Climate change, adaptive cycles, and the persistence of foraging economies during the late Pleistocene/Holocene transition in the Levant

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Climatic forcing during the Younger Dryas (~12.9–11.5 ky B.P.) event has become the theoretical basis to explain the origins of agricultural lifestyles in the Levant by suggesting a failure of foraging societies to adjust. This explanation however, does not fit the scarcity of data for predomestication cultivation in the Natufian Period. The resilience of Younger Dryas foragers is better illustrated by a concept of adaptive cycles within a theory of adaptive change (resilience theory). Such cycles consist of four phases: release/collapse (Ω); reorganization (α), when the system restructures itself after a catastrophic stimulus through innovation and social memory—a period of greater resilience and less vulnerability; exploitation (r); and conservation (K), representing an increasingly rigid system that loses flexibility to change. The Kebarans and Late Natufians had similar responses to cold and dry conditions vs. Early Natufians and the Pre-Pottery Neolithic A responses to warm and wet climates. Kebarans and Late Natufians (α-phase) shifted to a broader-based diet and increased their mobility. Early Natufian and Pre-Pottery Neolithic A populations (r- and K-phases) had a growing investment in more narrowly focused, high-yield plant resources, but they maintained the broad range of hunted animals because of increased sedentism. These human adaptive cycles interlocked with plant and animal cycles. Forest and grassland vegetation responded to late Pleistocene and early Holocene climatic fluctuations, but prey animal cycles reflected the impact of human hunting pressure. The combination of these three adaptive cycles results in a model of human adaptation, showing potential for great sustainability of Levantine foraging systems even under adverse climatic conditions.

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Social collapse is a theme most often applied to complex societies, but the shift from foraging to fully farming lifestyles represents a profound social change that many researchers implicitly or explicitly attribute to a failure of forager economies in the wake of abrupt climate change. This belief is especially true for the Near East, the center of domestication of founder crops, including wheat and barley. In this paper, we argue that, in the context of climate change, foraging societies in the southern Levant were highly resilient and robust in terms of diversity of options and mobility and forager responses relied on solutions that recur in a broadly cyclical manner over the longue durée. This argument is in contrast to the perception of economic vulnerability and collapse of forager economies. We emphasize three main concepts that apply to foragers as well as more complex societies: cultural systems are resilient and do not collapse as a simple stimulus–response to climate change; a broad range of economic strategies enhances social resilience; and long-term social memory of accumulated experiences is an important resource for preparing and responding to economic challenges.

The archeology of late Pleistocene foragers in the southern Levant has yielded significant quantities of faunal remains, but it is plagued by a dearth of archaeobotanical data, primarily because of poor preservation of charred residues (1). Therefore, the way that foragers used plant resources and eventually initiated predomestication cultivation of wild cereals requires researchers to use conjecture and models to help understand the processes that eventually led to farming communities in the Holocene. Traditional climate-forcing models for the origins of agriculture in the Levant proposed that the shift to wild cereal cultivation was a solution to the failure of foraging systems driven by the Terminal Pleistocene Younger Dryas (YD) climatic deterioration (2–5). The work by Weiss and Bradley (4) referred to this deterioration as "the earliest well-documented example of societal collapse" (4).

However, here, we argue that hunter–gatherer subsistence systems in the Near East were highly adaptable, and climatic fluctuations leading to major restructuring of vegetation only resulted in a shift in resource focus rather than forcing a collapse of foraging economies hence requiring a major change in social and economic organization (6, 7). This argument is not to say that there was no occurrence of low-level predomestication cultivation at any time in the late Pleistocene or early Holocene (8). This cultivation is certainly a possibility; however, we maintain that low-level cultivation would have been one of many options available to foragers and did not have a significant impact on foraging economies until well into the Holocene (9). The shift in resource emphasis during the YD was merely a common response used by hunter–gatherers worldwide when faced with climatic deterioration (6, 10, 11). We suggest that this argument is illustrated best through the heuristic use of an alternative model, the theory of adaptive change (TAC; also known as resilience theory).

TAC (12) facilitates interdisciplinary analyses by considering the relationships between plant and animal resource selections and the dynamics of human decision-making within contexts of climatic and cultural change. Although the archaeological record is patchy throughout the time periods represented in this study, a TAC model allows us to connect the dots and suggests an overall interpretation of archaeological snapshots at different phases within the adaptive cycles. TAC provides a deep-time perspective for integrating the short-term datasets inherent in the record.

Theoretical Framework

TAC states that processes in human and environmental systems are interlinked at different spatial/temporal scales of operation and modeled as adaptive cycles (Fig. S1) (12–14). The cycles move dynamically through four phases (r, K, Ω, and α); r-phase is

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defined as growth or exploitation, with trends to cultural conservatism and eventual high interconnectivity of the components in the K-phase (see the foreloop). The K-phase exhibits the least flexibility and the lowest resilience and potential for change, leading to a release and reshuffling in the Ω-phase. Many researchers equate the end of a K-phase with the collapse of a civilization. This interpretation is especially the case with respect to the impact of adverse climate change on societies (4). The K-phase is followed by reorganization and renewal in the α-phase (see the backloop) (15). The α-phase has the highest potential for innovation and adaptability, drawing both on traditional solutions maintained within social memory as well as innovations that later contribute to the array of known possible solutions within the cultural repertoire, and a new cycle begins. The activation of social memory and traditions in the α-phase reorganization is a key factor that argues against the concept of a cultural collapse.

In this paper, we group the adaptive cycles at micro-, meso-, and macroscales. Although the act of daily to yearly food provisioning is on a microscale cycle, the accumulation of subsistence decisions over multiple years constitutes a larger mesoscale cycle and ultimately, results in a traditional lifestyle. The long-term functioning of cycles at this larger scale enhances the memory of multiple successes, failures, and experimentations. The accumulation of many mesoscale cycles over the long term constitutes a macroscale cycle of social memory.

The TAC framework broadens our perspective away from the microscale of variability and allows the examination of a system of forager provisioning that takes into account thousands of years of learned knowledge, socially prescribed behaviors, and memories of how to respond to changing climatic conditions. It frees us from focusing on a point in time when the first forager planted the first wild cereal grain, and it allows us to examine the social and environmental factors that contextualize the events leading to those economic shifts from a deep-time perspective. We can then investigate social changes within dynamic environmental contexts and apply the results to an understanding of hunter–gatherer adaptations to late Pleistocene climatic changes.

Environmental Background

To operationalize the TAC models, we need to consider the dynamic environmental context for human decision-making. Here, we identify the relevant cycles for climate, vegetation, and fauna.

Modern Context. The southern Levant is within the Mediterranean climatic zone, with cool moist winters and warm dry summers (16). Vegetation zones are complex, with Mediterranean woodland in the west and north consisting of nut- and fruit-bearing trees dominated by evergreen oak (*Quercus calliprinos*) and the deciduous pistachio (*Pistacia palaestina*) in the moister denser forest zones, with deciduous oak (*Q. ithaburensis*) in the open woodland. Olive (*Olea europaea*) and almond (*Amygdalus communis*) also had wild antecedents growing in this area. The Irano–Turanian vegetation complex is in the drier areas to the east and south of the Mediterranean zone, and it consists of grasses and other steppic plants (17). This configuration of vegetation has a long history within the Levant and existed at least throughout the Pleistocene (18). The vegetation responded to the cooler, drier episodes and warmer, wetter phases by shifts in boundaries and shrinking or expanding within their respective zones. In this paper, we restrict our focus to the Epipaleolithic populations living in the Mediterranean woodlands and its ecotonal boundary with the Irano–Turanean steppe zone in the southern Levant.

Late Pleistocene/Early Holocene Climate. Isotope data from the Nahal Soreq Cave outlines the highest resolution and longest continuous paleoclimatic record to date (6, 19, 20). This sequence closely follows the general global paleoclimatic record from the Greenland ice core, GISP 2. The δ^{18}O indicators are calibrated to rainfall, and the record was dated by uranium/thorium, with results given in calendar years. It is used to reconstruct humidity beginning with the Last Glacial Maximum (LGM) through the present day. The sequence shows a pronounced cold/dry episode corresponding to the LGM at *ca.* 23 ky B.P. (Fig. S2). There is a steady decline in δ^{18}O values until around 15 ky B.P., when a plateau of warmer/wetter climate marks the Bølling/Allerød (B/A) climatic phase. The YD episode is indicated by a rapid return to cooler and drier conditions, which lasted from *ca.* 13 to 11.5 ky B.P., ending with an abrupt shift to the warmer and wetter early Holocene (21). The Holocene began with temperatures and rainfall levels roughly similar to the levels today and progressed steadily to increasing warmth and greater humidity until reaching a long-term optimum beginning around 10.5 ky B.P. (19, 20).

Late Pleistocene/Early Holocene Vegetation. Vegetation fluctuations over the late Pleistocene form adaptive cycles of their own, primarily driven by climate changes. To understand how these phases interface with human foraging cycles, we focus on changes in the elements of economic significance to Epipaleolithic populations, such as forest and grassland resources.

The ecotonal areas between the Mediterranean woodlands and Irano–Turanean steppe generally cycled between dominance of forests under warmer/moister climates and predominance of steppic species under drier regimes (6, 19). The woodlands were characterized by a naturally high biodiversity (22) during warmer/wetter episodes, and they would have provided a range of nuts and fruits that were rich in calories, protein, and nutrients as well as easily collected, processed, and consumed. The parkland and wetland vegetation in this zone is host to wild wheat and barley as well as abundant edible small-grained grasses and sedges such as *Stipa* sp., *Bromus* sp., and *Scirpus* sp. Numerous archaeological and ethnohistoric records of forager adaptations to drying climate indicate that hunter–gatherers typically shift their subsistence priorities in favor of greater grass seed exploitation in times of environmental hardship (6, 23). Therefore, we suggest that woodland resources would have been favored during forest expansion, but at times of forest contraction, parkland/steppe/wetland species would have received increased attention.

Late Pleistocene/Early Holocene Fauna. Although the accessibility and acquisition of plant resources seems to be closely linked to cycles of climatic change, the relationship between climate and hunting selectivity is less clear, suggesting that relative resource ranking of fauna is more closely related to cultural factors, such as intensification, than simple availability. However, climate does influence encounter rates with hunted animals. From the Epipaleolithic through the earliest Neolithic, large and small animals were targeted for exploitation, particularly gazelle (*Gazella gazella*), deer (*Dama mesopotamica*), tortoise (*Testudo graeca*), hare (*Lepus capensis*), and partridge (*Alectoris chukar*). Gazelles were the highest-ranked prey among large animals, whereas hares and tortoises were highly ranked among the small animals (7, 24–26). These three species respond differently to changes in environmental conditions and hunting patterns. Gazelles are adapted to living in dry settings, but their birthing is influenced by temperature and moisture (27). Hares (*L. capensis* and *L. europeus*) (28) are also adapted to living in dry environments, preferring ecotonal zones with high biodiversity (28). Tortoises also prefer areas of high vegetation complexity with intermediate grass cover. Fire frequency and intensity can affect tortoises, because their numbers decrease with frequent occurrences (29).

The climatic information indicates that, during the Epipaleolithic Period, the weather cycled through times of variable moisture and temperature. These changes affected the vegetation by altering the distribution of woodland and steppe zones, thus changing the location, diversity, and accessibility of resources. The biological requirements of highly ranked animals also suggest that their behavior could have been altered by the variations in climate and associated changes in vegetation. These data set the stage for understanding the dynamism of the environment, and they will permit the contextualization of a range of human subsistence strategies.

Epipaleolithic Archaeological Background

The Epipaleolithic Period began with the LGM and ended with the transition to the Holocene (30). For the purposes of this paper, we are restricting our discussion to the Epipaleolithic groups that inhabited the Mediterranean woodland/Irano–Turanean steppe ecotonal areas. The sites that we use for this study are those sites that have yielded information on botanical and/or faunal assemblages (Fig. S3).

Early Epipaleolithic Period [*ca.* 21–17 ky calendar years before present (cal B.P.)]. Kebaran populations existed in the Levant during the LGM. Their sites are generally small, and at Ohalo II, they are characterized by kidney-shaped huts. The material culture shows major diversity, which would be expected in a resilient society. The site of Ohalo II, located on the shore of Lake Kinneret, is on the cusp of the upper Paleolithic and the early Epipaleolithic Periods. It is unique in that it has yielded abundant archaeobotanical remains dominated by seeds from small-grained grasses as well as wild cereals, although nuts, fruits, and legumes were also present; additionally, ground stone mortars were used for plant processing (31, 32).

Geometric Kebaran (17–14.6 ky cal. B.P.). The Geometric Kebaran (GK) extends over a broad geographic region from the Euphrates to the Sinai Desert (33). No complete structures have been reported for GK sites, but there are features such as pit caches. Sites, such as Neve David or Hefzibah, indicate ephemeral occupation (34). There are few excavated sites in the Mediterranean zone and no sites in the southern Levant that have archaeobotanical remains.

Early Natufian (14.9/14.7–13.2/13 ky cal. B.P.). Early Natufians appeared in the Levant during the B/A climatic phase (35, 36). Their sites vary in size, but the largest have features that indicate that they may have been semi- or even fully sedentary. Settlements such as Eynan (Mallaha) on the shore of the Hula marsh are significantly larger than many forager sites in the Levant. They typically include structures with stone foundations and superstructures composed of reeds, burials, possible storage installations, and the remains of grinding stones (35, 37). Phytolith evidence suggests heavy use of woodland resources (Fig. S4) (38).

Late Natufian (13/12.8–11.5 ky cal. B.P.). The Late Natufians, coinciding with the YD, marked a change in settlement patterns, with smaller, more ephemeral sites and all appearances of a more mobile population (33, 35). Unfortunately, paleobotanical information for Natufian sites in the southern Levant is scarce. Toolkits containing large numbers of sickles and an increase in grinding stones from the previous periods led some researchers to argue that the Natufians were intensively collecting wild cereals and possibly planting them (3, 39). Evidence from Abu Hureyra on the Syrian Euphrates indicates that Late Natufians exploited a broad range of grass species and sedges (40), which is in line with phytolith evidence from Eynan, el-Wad, and Hilazon Tahtit that suggests a shift away from woodland products in the Early Natufian to heavier emphasis on small-grained grasses as well as wild cereals (Fig. S5) (38).

Pre-Pottery Neolithic A (11.7–10.5 ky cal. B.P.). The Pre-Pottery Neolithic A (PPNA) saw the renewal of village life reminiscent of the Early Natufian. The largest PPNA sites in the southern Levant are from the Jordan Valley on both the east and west sides of the Jordan River. These sites include Jericho, Netiv Hagdud, Wadi Feynan, and Dhra. The sites are characterized by oval houses made of stone foundations with superstructures of mud brick. Toolkits include sickles and grinding stones. Population increased notably, and villages became substantial in the later phase of the PPNA (41, 42).

There has been much speculation on whether wild cereals identified from PPNA sites were cultivated or collected from wild stands (43–45). Recent reevaluations of the limited archaeobotanical data for the most part agree that there is little direct evidence for cultivation in the southern Levant until the first signs of domesticated barley containing percentages of non-shattering rachises exceed those percentages found in wild populations. For the PPNA, the only such evidence comes from ZAD I in Jordan (46). Data supporting grain size increase in the PPNA is also inconclusive but might suggest a slight trend to larger grains (1). The presence of arable weeds might indicate landscape disturbance associated with predomestication cultivation, but fires, both natural and started by foragers, might also increase annual weed populations. Wilcox reports on arable weeds that extend back through the Pleistocene, including those weeds at the LGM site of Ohalo II (9), and Fuller et al. (43) cite genetic data indicating phases of nondomestic cultivation coming and going over thousands of years. These suggestions point to the possibility that intervals of low-level cultivation could have taken place at any time in the late Pleistocene and early Holocene. However, there is no evidence that cultivation was a significant portion of forager economies until late in the PPNA or even with the early PPNB. The work by Fuller et al. (43) suggests that predomestication cultivation was highly variable, and when it did exist, it went hand in hand with significant quantities of wild food collection as well (44).

TAC Model of Forager Resilience

As stated above, the TAC allows us to examine the interrelationships between climate change, cultural change, and human decision-making about selection of plant and animal resources. This can help us evaluate hunter–gatherer resilience during episodes of adverse climate change. Although there have been a number of superb studies of late Pleistocene plant use (40, 45) and animal resource ranking (7, 26, 47), very few studies have considered them together as a part of a unified system of provisioning through time. Here, we consider both categories of resources within two separate schemes defined as collectable provisions (plants and tortoises) and hunted resources (hare, game birds, and gazelle). This system allows us to model foraging decisions more holistically, because they represent different exploitation strategies, often reflecting diverse specialist activities and decision-making at the household level.

The archaeological evidence allows us to express human decision-making about provisioning at the microscale (the site), and project trends through time at the mesoscale as adaptive cycles occurring throughout the late Pleistocene Epipaleolithic periods. At this scale, we model the changing productivity of the home range and the intensity of exploitation and domestication of the landscape (48) as strategies for adapting to long-term climatic changes. We propose that, for the Epipaleolithic and PPNA, multiple mesoscale cycles should articulate into one macroscale cycle of social memory that remains in place throughout the late Pleistocene and early Holocene, and the cycle only ended in the Levant with the introduction of full-scale farming economies in the PPNB. This social memory can go back thousands of years on the macroscale, but it is kept alive at the microscale of generational memory in the form of occasional short-term droughts and the socially prescribed methods to survive them.

Kebaran: First α-Phase. The LGM climatic deterioration triggered a restructuring of resource distributions over the landscape. The flexibility of territorial boundaries in the Kebaran Period led to greater resilience and increased the potential for social groups to adjust. High mobility (26, 49) allowed the exploitation of diverse resource options (animals and plants) distributed across the landscape. Emphasis was placed on gazelle and deer, which can be seen in Nahal Meged, Hayonim Cave (26), and other Kebaran sites. The small game index is low, but analysis of the assemblage shows that hares, partridges, and tortoises were being consistently exploited. Archaeobotanical evidence from Ohalo II indicates that a broad range of plants were also used, although the heaviest exploitation seems to have been small-grained grasses (32).

The characteristics of the Upper Paleolithic/early Kebaran populations living in the Mediterranean vegetation zones during the LGM are consistent with the Ω- and α-phases of the adaptive cycle. They were small-scale bands with low organizational and economic connectedness. They had a flexible investment in resilient broad-spectrum plant collection strategies, high mobility, and high potential for innovation, which is shown by the increased use of mortars and grinding stones at Ohalo II over earlier periods. This finding suggests that different plant collection strategies were being implemented, particularly the increased use of small-grained grasses, wild cereals, and other monocotyledons. Although the faunal assemblage shows specialized interest in gazelle and deer, the resilience of the α-phase supported the innovation of exploiting hares and partridges as food resources. These species were known before, but it is in the Kebaran that their presence starts to increase in the record (25).

Geometric Kebaran (GK): First r-Phase. During the B/A, the climate was becoming progressively warmer and wetter, and the Mediterranean forest zone began to expand, with a corresponding shift in plant and animal resources. Territorial rigidity increased in the GK, which is shown by increasingly larger sites (34, 49). The selection of animal resources remained similar to the selection of the Kebaran, which was seen at the sites of Neve David and Hefzibah (26), although the assemblage of Hefzibah suggests a slightly growing investment in capturing fast-escaping fauna (47). The decreasing mobility and the fact that hunting patterns indicate no major restructuring suggest increasing conservatism and connectedness to the home range. This finding is consistent with the r- to K-phases of the adaptive cycle (front loop) (Fig. 1) that culminated in the highly connected K-phase of the Early Natufian.

Early Natufian (EN): First K-Phase. Social rigidity on territorial boundaries in the Mediterranean zone dramatically increased during the Early Natufian, which was indicated by sedentary villages with permanent structures and increased evidence of ritual behavior (35). This rigidity was accompanied by the intensification of resource use within the home ranges. The continued expansion of the woodland zone allowed for the exploitation of nut and fruit resources. Although we have little direct evidence of plant exploitation for the Early Natufian, phytolith data from el-Wad and Early Natufian levels at Eynan (38) suggest that woodland resources were significantly more important in the Early Natufian than in the Late Natufian (Fig. S4). This finding is supported by evidence from Wadi Hammeh 27 in Jordan (50). The collection of nuts and acorns would have been sustainable even as human population densities grew because of the increasing density of productive nut-bearing tree patches under conditions of the B/A warming and wetting. This

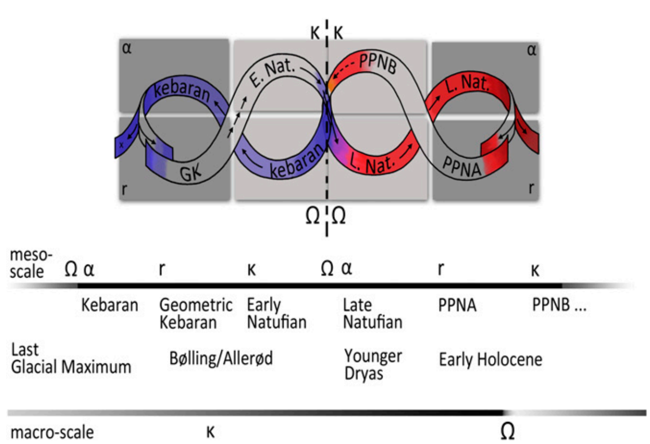

Fig. 1. The adaptive cycle model applied to late Pleistocene and early Holocene foragers in the southern Levant.

change might have allowed for a narrowing of the plant resources targeted.

Hunting pressure on animals meant that people had to invest much more energy and effort to obtain their resources from their home ranges. Within this context, the forager populations invested more in the exploitation of lower-ranked animals, which were known and exploited in the previous periods. This finding is reflected in a significant increase in hunting diversification, particularly the presence of fast-moving hares and partridges, which was seen at the sites of el-Wad and Hayonim Caves (25). Although gazelle are usually associated with grassland expansion and the Early Natufian existed at a time of woodland expansion, the presence of warmer/wetter weather actually supports increased fecundity in the gazelle and multiple births per year. Therefore, it is possible that gazelle encounters were more common than in previous periods.

Small game exploitation indicates a much higher investment in catching prey near the permanent base camp. Woodland expansion and thus, increase in shade could have negatively affected the tortoise population, which was already under pressure from human exploitation, by reducing their ideal habitat and potential for thermoregulation in sunny areas. Although tortoises were still collected whenever encountered, hares and partridges, which take much more effort to catch, became particularly important, because more productivity was required from the same geographical area. This investment, combined with an increase in processing of gazelle (including marrow and fat extraction from bones) (24), suggests that, during the Early Natufian, all of the known potential animal resources within the home range were being exploited to their highest known productivity, suggesting a broadening of animal resource exploitation. At this time, the pronounced exploitation and connectedness to the home range, the intensification of the productivity of exploited resources, and the increasing territoriality linked to decreased mobility and sedentary residence are all consistent with the highly connected and rigid K-phase of the adaptive cycle.

Late Natufian (LN): First Ω- and Second α-Phases. The greater connectedness of the Early Natufian to a particular structure of resource distribution within the home range made them increasingly vulnerable to the impact of climate change. As the climate shifted to the cool/dry YD, the woodlands retreated, and steppic ecosystems expanded. Late Natufian foragers entered a release and reorganization phase (Ω- and α-phases) generated by the instability of habitat restructuring in the home ranges. This change in resource distribution over the landscape occurred at a time when the social adaptive cycle was in a K-stage of high connectedness and low flexibility. Rather than investing in cultivation of wild cereals as a major subsistence strategy (a high risk activity at this time), we suggest that the downturn in climate triggered the social memory of past cold/dry conditions (kept alive during occasional drier weather events) and the adoption of subsistence strategies that had been successful in the past. This adoption entailed the broadening of plant collection to include a greater investment in the collection of both small and large grass seeds, leading to a restructuring of a different mesoscale adaptive cycle.

Grasses and other monocotyledons (e.g., sedge seeds and tubers) are highly resilient annual plants that are far more sustainable than nuts and other forest resources, because they can endure intensive exploitation and return in great abundance year after year. Increased wild grass seed collection, with an emphasis on small-grained weed grasses in addition to wild cereals, is supported by phytolith evidence from the sites of Hilazon Tahtit and Eynan (Fig. S5) as well as macrobotanical data from Abu Hureyra (38, 40). Heightened exploitation of grass seeds is a strategy reminiscent of the one used by early Epipaleolithic inhabitants of Ohalo II in the LGM.

The faunal assemblages from the sites of Hayonim Cave, H. Terrace, and Hilazon Tachtit indicate a very significant presence of tortoises and less energy investment in the capture of fast-escaping fauna (hares and partridges) (25), similar to the strategies practiced in the early Epipaleolithic period. The emphasis on tortoises in the Late Natufian might reflect the expansion of the tortoise habitats during the YD, but it also may be linked to an increased exploitation of wild grasses from the expanding steppic/parkland ecosystems into the social home ranges, where the tortoises would have been easily found and collected by the gatherers of the community.

The settlement patterns returned to smaller, more dispersed sites, with less investment in permanent residential structures. The restructuring of the settlements also suggests increased emphasis on identity with a specific geographic zone and home range territoriality, which was suggested by the change in character of Natufian habitation sites to a more ritualistic entity in the Late Natufian (7, 34, 51, 52). Rather than representing a failure of vulnerable foraging societies that could not adjust to climate change, the characteristics of these shifts in behavior are consistent with the resilient transformation of a flexible system, which could use memory and long-term experience to respond to changes in resource distribution and availability.

PPNA: Second r-Phase. Woodlands expanded after the abrupt end of the YD and the return of the warm/moist conditions in the early Holocene. With the beginning of the Holocene, the significant increase in microcharcoal seen in pollen cores at Ghab (northern Syria) and Lake Hula (northern Israel) (53, 54) suggests heightened landscape domestication through more intense intervention and control of the landscape and its productivity during the PPNA. We suggest that, as woodlands began to expand, PPNA communities invested significant energy in maintaining the parkland structure of the home ranges by burning forests and encouraging grasslands (55). We believe this intensification of land management was a method for increasing the foraging productivity of the landscape by opening up the area for growth of more wild cereals and other grasses as well as possible low-level cultivation in some cases. It should be noted that the amount of microcharcoal appearing in pollen diagrams across the Near East seems to exceed expectations for the occasional low-level type of cultivation proposed for the southern Levant, suggesting that this strategy was for foraging rather than cultivation (1, 44). This manipulation of the resource structure of the home range also would have favored gazelle herds, which graze on the new grass growth. Gazelles would also have been particularly productive during the warm and moist early Holocene. Recurrent fire, however, might have disturbed the tortoise life cycle significantly, possibly reducing their numbers on the landscape.

With heightened control of resource distribution within home ranges and the intensification of their productivity, beginning in the GK and EN, settlements shifted to areas with abundant freshwater resources, resulting in increased sedentism. Intensification of home range productivity is also supported by a return to previous knowledge regarding the exploitation of hares and partridges, which was seen at the sites of Netiv Hagdud and Gilgal (7). The new structure of the adaptive cycle that started with the α-phase of the Late Natufian also placed increased focus on the exploitation of a smaller number of plant species in the PPNA, with a shift from the collection of both small- and large-grained grasses to more emphasis on a narrower range of highly productive plant foods, such as large-seeded wild barley. This finding is evidenced by an abundance of wild barley in the Jordan Valley sites of Netiv Hagdud (56), Wadi Faynan, and Dhra (42). Settlement patterns in the PPNA indicate a return to permanent communities often larger than those settlements of the Early Natufian, with a greater investment in permanent architectural features (49, 57).

The PPNA is consistent with an r-stage in which the social cycle increased its connectedness to the control of resources in home ranges, the rigidity of territorial boundaries, and the intensification of the productivity of those territories. In this sense, PPNA groups share more of an affinity with the Early Natufian (also within the r- or K-phases) than to their immediate Late Natufian predecessors.

PPNB: Second K-Stage and the Longue Durée. When these mesoscale phases are considered within a long-term macroscale perspective, the eventual Late Natufian transition into the PPNA is not a result of the collapse of Epipaleolithic foraging economies but rather, a continuation of social processes that started even before the Kebaran Period and culminated in the very high organizational connectedness and rigidity of social groups at the beginning of the PPNB (K-phase; macroscale is shown in Fig. 1). The process of landscape domestication for the control of home range productivity and social investment in a narrower spectrum of resources is directly linked to the significant socially driven narrowing of options that culminated in a greater investment in agricultural lifestyles, fully formed agricultural villages, and highly connected organizational subsystems in the PPNB. Throughout the Epipaleolithic period, we see a gradual rise in connectedness to the home range from the flexible Kebaran to the increasingly connected PPNA. Although the YD presented a crisis that triggered a renewed cycle during the Late Natufian, the mesoscale variability was reinforced by the stability of an r- to K-phase of a macroscale lifestyle cycle of forager social memory. We suggest that the greater commitment to agricultural economies in the PPNB was a response to social pressures, which stimulated a release from the foraging lifestyle and catapulted PPNB populations onto a new macrocycle of village farming communities. This change occurred at a time in which climatic conditions were among the warmest and wettest of the Holocene, thus facilitating this major shift in the economic macrocycle.

Conclusions

In this paper, we use the TAC concepts of adaptive cycles to show the robust nature of foraging systems in the face of Terminal Pleistocene climatic changes. We argue that the YD did not initiate the eventual collapse of foraging systems that lead to the earliest cereal cultivation in the southern Levant. Rather, the Late Natufians relied on the long-term social memory of past experience, and they initiated a series of subsistence procurement responses that were similar to those responses of early Epipaleolithic peoples who faced the cold and dry climate of the LGM. The influence of climate change seems to have been particularly important with regards to gathered resources such as nuts, fruits, seeds, and tortoises. Animal prey selection was more a function of social factors such as territoriality. Although we do not have enough sites with enough archaeobotanical remains to allow us to test proposed patterns, we tentatively suggest that, under warmer and wetter conditions, the spectrum of gathered resources narrowed to collection (or cultivation) of highly productive protein-rich nuts or large-seeded grasses. At the same time, increased sedentism demanded a broad spectrum of prey to avoid depletion of animal resources within increasingly rigid home range boundaries. Conversely, during cool and dry episodes, the plant spectrum broadened to include small-grained grasses caused by decreased availability of woodland products, but at the same time, social and environmental conditions supported an emphasis on a lower diversity of prey animals targeted.

We propose that the reactions of Levantine hunter–gatherers are consistent with α-, r-, K-, and Ω-phases of mesoscale adaptive cycles throughout the LGM, B/A, YD, and early Holocene periods. These cycles and socially prescribed responses to environmental change were embedded in a social macroscale of memory and kept current through similar adjustments and responses to environmental stress on the microscale of years to generations, shaping the Epipaleolithic economic traditions. These memories, coupled with successful innovations, allowed foragers to adjust their procurement strategies with changing resource availability during the release of the Ω-phase and readjustments of α- and r-phases caused by their increased range of socially acceptable options and greater flexibility. This macroscale cycle was only broken during the Holocene Climatic Optimum (*ca.* 10,000 cal. B.P.) when increased organizational rigidity (overconnectedness) during the PPNB led to a change in the characteristics of the traditional foraging lifestyle to a more intensive food production system. In this sense, forager responses to environmental stress were similar to more complex societies of later time periods. Our model illustrates and helps explain transformations in a context without written records. It also suggests that breakdown was not an integral part of change in this particular setting. In the past (as in the present day), economic adjustment to climate change was not a product of climatic forcing in a simple cause and effect relationship, leading to an hypothetical collapse, but rather, it was a complex interplay between the environment and social behavior in response to change within the context of past experience and increasing potential for landscape domestication. Therefore, understanding the effect of climate variability on society requires a more holistic consideration of the environment, the effect of human behavior on landscapes, and the possibility of social memory and traditional knowledge enhancing the social capacity to adjust and respond to change.

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