornis</i>	Extinct



**Fig. 4.** Interpreted principal edaphic characteristics of the Carmel, Galilee and Golan regions, plotted on a relief map. Edaphic characteristics are based on the geology. Site colours as in Figs. 1 and 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

underlying rocks. We have taken this into account in offering the broad areas of relative edaphic quality shown in Fig. 4.

### 5.2. Water and 'dry season' fodder

Dry season (late summer–autumn) fodder supplies, adequate for animals such as elephants, would form a considerable constraint. Fig. 5 offers a broad-brush approach to illustrate the relative water retentiveness of the soils. The highest-ranked areas are in the western portion of the Jezreel valley, where lake and marsh deposits from various Neogene periods provide good water retention, and in the Harod valley in the Eastern part of the Jezreel valley down to the Dead Sea, where wet areas, marsh and some permanent lakes are supplemented by the large springs bringing water from the aquifers of the Samarian hills. Alongside these areas, where dry-season vegetation would provide a vital seasonal resource, the main lakes of the Jordan valley and the perennial streams of the Jordan and Harod provide free water. In general the dry-season vegetation of the eastern Jezreel valley would have been of critical importance because it is of higher quality than the vegetation in the western part due to the edaphic factors.

Next in water-retentiveness value are the basalt soils of Eastern Galilee and the Golan Heights. These vary in their ability to take up water (Scharpenseel et al., 1995) but in general are intermediate in this respect between the limestone and coastal dune-rock areas on the one hand, and the Jezreel area on the other. The sediments which have accumulated in the basins between the ridges of the Galilee area are also intermediate in terms of water-retentiveness, because in many cases there is a considerable depth of soil. Few

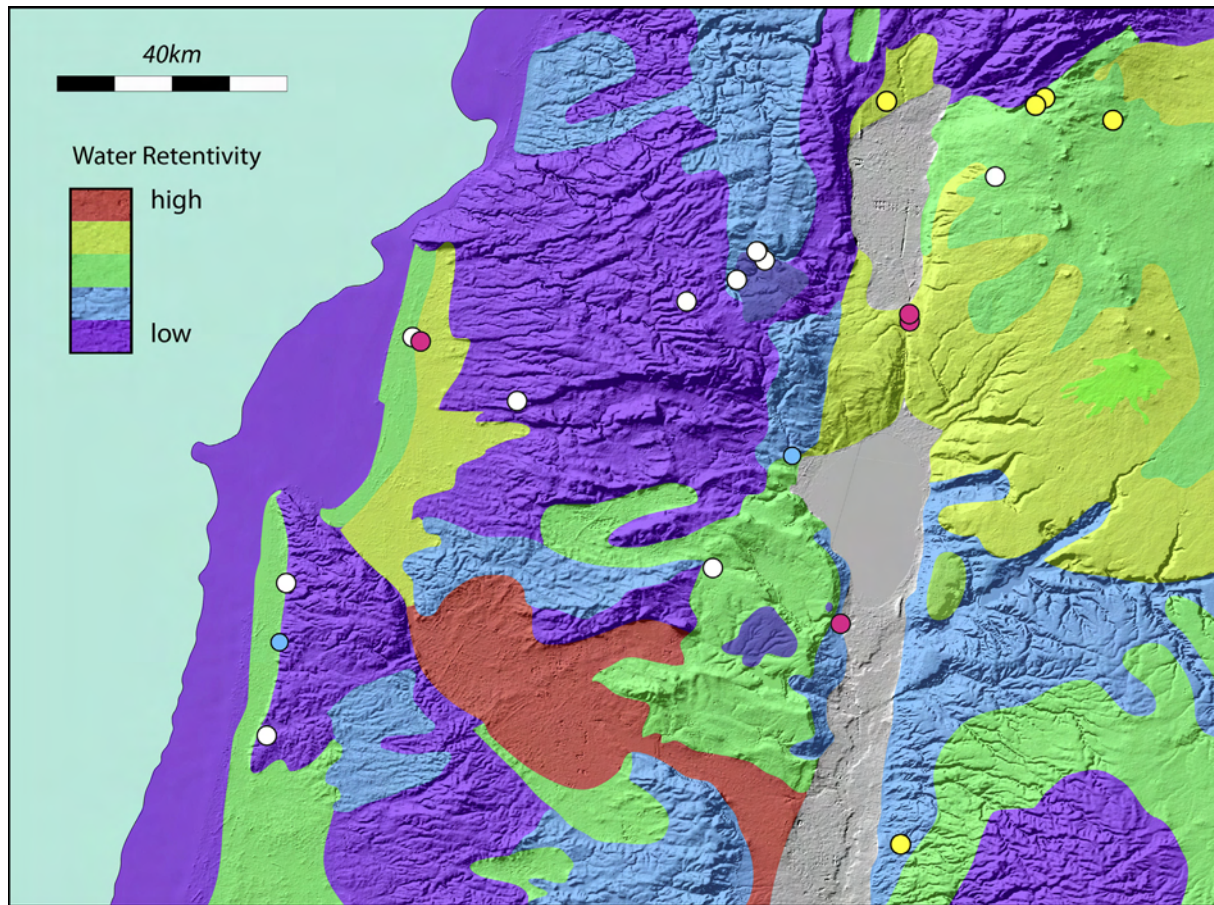
of these basins, however, have much surface water in the dry season.

The limestone areas are famously porous (karstic) and offer little in the way of dry-season water or vegetation for the large herbivores such as elephants. There is typically a difference between the areas of the limestones from later in the Mesozoic–Palaeogene sequence, and those from earlier in the sequence. The later limestones provide thicker, rendzina type soils with rather better water retention than the earlier. The finer, more massive limestones, typically from earlier in the Mesozoic–Palaeogene sequence, provide terra rossa soils which are potentially quite water retentive – more water retentive per unit of volume than the basalt soils (Singer, 1987) – but are typically thin. In terms of area, therefore, none of the limestone soils can be classified as anything but poor from the point of view of dry-season grazing.

Water-retentive soils are rare in the coastal areas, which are mainly based on cemented dune sands. Areas of loams and pockets of marsh soils and dense clay soils certainly occur, and Lower Palaeolithic sites are specifically associated with them at, for example, Evron (in Fig. 6), and at Holon and Bizat Ruhama further south. The inland side of the coastal plain receives sediments with terra rossa and rendzina components and therefore develops a relatively more water-retentive regolith than the seaward side.

### 5.3. Altitude constraints

Although the higher areas enjoy higher precipitation, this can turn to snow, producing winter conditions which animals such as the



**Fig. 5.** Simplified map of relative water retentivity of soils in the Carmel, Galilee and Golan regions. Typical soil thickness as well as water retentivity are used to construct the figure. Sea level in this figure is shown at  $-50$  m. Site colours as in Figs. 1 and 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

elephants and rhinoceros of our period could probably not endure (see Fig. 2). Today, winters in the Northern Golan and in the Upper Galilee are certainly harsh enough to make them unattractive to many of the herbivores we are considering. In the wetter and cooler phases of our period, this situation would have been accentuated.

#### 5.4. Roughness constraints

Fig. 6 shows roughness and steep slopes. As noted above, animals such as elephants, rhinoceros and giraffe are limited by rocky, jagged or steep terrain. Their weight, and their limb configuration in the case of giraffes, excludes them from such areas. This means that quite large areas of our region, particularly the Upper Galilee, could not be exploited by these animals – the smaller herbivores, especially deer and gazelle, do not suffer from these constraints to the same degree, while goats are almost unaffected by them (see also Table 3).

This is important not just for grazing areas, but for routes between grazing areas. As Fig. 6 indicates, between the Golan and the dry-season pastures of the Jezreel and the coast, there are limited routeways available to large herbivores, and the grazing areas available along or beside them are relatively small.

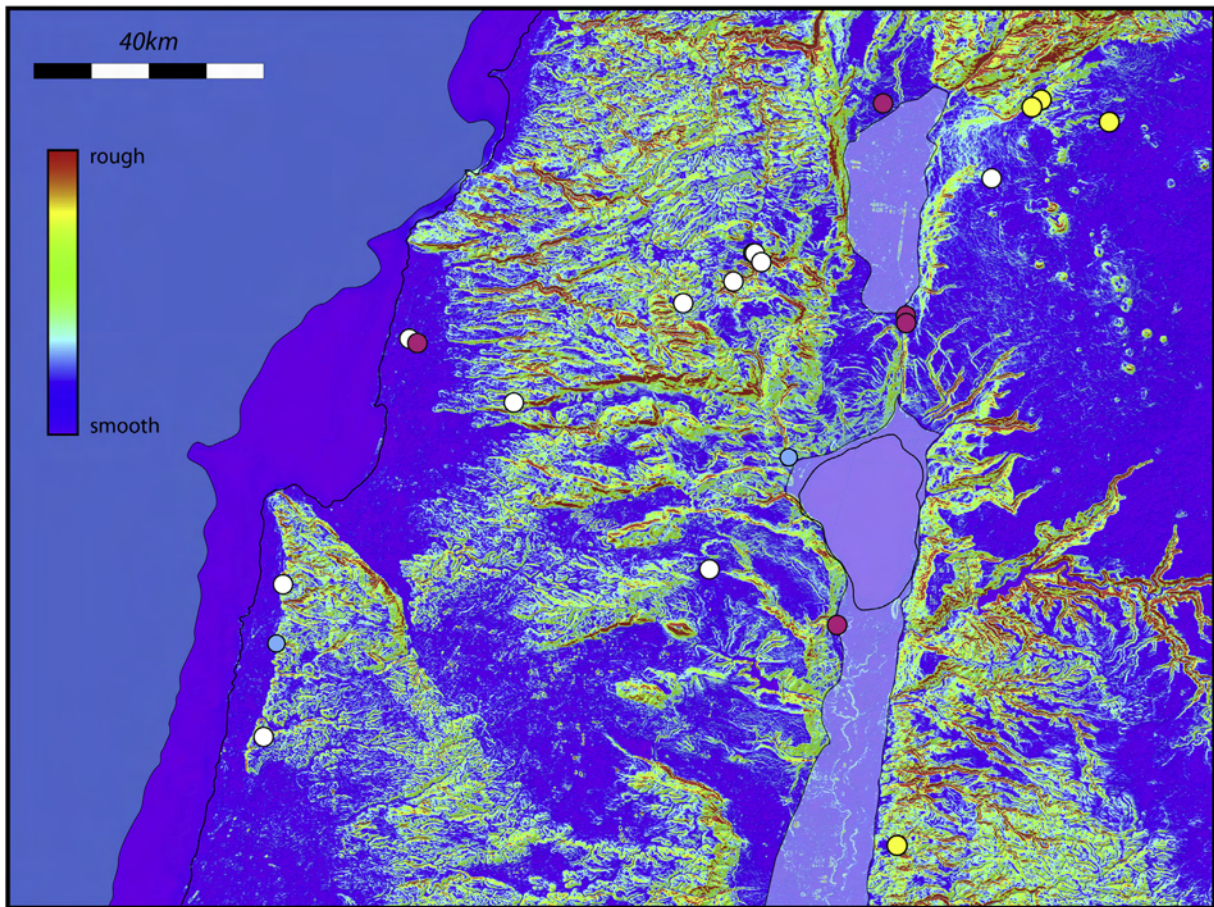
#### 5.5. Synthesis of large herbivore seasonal movements

##### 5.5.1. The essential pattern – eastwards in spring, westwards in autumn

Fig. 7 pulls together these various threads to present the possible seasonal rounds of large herbivores. Starting with the

spring season, the animals would have moved eastwards from the coastal plain towards the more edaphically productive areas to take advantage of the best nutrition of the year. They would follow the growth on such limestone areas as were available, for example, the easier ground south of Carmel between the coastal plain and the Jezreel valley, eastwards towards the more phosphate-rich basaltic soils. Henkin et al. (2007) stress that the first flush of new forage is the most nutritious, and here altitudinal differences would give large herbivores an incentive to follow the new forage at higher altitudes as it became available. The low-lying basalt soils of the eastern Galilee would be the earliest, and the animals would then move into the Golan, crossing the Jordan valley where they could. The altitudinal effect greatly extends the season of the most nutritious fodder, and thus provides an important driver of animal movement.

Bischof et al. (2012) provide a useful discussion of this 'plant maturation hypothesis' and the benefits to migrating herbivores of following the sequence of fresh plant growth in spring as it matures at successively higher altitude. They also provide an interesting alternative view for red deer in a specific Norwegian study area, suggesting that the deer 'jump' rather than 'surf the green wave', moving rapidly from winter to summer grazing. However, the distances they discuss are smaller and other factors may drive this phenomenon, including the vulnerability of migrating animals to predation and the competitive drive to reach the vital early summer final areas 'first'. This suggests that it might be unwise to seek for too much detail about the exact nature of the spring movement, but the general outline remains clear: the more than 1000 m of



**Fig. 6.** Slopes and roughness in the Carmel, Galilee and Golan regions. The range of slopes that would be difficult or impossible for large herbivores to negotiate is indicated. See discussion in the text. Note that the eastern flank of the Upper Jordan valley and the western part of the Jordan plateau are heavily dissected, limiting their use even when climate was favourable. Site colours as in Figs. 1 and 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

altitudinal difference between winter and summer grazing would have had the important advantage for large herbivores of providing an extended 'spring' season of the best forage.

The highest point of the southern Golan, close to the Acheulean sites of Berekhat Ram and its neighbours, represents the limit of the new forage. After reaching the Northern Golan, much of the summer would be spent in making use of the available grazing east of the Jordan River. At times during our period, recent lava flows would provide local no-go areas, while the lower nutritional value of the Southern Golan, compared to the Northern, would be offset by the availability of fodder through the summer.

With the late summer/dry-season approaching, the animals would move back towards the limited resource of the Harod-Jezreel areas, where water-retentive soils, and marshlands, provided important dry-season fodder. The winter rains would then make the coastal plain the obvious main grazing area for winter.

#### 5.5.2. Routeways

As we noted above, landscape roughness creates important constraints not just on animal grazing areas but on routeways. There are certainly limited routes that would be available to animals such as elephants, rhinoceros and giraffe, and to a lesser extent the large bovids.

Crossing the Jordan valley would normally have been highly restricted. The larger Central Jordan Valley lakes, and the extended Hula Lake in the north, would typically restrict large herbivore movement between the coast and the Golan to a crossing at Gesh

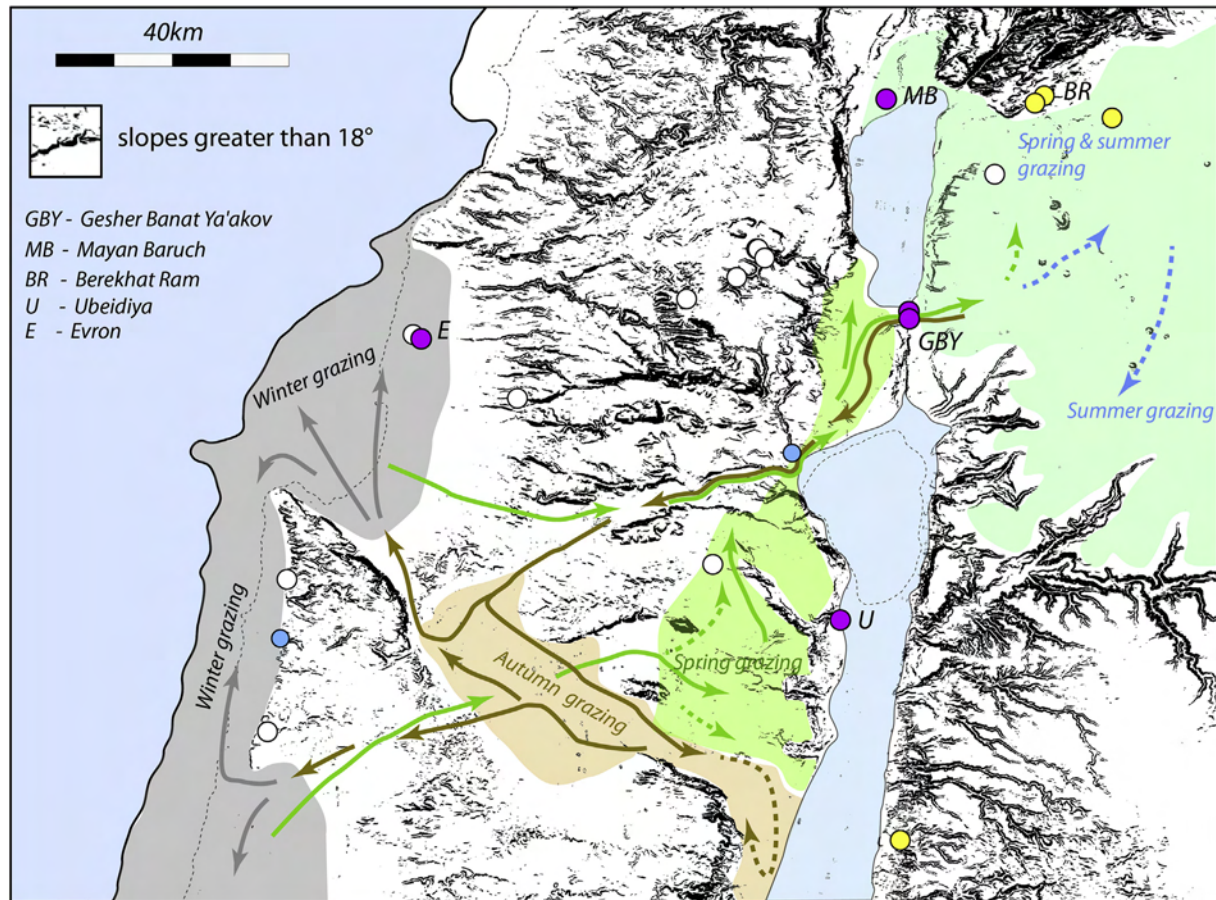
Benot Ya'aqov. At times, a crossing below the Lake Kinneret would also be theoretically possible, but the steep and rugged valleys on the Jordan side would have blocked access to the Golan via this route for larger herbivores regardless of their swimming abilities (Figs. 6 and 8). Crossings in the Central Jordan valley between the areas of the current Lake Kinneret and the Dead Sea would be the atypical situation for most of our period. At all times, the crossing at Gesh Benot Ya'aqov was a vital pinch point.

The available routeways would also be seasonally affected by the differing requirements for forage. Spring routeways would concentrate on following the new flush of nutritious forage, as noted above. In autumn, the emphasis would be on the quantity, rather than the quality, of forage available and water supplies.

#### 5.5.3. Interaction of large and small herbivores

**5.5.3.1. The elephant periods.** During our period we would expect the large herbivores to have maintained open pasture conditions on their favoured grazing areas. Modern elephants, in particular, pull up and eat young trees, inhibiting woodland growth (Estes, 2012). However, the limestone areas may have been relatively unaffected by large animal behaviour because these areas would have been too rough for them. On the limestone areas, woodland would have been more common, varying from closed woodland to open parkland, depending on both the amount of rainfall, soil depth, and the intensity of smaller herbivore usage, as it is today.

We would therefore expect the main areas available to the deer and gazelle species to be more or less distinct from those favoured



**Fig. 7.** Reconstructed seasonal movements of large herbivores in the middle Pleistocene of the Carmel, Galilee and Golan regions. Green arrows show suggested spring movements, blue arrows possible summer movements, and brown arrows suggested autumn movements. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

by the large animals, because of the competitive pressures on forage availability exerted by the large animals. Seasonal movements of the larger deer species would be altitudinal, exploiting the high Galilee in summer, but the smaller species (fallow deer and gazelle) would probably have made only limited seasonal movements.

**5.5.3.2. After the elephants.** When the large animals became extinct in the region, this dichotomy would probably continue, though in a less marked manner. Equid (horse, ass and zebra) and large bovid herds, including *Alcelaphus* when it was present, could be expected to make use of the same flatter grazing as the preceding large herbivores, probably expanding in numbers to fill the ecological gap, but following the same seasonal rounds. In some ways we can envisage the large bovid/horse herds emulating the modern association of wildebeest and zebra in East Africa, eating different components of the forage, but essentially sharing both grazing areas and migration routes.

The larger cervids would make use of altitudinal differences in the limestone areas as always (e.g. Sturdy et al., 1997; Sturdy and Webley, 1988), and the smaller cervids and gazelles would perhaps expand their ranges, as (or if) the amount of woodland increased in the absence of the large herbivores. The main result of this effect would be to 'blur' the distinction between the large herbivore and medium/small herbivore ranges, resulting perhaps in increasing food-source complexity for hominin groups.

## 6. Hominin responses

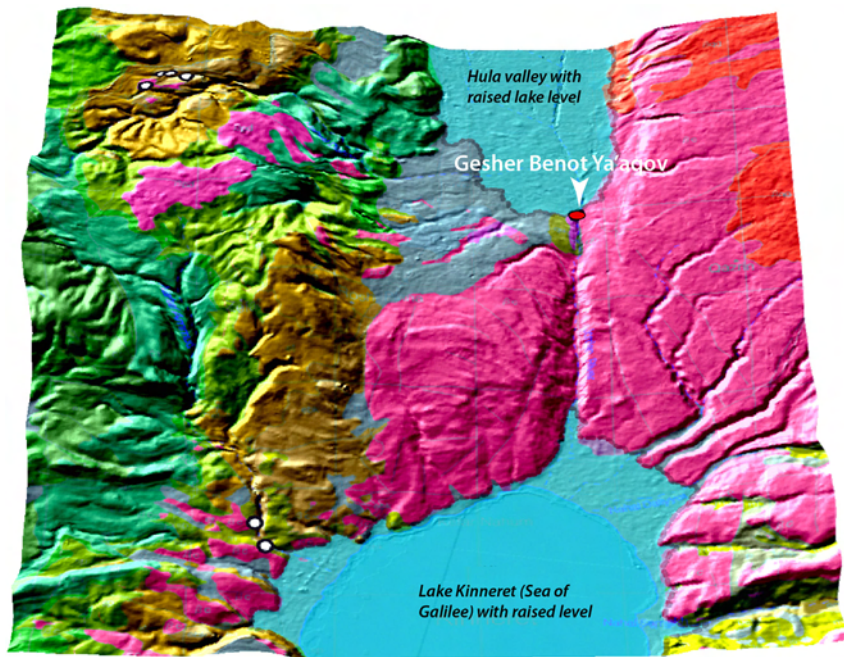
### 6.1. Sites on migration or seasonal movement routes

Migration hunting is typically a very high-risk strategy because it depends on positioning most of the available humans where they believe a migration of animals is due to pass. If the migration route varies, the humans will probably starve, as exemplified by the short-lived and unsuccessful attempts of Barren Ground Eskimo to adopt this strategy after the introduction of guns to the Canadian North (Mowat, 1952; Hurst, 2004). If migration hunting is to work, there must be a real certainty that bypaths are not available to the animals. Two sites, one relatively early in the Acheulean sequence and one right at the end of it, appear to be closely related to migration routes.

#### 6.1.1. Gesher Benot Ya'akov (GBY)

Faunal remains are dominated (numerically and in terms of dietary contribution) by elephant (*Palaeoloxodon antiquus*) and fallow deer (*Dama* sp.) (Goren-Inbar et al., 1994; Tchernov et al., 1994; Rabinovich and Biton, 2011; Rabinovich et al., 2011). Many other herbivore species are present, including hippopotamus, steppe rhinoceros, horse, warthog, pig, giant and red deer, gazelle and large bovinds.

When the central Jordan valley was filled with a single lake from the north end of Lake Kinneret to the southern end of the Dead Sea (Feibel, 2009), GBY is on the only practical route from the coast to the



**Fig. 8.** The location of Geshher Benot Ya'aqov at a highly restricted pinchpoint on the route between the Golan and the grazing lands west of the Jordan Valley. Note the small crossing point between the expanded Lake Huleh and the steep-sided Upper Jordan valley.

Golan summer grazing, and this would have been true for all but small animals at all times regardless of lake levels (see Fig. 8). If hominins or other predators at the crossing were sufficiently threatening, animals might be forced to try alternative routes to the South – some possible routes 2–10 km to the south would be available – but these involve much harsher and rockier terrain and would be unattractive to very large herbivores except in the last resort.

But GBY also offers other advantages to hominins (Stekelis et al., 1937, 1938; Alpersen-Afil et al., 2009; van Zeist and Bottema, 2009). Unlike many potential migration-hunting sites, the migratory animals are not the only resource (Goren-Inbar et al., 1992, 2000; Shoshani et al., 2001; Rosenfeld et al., 2004; Rabinovich et al., 2011). Because of its lake-side/riverine location, non-migratory animals (pigs, fallow deer, even hippopotamus) were available locally, so that hominin groups arriving to exploit the spring or autumn herd migration could not only support themselves while they waited, but support themselves if the migration, for whatever reason, failed to materialise (Rabinovich and Biton, 2011). Given this remarkable concatenation of advantages, it is not surprising to find more than one site, several periods, and indications of repetitive use of the site not only for perhaps 100 ka in the Acheulean period, but at many other periods as well.

#### 6.1.2. Zuttiyeh

The herbivore fauna of the Lower Palaeolithic layer of Zuttiyeh includes large bovinds (*Bos/Bison*), fallow deer (*D. mesopotamica*), goat, red deer and gazelle (Bate, 1927a,b).

The Amud valley runs in a gorge for a considerable length northwest of Lake Kinneret. Where the valley debouches on to the northwest margins of Lake Kinneret, the various possible route-ways leading from (or to) the West and South converge into a single narrow passage along the lake margins. This margin would vary in width with the height of the enlarged Lake Amora in wetter phases. It is also possible to cross the Amud a kilometre from the mouth of the gorge (a crossing used by the modern main road) between the sites of Amud and Zuttiyeh. The three Palaeolithic sites in the valley,

Amud cave, Zuttiyeh and Emireh (Turville-Petre, 1927; Bate, 1927a; Garrod, 1955; Hovers et al., 1991; Rabinovich and Hovers, 2004) all offer the opportunity to monitor or exploit seasonal animal migrations where routeways are highly restricted, and testify to a long period in which hominins found this location useful, from the late Lower Palaeolithic to the Upper Palaeolithic.

Zuttiyeh is the site in the Amud valley which has a final Lower Palaeolithic component, based on dating and the Amudian assemblages, which are found interstratified with Acheuleo-Yabrudian industries elsewhere (Bate, 1927c; Gisis and Bar-Yosef, 1974). The most important food animals in the Final Lower Palaeolithic were probably large bovinds, taken on migration, though the site is probably not itself a large game kill site (the animals would be passing about 1 km to the South). Although not as abundant as at GBY, smaller local, non-migratory herbivores (*Dama*, *Gazella*) were available to reduce the reliance of the site users on a single hunting tactic.

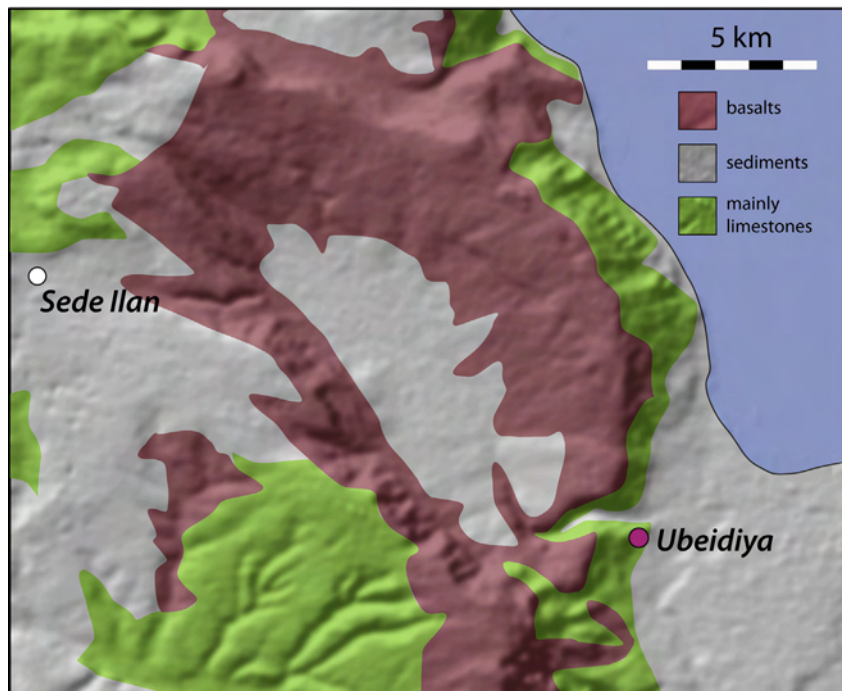
### 6.2. Sites related to seasonal grazing

#### 6.2.1. Spring grazing in the Eastern Lower Galilee

The famous Early Pleistocene site of 'Ubeidiya is a good example of a palimpsest of frequently repeated hominin behaviour and activities, probably over quite a long time period. Fig. 9 shows a close-up view of the area, with the expanded Lake Amora to the East. Note the 'jumbled' appearance of the western edge of the Jordan Valley. For a distance of 1–2 km west of the lake, very complex gullying and active landscapes are clearly visible, but moving west beyond this valley margin, a much more mature landscape is evident.

The fauna from 'Ubeidiya is substantial with many species (Tchernov, 1986; Tchernov et al., 1994), including elephants, hippopotamus and rhinoceros, horse, warthog, giant deer, large bovinds, giraffe, camel and gazelle.

The modern local environment does not represent exactly how the site appeared when hominins used the area 1.4 million



**Fig. 9.** The location of 'Ubeidiya in relation to prime grazing areas to the west of the site. While the detailed topography local to the site has changed very considerably, the larger-scale relationship of the site location to the landforms, rock formations and sediments to the west is essentially unchanged in the last 1.4 Myr. Note that at lower lake levels when access was possible to the east flank of the Jordan valley, the rough topography limited its usefulness (see Figs. 6 and 7).

years ago. The tilting of sediments, and changes in the immediate location, make an exact reconstruction difficult. The site shows evidence of lakeside, or near lakeside, occupations, associated with outwash fans and small valleys coming down from the higher ground to the West (Bar-Yosef and Tchernov, 1972; Bar-Yosef, 1989; Guerin et al., 1996; Gaudzinski, 2004; Belmaker, 2010). In general terms, therefore, using examples of these landforms from the modern Lake Kinneret shores, and landforms to the South of the site, it is not at all hard to imagine what the local environment was like at the time of occupation (Mallol, 2006).

But the key to 'Ubeidiya lies above the site to the West (Fig. 9). We observe that 'Ubeidiya lies below a fine example of basalt-area grazing, in the relatively undisturbed landscape which is reached as soon as the immediate margins of the Rift are left. A long, smoothly shaped valley, lunate in shape, and 75–80 sq km in area, extends to the Northwest. Its sediments are fertile and deep, being largely composed of the erosion and chemical breakdown of the basalts that form the upper edges of the valley. Such a site would form a natural spring grazing location for very large herbivores, which would need to descend periodically to the lake below to obtain their water. The hominins would be in a position to make use of natural features such as marsh, and a concentration of the animals at specific times of day, to make their kills (Tchernov, 1988; Bar-Yosef, 1995; Belmaker, 2010; Martinez-Navarro et al., 2012).

### 6.2.2. Summer grazing on the Golan

The Acheulean sites in the Northern Golan are located around the high point of the annual migration round, whether of very large herbivores (elephants, rhinoceros) or large bovinds. Berekhat Ram and other sites nearby suggest from the size of the Acheulean find scatters that regular visits were made to this area (Goren, 1982; Singer, 1983; Goldberg, 1992). Further detail of interpretation is limited by landscape changes that have occurred subsequently: the

crater lake of Berekhat Ram, for example, did not exist at the time of the Acheulean site.

### 6.2.3. Specialist grazing on the North Hula margin

Mayan Baruch includes finds of *Elephas/P. antiquus* remains (Stekelis and Gilead, 1966; Ronen et al., 1980). The Mayan Baruch Acheulean handaxe collection is remarkable not only for the large number of flint implements in the basaltic area, but also the very slender evidence for their manufacture. Flakes and chips are so rare that Bar-Yosef and Belmaker (2011) have suggested that the actual manufacture of the handaxes may have taken place further north in the Litani valley. With even a slightly expanded Lake Hula, Mayan Baruch occupies a relatively small area of flat, valuable grazing, perhaps most useful in late summer, where the movements of animals were highly restricted and could be closely monitored. Movement to the West is cut off by the steep slopes coming straight down to the lake (Fig. 4), to the North by the rough country which separates the Hula valley from the Beqaa valley, to the East by the hostile slopes of Hermon, and to the South by the lake itself. Lakeside opportunities for miring large herbivores could have been an attraction.

### 6.2.4. Winter grazing on the coastal plain

The build-up of dune material and the atypically high modern sea level mean that Lower Palaeolithic sites are not easy to find on the coastal plain. Some indications come from Evron, where earlier hominin activity (perhaps as old as 1 Ma, perhaps closer to 0.65 Ma) as well as late Acheulean finds again suggest that the site repeatedly offered scope to hominin groups to exploit the herbivores whose bones occur at the site (Ronen and Amiel, 1974; Ronen and Prausnitz, 1979; Tchernov et al., 1994; Ronen, 2003).

The fauna from the main Acheulean site at Evron (Issar and Kafri, 1969; Tchernov et al., 1994) includes elephants, hippopotamus, rhinoceros, horse, warthog, red deer, large bovinds, hartebeest and gazelle.

The loam from which the main Evron finds come is thick and well weathered, suggesting that the site enjoyed good local vegetation. The later finds are associated with a thick clay which implies unusually good water supplies.

In the Carmel region, the Misliya cave site (Weinstein-Evron et al., 2003, 2012; Zaidner et al., 2006) and the earlier layers of Tabun (F and G) (Bate, 1937; Rollefson et al., 2006; Yeshurun et al., 2007; Rabinovich et al., 2012) provide evidence of Lower Palaeolithic occupation. There is little identifiable fauna from the lower layers of Tabun. By the latest Lower Palaeolithic of Tabun E and the Lower Palaeolithic horizon at Misliya, the largest herbivores were the large bovids, though rhinoceros still occurred occasionally. The sites provide access not only to the coastal plain but to the limestone hill country of Carmel, where the smaller herbivores (*Dama* and *Gazella*) provided a year-round resource.

### 6.3. Quarry sites

We exclude from this discussion the very interesting sites of Mount Pua, Sasa, Sede Ilan, and so on (Barkai et al., 2002, 2006; Verri et al., 2004; Gopher and Barkai, 2006), because they are apparently factory or quarry sites related to the manufacture of implements rather than to the direct exploitation of animals.

### 6.4. Comparisons with sites in the wider Levant region

At this time we lack the information to make a detailed study of a wider region than that shown in Fig. 2. However, the particular concentration of activities suggested above finds some parallels elsewhere as well as some contrasts.

#### 6.4.1. Sites related to animal movement

The Fjaje locality in south west Jordan is an enormous, probably late Lower Palaeolithic, concentration of artefacts (Rollefson, 1981, 1985), extending along the edge of a long plateau overlooking the Wadi el-Bustan. This valley provides an obvious, major migratory route for animals moving between the lowlands of the Wadi Arabah (the southern part of the Rift Valley, south of the Dead Sea) and the Jordanian highlands – a movement with parallels to the seasonal round we have postulated for the Galilee coast – Golan movement. The artefacts are not precisely on this route, but immediately above it: the inference is that the hominins repeatedly camped on the plateau, preparing their tools and waiting for the migratory animals to pass below.

Abu Habil, a middle Lower Palaeolithic locality close to the Jordan valley, offers another intriguing parallel (Macumber, 1992). At this point in the Central Jordan valley, the valley floor currently rises to a level comparable with the 'lip' of Lake Kinneret at the southern end of the current lake. The valley is also narrow at this point. The location suggests that at a time when the central valley split into two lakes – one an extended Dead Sea to the south and one an extended Lake Kinneret to the north – Abu Habil would have been located on the bridge between them.

#### 6.4.2. Winter grazing on the coastal plain

Both early sites, such as Bizat Ruhama, and later Lower Palaeolithic sites, such as Holon, show the importance of marshy, wet localities to the hominins who produced the various assemblages. Like Evron, the Ruhama sites (Ronen et al., 1998; Tsatskin et al., 2001; Zaidner et al., 2010; Mallol et al., 2011; Yeshurun et al., 2011) reveal stone flake industries which are not precisely associated with the bifaces also found in the vicinity, but unlike Evron, the larger herbivores are not elephants, but horse and bison – a typical grassland pairing. The Ruhama fauna (Yeshurun et al., 2011) includes, alongside the horse and large bovids (*Bos/Bison*), antelopes

and some gazelle. The samples are small, and it would be unwise to infer too much from them, but while in numerical terms horse is dominant, in meat-weight terms horse and the large bovids may have been roughly equal.

Holon (Yizraeli, 1967; Horwitz and Tchernov, 1990; Chazan et al., 2001; Horwitz and Monchot, 2007; Monchot and Horwitz, 2007), which includes hippopotamus remains, shows that the unusual presence of marsh/lake was the attraction for the hominins. This is chronologically one of the latest elephant sites in the Southern Levant.

Revadim (Marder et al., 2011; Rabinovich et al., 2012), a Middle Pleistocene Acheulean site with substantial elephant remains, occupies a position somewhat analogous to Misliya, being on the eastern margin of the coastal plain at the edge of the hill country.

#### 6.4.3. Specialist, possibly summer grazing exploitation

Jubb Jannine, at the southern end of the Beqaa valley, shows a plentiful scatter of sites attesting to repeated hominin behaviour, although no faunal remains have been recorded (Besançon et al., 1970, 1982). The sites are related to an area of the Beqaa valley which, at various times, supported lake or marshy environments. Like Mayan Baruch, the sites overlook a cul-de-sac, since the steep sides of the Beqaa and the rough country today associated with the Litani gorges implies that animals moving down to the wet areas would normally have to move north again to leave the Beqaa region when the cold weather, exacerbated by cold-air sinkage phenomena, made the valley unattractive.

#### 6.4.4. Site types not found in the Galilee-Golan area

The oasis sites of the el-Kowm/al-Kawm region (Cauvin et al., 1979; Besançon et al., 1981, 1984; Copeland, 1988; Le Tensorer and Hours, 1989; Wilson et al., 2001; Le Tensorer et al., 2005, 2007; Hauck et al., 2006) are clearly without obvious direct parallel to the sites discussed above. However, the purpose of these sites seems most closely related to exploiting animals where they are forced to visit restricted localities for water. In this respect, there are parallels to the coastal plain sites, where the limited open water supplies made marsh locations such as Holon and Ruhama attractive to herbivores and hominins alike. That the area could provide excellent forage at times is shown by the giant camelid from Middle Pleistocene horizons (Le Tensorer et al., 2003; see also Dirks et al., 1998, for reference to elephants at a later period).

The sites associated with river valleys, and possibly small lakes, are the principal site types which have no direct parallels with the sites discussed in this study. Latamne and Gharmachi, respectively quite early and rather late Lower Palaeolithic sites on the Orontes, and the Wadi Zarqa sites, north of Amman in Jordan, again of varying Lower Palaeolithic ages, attest to a specific type of behaviour which we cannot yet assess in detail (Hooijer, 1962; Clark, 1967, 1968). The river sites may, perhaps, have been on migration route ways, since the upper terraces of the rivers, especially of the Orontes, suggest wider valleys than at present (Besançon et al., 1978; Sanlaville et al., 1993) but the attraction may simply have been the supply of water in an otherwise quite arid environment, while the wide alluvial plains of the period would have contributed to forage supplies. In this respect, the river sites may have performed the same function as the coastal plain sites.

The fauna of Latamne (Hooijer, 1962; Clark, 1967, 1968; Guerin et al., 1993) includes elephants, rhinoceros, horse, giant deer, fallow deer (*Dama* sp.), giraffe, camel, large bovids and gazelle, suggesting a mixture of steppic and woodland (perhaps riverine) communities. The fauna of Dauqara (Parenti et al., 1997) includes elephant, large bovids (*Bos*), and horse.



### 6.5. After the elephants

The major change which occurred in the later Lower Palaeolithic, from the point of view of this study, is the reduction in importance, and eventual disappearance, of the largest herbivores, especially the elephant. Ben-Dor et al. (2011) have illustrated the profound impact which this could have had on the hominin groups, and the changes in behaviour they must have had to make to adapt to this change.

We have suggested above that the large bovids, and *Alcelaphus* when in sufficient numbers, would have taken over the main seasonal rounds we have proposed above, especially in order to exploit the summer flush of excellent grazing on the Golan.

However, the rising importance of species which make much smaller movements, especially fallow deer and gazelle, is not only reflected in the site faunas, but in sites on the edge of, or in, the limestone areas. A wider range of exploitation methods emerges. For example, the late Acheulean/Acheuleo/Yabrudian lowland sites of Adlun (Roe, 1983), the lowest level G at Hayonim (Stiner, 2005), Misliya (Weinstein-Evron et al., 2003), Tabun (Bate, 1937), and Qesem (Stiner et al., 2004, 2009; Bar-Yosef and Belmaker, 2011) are based on a different resource mixture with bovids, fallow deer and gazelle assuming major components of the diet in notably different environments. At the same time, late Acheulean sites in the Samarian and Judaeian hills, for example Sahl el-Koussin (Roche, 1936) and Emek Refaim (Stekelis, 1948; Arensburg and Bar-Yosef, 1967), suggest that exploitation of the medium and smaller herbivores expanded into upland limestone areas. Sites such as Umm Qatafa (Neuville, 1931; Porat et al., 1992) in the Judaeian desert, and Yabrud in southwest Syria (de Heinzelin, 1966; Solecki and Solecki, 1986), are in areas where it seems that horse/zebra/steppe ass formed the principal attraction.

In some ways it might seem surprising that the limestone areas were, apparently, not used until the late Lower Palaeolithic, but new site discoveries may yet alter this view. Nonetheless, the substantial change in behaviour which must have followed the disappearance of the very large herbivores can be seen in three, presumably inter-related pieces of evidence: in the toolkits, with the rise of Yabrudian and Amudian industries; in the diet, as reflected by site faunas, with increasing dependence initially on the large bovids and equids, and then on fallow deer and gazelle; and in new site locations in the limestone areas.

## 7. Conclusions

In this study we have set out a methodology for mapping a series of variables that would have constrained the distributions and movements of the large herbivores, especially the elephants, in the Lower Palaeolithic of the Southern Levant. We have considered the factors that may have influenced seasonal movements and shown how the combination of edaphic factors, the water retentiveness of soils, terrain that limits animal movements, and altitudinal factors allow the reconstruction of such seasonal distributions.

The relationships of the Lower Palaeolithic sites to particular elements of this seasonal distribution suggest that the hominin groups were well aware of the movements made by elephant herds, and selected locations in the landscape which provided the best tactical opportunities for intercepting migrating prey and/or finding alternative food resources. The evidence also includes suggestive associations between hominin exploitation of elephants and marshy/lakeside conditions – not exclusively, but frequently enough to suggest that miring was one way in which hominin groups could reduce risk when attacking large animals. We also see how, at the present state of our knowledge, hominin groups confined their activities to the less rugged terrain so long as the

elephants and other large herbivores remained available, and only started to exploit the rougher terrain in the Late Acheulean, when they were forced to turn their attention to smaller herbivores such as deer and gazelle following the disappearance of the elephants.

We have drawn attention to the importance of edaphic potential as an important and useful proxy measure of which areas were more or less attractive to herbivores, and one that has previously attracted little attention, and have shown how mapping of topography using measures of roughness can identify landscape features that would have enhanced tactical access to the large herbivores. For edaphic potential, we have had to rely on the assumption that there is a close relationship between the mineral composition of the underlying bedrock and the soils that supported vegetation, and we have supported that with numerous field observations. However, this is clearly one aspect of the method that would benefit from further investigation, using more detailed and extensive soil analyses to test more fully the uniformity of this relationship, including analyses of palaeosols where these are available.

We have shown how the resulting maps can be used to highlight relationships between locations of archaeological material, their archaeofaunal associations and the surrounding landscape. We have also touched on ways in which this approach provides a framework for considering a wider range of issues, including the functions of individual sites, the nature of the associations between humans and animals, the size of territory required to support viable human populations, the pattern and causes of time trends in faunal exploitation, the interaction between these trends and climatic and tectonic changes, group size and social organisation, cultural preferences, and more broadly the pattern and causes of human dispersals and extinctions (e.g. Hovers, 2001, 2006; Bar-Yosef and Belfer-Cohen, 2013). These are matters that await further investigation.

To those who consider that we have oversimplified measures of species habitats and environmental variables, we acknowledge the charge, but emphasise that many of the additional variables that might be added to the analysis of past habitats, such as small-scale variations in vegetation, climate and soil properties, will require more detailed investigation before modelling can proceed much beyond broad generalisation or guesswork. The purpose of a model such as ours is to create a framework of investigation based on some simple and relatively easily measured variables, which can highlight areas of ignorance, and can be variously refined or modified in subsequent investigations, and ultimately be replaced by improved alternatives.

To those who consider this approach too overly deterministic or too confined to functional factors, we emphasise that it is deterministic only in the methodological sense of this term but not the substantive. Substantive determinism would entail the assumption that there is only one possible human response to a given environment, and that environmental reconstruction can be used as a direct proxy for human behaviour and hence a primary determinant of it. On the contrary, we emphasise that our reconstructions provide an independent framework based on knowledge about physical landscape processes and animal behaviour, in principle open to independent verification, which can then be used to calibrate variations in human response as inferred from other lines of evidence.

Ultimately, a regional framework of the type presented here could be extended to other regions on a larger geographical scale, providing an essential contribution to understanding the circumstances in which expansion of the human range and ultimately the colonisation of new continents took place, and the relative influence of environmental, social and technological factors in this process.

## Acknowledgements

We acknowledge funding support from The Southern Levant Human Environment Project, a charity registered in the UK, the Institut de Physique du Globe de Paris, and the European Research Council (ERC) through Advanced Grant 269586 'DISPERSE: Dynamic Landscapes, Coastal Environments and Human Dispersals' under the 'Ideas-specific' Programme of the 7th Framework Programme (FP7). This is IPGP contribution number 3532 and DISPERSE contribution number 0009. GK would like to thank the Hebrew University of Jerusalem for a 3-month fellowship during which some of the ideas in this paper were developed. We greatly appreciate help from Kate Raphael and Amotz Agnon.

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