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42 The Kaleidoscope of Mammalian Faunas during the Terminal Pleistocene and Holocene in the Southern Levant

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42.1 INTRODUCTION

High rates of species extinction and loss of biodiversity due to human activities make the Holocene a unique period in comparison to the entire Quaternary. Major waves of mammalian extinction of the scale documented in the Americas across the Pleistocene–Holocene boundary or earlier in Australia (e.g. Martin 1984; Brook & Bowman 2002; Burney & Flannery 2005) never occurred in the southern Levant. Nonetheless, local faunal communities were disrupted during the Holocene by the elimination of many species and addition of others (Tchernov 1982, 1984, 1988). The geographic pattern, timing, and cultural and environmental contexts of these critical events remain poorly understood. Thus, the contrast between modern and Pleistocene faunas has often provided a crude baseline in assessing impacts of Holocene palaeoenvironmental fluctuations and the history of anthropogenic landscape transformation.

It is generally thought that during the Holocene (~11,700 cal BP to present), the growth of human settlement, agricultural and industrial activities has played a major role in environmental change (Blondel 2009). This is especially true in the Levant where such developments began early. At the same time, the climate became drier, and amplitudes of its fluctuations appear to have been milder in comparison to the Pleistocene (Bar-Matthews *et al.* 1999). Where mammalian communities are concerned, little is known regarding the pace of, or which phases in the sequence of cultural development had the most influence on the distribution of different species or their local extinction.

The southern Levant is situated at a unique biogeographic intersection of different continents and ecoregions. These circumstances account for the relatively high diversity of species in the region and account for the hypersensitivity of its mammalian communities to human pressure and environmental fluctuations (Tsahar *et al.* 2009; Bar-Oz *et al.* 2015). Many species here are either on the northern or on the southern edges of their range of distribution. It is, therefore, likely that the composition of local communities should react to even minor changes in environmental conditions through either losses or gains of species from different types of ecoregions.

Data available to examine long-term community dynamics in mammalian species are obtained from archaeological sites accumulating through human activities and in some cases through non-anthropogenic processes. The records used in this review are from areas characterized by mean annual precipitation of > 200 mm in ecoregions of Mediterranean vegetation community and adjacent semi-arid environments. Arid environments have so far furnished a sparse and discontinuous fossil record. Consequently, the spectrum of species adapted specifically to these arid settings is underrepresented in the available record and not included in this chapter.

The types of archaeological contexts producing the relevant faunal assemblages changed with the onset of the Holocene. Dense, long-term settlement and sites that are more complex replaced occupation of caves and ephemeral open-air settings. Long-term settlements contain large amounts of faunal remains, mainly of domestic animals such as sheep, goat, cattle and pig together with smaller amounts of hunted game. Accumulation of different predators typical of caves were rare in Holocene sites. Preying birds such as owls were in many cases responsible for the accumulation of small mammal remains in caves during the Pleistocene.

To assess the existence of trends in biodiversity of mammalian species at century and millennial scales, a refined framework of the pace of changes during the Holocene is needed. A critical question is whether such changes are mainly a product of recent, severe impingement on the environment by large-scale population growth, industrialization and urbanization. Alternatively, we may be looking at a long drawn-out and phased process involving multiple environmental and anthropogenic factors in contexts of different cultural developments in historical times.

In this review, we present data on temporal patterns in the composition and distribution of mammalian species in the southern Levant compiled from more than 80 years of research. We compare and contrast data on two groups of species with very different life-history traits, ecologies and mode of interaction with humans: the medium–large and small mammals. In spite of the

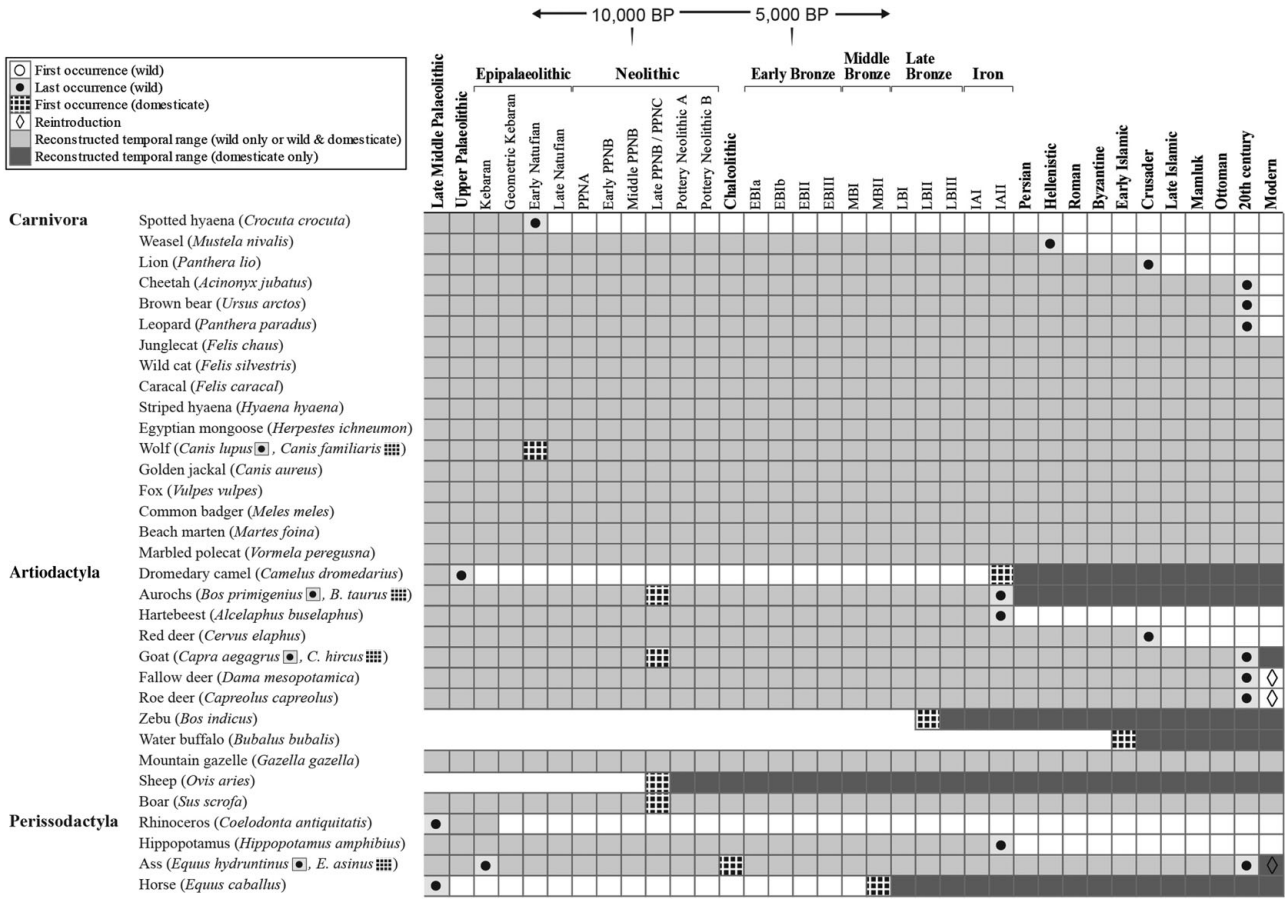

Figure 42.1 Chart of presence/absence of species of ungulates and carnivores between the terminal Pleistocene and present day showing local extinctions and introductions of wild and domesticated species. Chart is based on the Archaeozoological Database of the Southern Levant of the Laboratory of Archaeozoology, University of Haifa (see also Tsahar *et al.* 2009). The database includes 382 assemblages from 190 archaeological sites. For comparison, we include data for the late Pleistocene (taken from Tchernov 1984: Table 24.1).

abovementioned difficulties facing such a synthesis, a coherent dataset is now available from different terminal Pleistocene and Holocene archaeological sites in the southern Levant. This large dataset provides a sufficient basis for determining the patterns of presence or absence of species with high confidence.

42.2 THE DYNAMICS OF LOCAL EXTINCTIONS

42.2.1 MEDIUM TO LARGE MAMMALS

A high-resolution, temporal portrayal of south Levantine faunal data (Fig. 42.1) constructed during the 1990s and 2000s (e.g. Horwitz & Tchernov 1990; Grigson 1995) is employed here together with recent meta-analysis of the extensive dataset for medium–large mammals (Tsahar *et al.* 2009). The ~30 medium to large wild mammals of the late Pleistocene were halved to ~15 by the early twentieth century. Many of these 30 mammals were observed in the region until the nineteenth or early twentieth centuries; by then, most species of both ungulates and carnivores >10 kg had become extinct locally. In comparison, mammalian communities of the southern Levant lost nearly 30 species throughout the preceding million years (Tchernov 1984). The dynamic of local extinction was far from one fell swoop. Local extinction and displacements of multiple species affected both the predators (carnivores) and their prey (ungulates), involving extinctions of 5 species before the Holocene and 12 species spanning the late Holocene.

High-resolution data show that the Holocene wave of extinctions was in itself non-homogeneous. Rather, it encompassed two major events and a minor third one. (1) The first event occurred during the first millennium BC in the later phase of the Iron Age (IAII) and includes three large ungulates (aurochs, hartebeest and hippopotamus); (2) a minor event including one medium ungulate (red deer) and one large carnivore (lion) occurred during the early second millennium AD in the Crusader period; and (3) the second major event involving three medium ungulates (wild goat, and fallow and roe deer) and at least two carnivores (brown bear and cheetah) occurred during the beginning of the twentieth century and is known largely from historical documents (Yom-Tov & Mendelssohn 1988; Mendelssohn & Yom-Tov 1999). These events are linked to major historical developments, including large-scale human expansion in the Iron Age, and a surge in unregulated

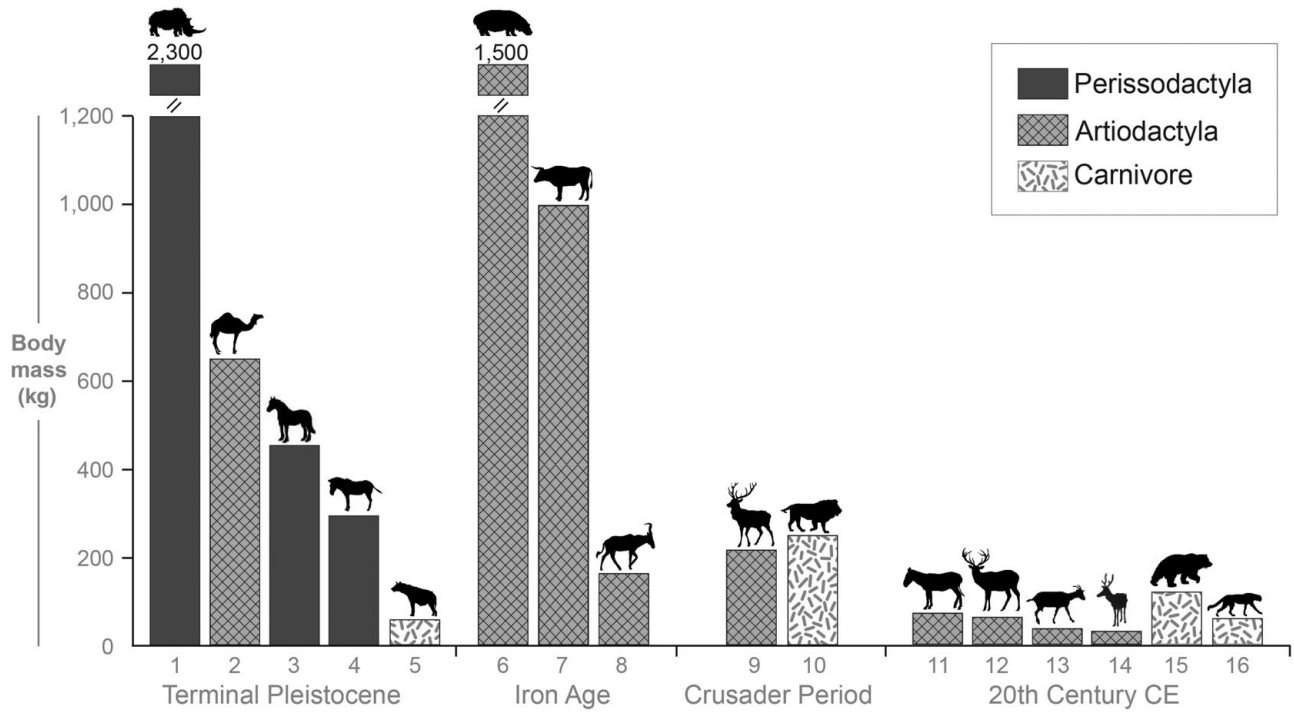

Figure 42.2 Body mass of ungulates and carnivores that became extinct in the southern Levant between the terminal Pleistocene and the present (extinct species shown in Fig. 42.1).

hunting of large game using firearms early in the last century (Tsahar *et al.* 2009; Bar-Oz *et al.* 2015). Both towards the end of the Iron Age and early in the twentieth century, political unrest and destabilization of local authorities may have contributed to an increase in hunting pressure on local game populations, for some of which a critical mass must have been reached at those times.

Among ungulates, species of comparatively large body mass including hippopotamus, aurochs, and hartebeest were the first to be extirpated regionally early on in the late Holocene, followed by medium-sized species in the first millennium AD (Fig. 42.2). Large-bodied species for which the southern Levant marks either the northern or the southern edge in the range of distribution were more vulnerable to combined pressure from human hunting and rapid habitat loss due to anthropogenic landscape transformation (Fig. 42.3). Large species are also more susceptible to such pressures than smaller ones owing to their slow rates of reproduction, which decreases population rebound following substantial losses in numbers. It is also likely that large ungulates inhabiting fertile plains came into direct competition for space with humans in some of the more populated parts of the region. Expansion in human settlement and agricultural activities would have fragmented the habitat of these species.

Similarly, lion, leopard, cheetah and brown bear became locally extinct in the late Holocene (Fig. 42.1). The leopard persists in the less populated dry region of the Negev Desert in southern Israel. The extirpation of large carnivores may have coincided with that of potential prey such as deer and wild goat. Predator–prey dynamics need not necessarily be implicated in these extinctions, nonetheless, as direct hunting of large carnivores by humans (especially royal hunting; Marom & Bar-Oz 2013a) is a highly probable and possibly a sufficient cause as well (Dolev & Perevolotsky 2004).

The spread of herding economies and grazing by domestic herbivores would have constituted another source of competition for wild herbivores of the region. Domesticated mammals occur in the southern Levant from the ninth to eighth millennia BP. Some, such as sheep and goats, were most likely introduced from centres of domestication in the northeast (Zeder 2008), whereas there is some indication that other species such as cattle and pig were domesticated locally (Marom & Bar-Oz 2013b). Ancient DNA analysis of pigs also indicates secondary introductions of European lineages during later periods in history (Meiri *et al.* 2013).

Species that have persisted and maintained stable populations through antiquity until modern times seem to be those capable of tolerating and even benefiting to some degree from human impingement on natural habitats. Small ungulates such as the gazelle venture into open fields in agricultural areas. Many species of carnivores including the striped hyena, canids, small felids, mongoose and mustelids tend to feed on refuse in the human environment or on abundant small prey present in these environments.

42.2.2 SMALL MAMMALS

Data on the occurrence of small mammals throughout the Holocene are insufficient to evaluate the local community dynamics in time in any detail. Substantial data are available only for the end of the terminal Pleistocene (e.g. Tchernov 1988, 1996; Weissbrod *et al.* 2005, 2013). The Iron Age is the only interval for which systematic collection and analysis of the remains of small mammals

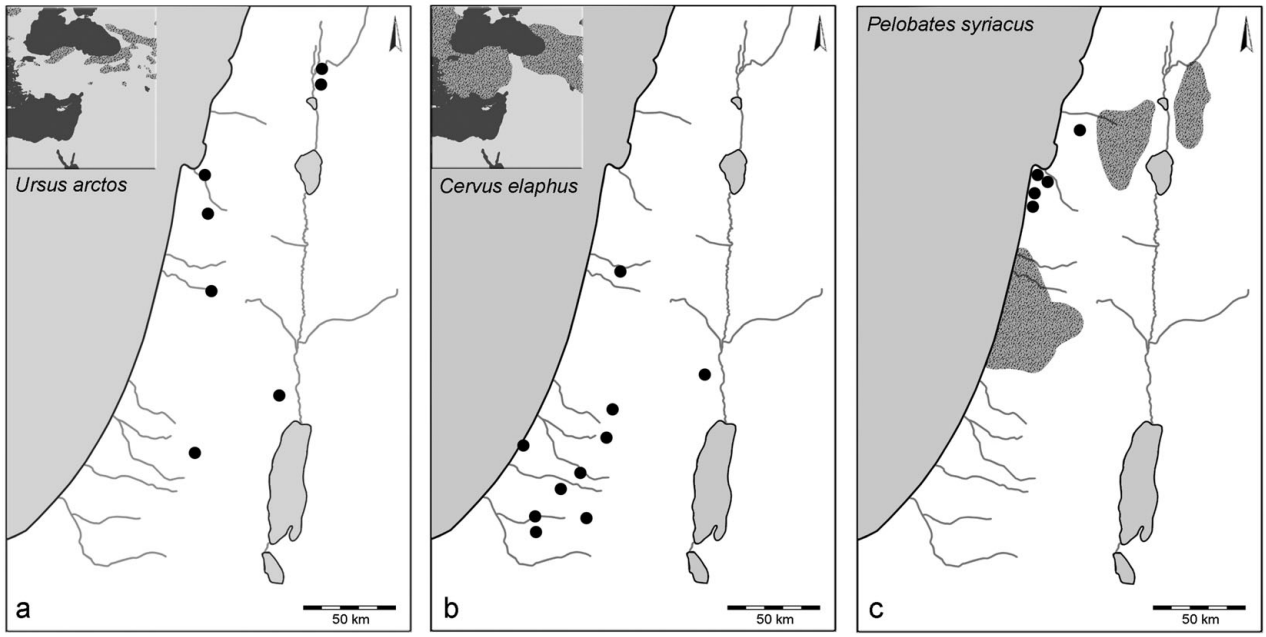

Figure 42.3 Distributions of species from terminal Pleistocene through Holocene intervals. These are based on remains in archaeological sites and compared with present-day ranges in the Levant (insets; species distribution ranges are based on distribution maps in http://www.iucnredlist.org). Bear (a) and red deer (b) retreated northwards as far as Anatolia, the deer within ca. 800 years and the bear within a single century; such habitat loss most likely proceeded through fragmentation as demonstrated (c) by the eastern spadefoot toad, *Pelobates syriacus*, for which the present-day range consists of isolated patches and the historic range (shaded regions) was more continuous (Delfino *et al.* 2007).

has been conducted (Weissbrod *et al.* 2013, 2014). The communities of small mammals demonstrate a very different sequence from that of the larger species, involving markedly fewer losses as well as several gains of species (Fig. 42.4). Two species of rodents are known to have invaded the Mediterranean ecozone of the Levant from adjacent arid regions just prior to or during the terminal Pleistocene (Tchernov 1988). These include the spiny mouse, of Saharan origin, and Wagner's gerbil, of Arabian origin, typically occupying open vegetation formations such as rocky slopes.

Following Tchernov (1988), it is possible that additional species of spiny mice, gerbils, jirds and jerboas which today are distributed in dry environments in Transjordan, the Negev desert and coastal

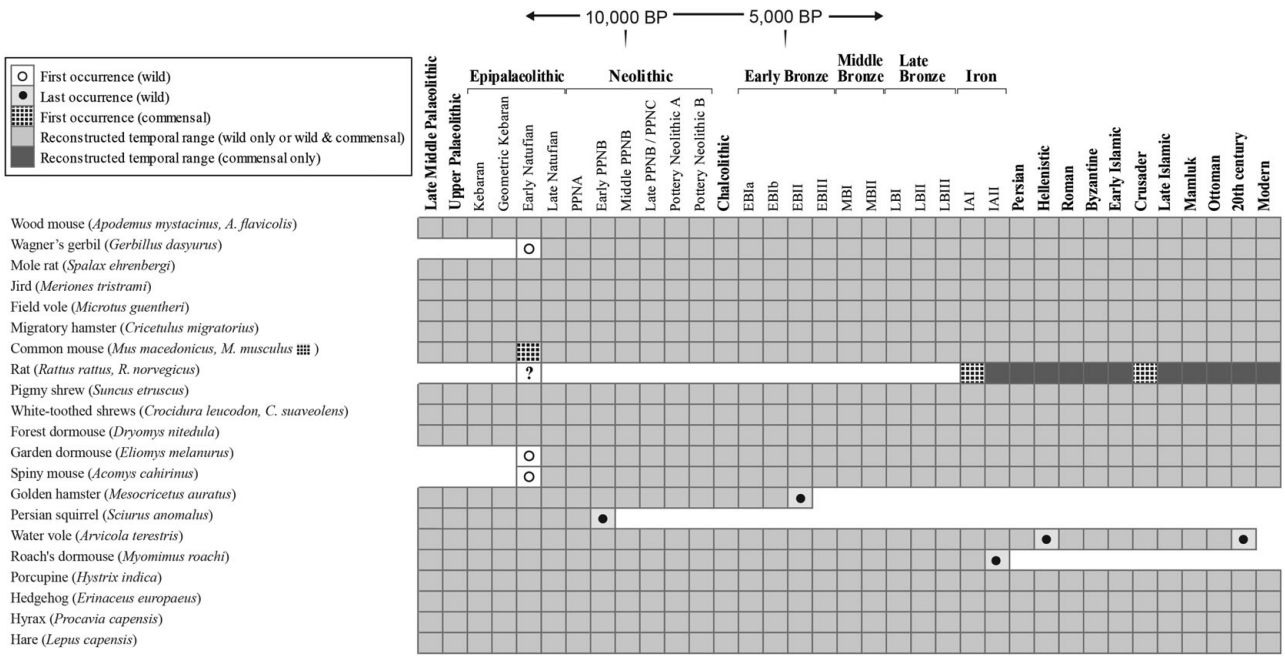

Figure 42.4 Presence/absence of small mammal species between the terminal Pleistocene and present day, showing local extinctions and introductions of wild and commensal species (data are from Tchernov 1984: Tables 24.2–3; Weissbrod *et al.* 2014).

sand dunes of the eastern Mediterranean invaded the southern Levant during the same period and in some cases emerged as the result of local speciation (e.g. Zahavi & Wahrman 1957). A record of these faunal events, occurring outside the Mediterranean ecozone, is not currently at hand. It is likely that the invasion and ongoing colonization of species adapted to open, arid environments goes hand in hand with the expansion of open landscapes at the expense of forested ones within Mediterranean environments of the southern Levant at least since the terminal Pleistocene.

Four species of small mammals became locally extinct between the early Holocene and present (Fig. 42.4). In contrast to the larger mammals, there is only a modest loss of small mammals in the Holocene. The record of local Holocene extinctions indicates that they occurred throughout this interval: Persian squirrel is last documented in the Neolithic, golden hamster in the Early Bronze Age, Roach's dormouse in the late Iron Age and water vole in the early twentieth century. The habitats of these species include woodland, open vegetation, and marsh or streamside. The ranges of distribution of all of these species shifted northwards to varying extents. The squirrel shows the least amount of range loss and continues to persist today in some high-elevation regions of Lebanon, Syria and Jordan. It is difficult to assess the role of predator–prey interactions in the community dynamics of small mammals during the Holocene. Most species of raptors and of small mammalian carnivores that feed on small mammals, except for the weasel (Fig. 42.1), have survived in this region to this day; changes in their population size and distribution are unknown.

Two additional species seem to have colonized the southern Levant in terminal Pleistocene–Holocene times. The earliest house mice were documented in sites preceding the Holocene by a few thousand years, and have invaded the region with the advent of more sedentary settlements and settled ways of life (Cucchi *et al.* 2005). The invasion of house mice may have been made possible through partitioning of the habitat with indigenous wild mice: within the area of sympatry in the Mediterranean region, house mice seem to be largely confined to settled and agricultural areas (Auffray *et al.* 1990). A second highly commensal species, the black rat (*Rattus rattus*), has been identified in several instances in deposits of the terminal Pleistocene (Tchernov 1984; Weissbrod *et al.* 2005; Edwards & Martin 2007). Pre-Holocene remains of black rat are rare, however, and have not been discovered in any Holocene deposits predating the first century BC (e.g. Bar-Oz *et al.* 2007). It has been argued using data from the fossil record that the black rat spread from its centre of origin in southeastern Asia only after the emergence of urbanism in middle–late Holocene times (Ervynck 2002). This species seems to have arrived in west Asia and subsequently in Europe late during the second half of the first millennium BC. A second species of rat, the brown rat (*Rattus norvegicus*), is thought to have been introduced to west Asia and Europe only in recent centuries.

42.3 SYNOPSIS AND FUTURE RESEARCH

Biodiversity of mammalian communities in the southern Levant today is the product of interacting biotic and anthropogenic factors during the last ca. 20,000 years. This observation is highlighted by the seeming contrast between the two groups of medium–large and small mammals in the dynamics of losses and gains of species. The medium–large mammals sustained merely a few losses in the latest Pleistocene or early Holocene, unlike the major extinction events of such species documented in the Americas (Grayson 2007). Subsequently, further losses occurred through a drawn-out and phased process during late Holocene to near-modern times involving three separate local extinctions. The largest species were extirpated early on in this sequence, probably because of their enhanced ecological vulnerability. Survivors include mainly those species that are relatively small, and those that have adapted to exploiting the human environment.

The community of small mammals demonstrates fewer losses as well as several gains of species. Invasions of new species occurred during the latest Pleistocene, probably in relation to the expansion of open vegetation environments at least since post-glacial times. Additional invasions involving commensal species populating the human environment occurred between the very end of the Pleistocene and the late Holocene. A few species retreated from the southern Levant to the north through a sequence widely spread out across the entire Holocene.

Owing to relatively narrow habitat requirements of small mammals, these species are particularly sensitive to fragmentation and loss of habitat. However, the apparent inconsistency in patterns of local extinction between the two groups indicates that direct persecution of larger mammals played a critical role in their eventual extirpation. Habitat loss and fragmentation due to climatic or anthropogenic impacts or imbalances in predator–prey interactions were important in their influence on extinction dynamics within the region. Nonetheless, it is hunting by humans that may have dealt the final blow. Intensified and uncontrolled hunting activities seem to correlate with periods of heightened social and political unrest in the southern Levant: the end of the Iron Age, the Crusader period and the nineteenth to early twentieth centuries. Thus, overhunting may have overwhelmed populations of otherwise resilient species persisting on the edges of their range of distribution in spite of pressures from landscape transformation and habitat loss.

Future research will combine intensive recovery of relevant archaeozoological materials with ancient DNA and isotopic studies to upgrade the existing knowledge base. Sophisticated modelling approaches to long-term community dynamics such as predator–prey interactions in the context of foodweb evolution are currently needed to address critical questions regarding the continued sustainability and conservation status of south Levantine biotas.

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