

Collapse of an ecological network in Ancient Egypt

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The dynamics of ecosystem collapse are fundamental to determining how and why biological communities change through time, as well as the potential effects of extinctions on ecosystems. Here, we integrate depictions of mammals from Egyptian antiquity with direct lines of paleontological and archeological evidence to infer local extinctions and community dynamics over a 6,000-y span. The unprecedented temporal resolution of this dataset enables examination of how the tandem effects of human population growth and climate change can disrupt mammalian communities. We show that the extinctions of mammals in Egypt were nonrandom and that destabilizing changes in community composition coincided with abrupt aridification events and the attendant collapses of some complex societies. We also show that the roles of species in a community can change over time and that persistence is predicted by measures of species sensitivity, a function of local dynamic stability. To our knowledge, our study is the first high-resolution analysis of the ecological impacts of environmental change on predator–prey networks over millennial timescales and sheds light on the historical events that have shaped modern animal communities.

community stability | historical ecology | trophic interactions | dynamic sensitivity | redundancy

Modern biological communities are vestiges, with rich ecological ancestries shaped by evolutionary, climatic, and more recently anthropogenic effects. Determining the consequences of past ecological disturbance will inform predictions of how modern communities may respond to ongoing anthropogenic or climatic pressures. Of particular importance are extinction cascades (1, 2), which can lead to trophic downgrading and community collapse by altering the structure (2) and relative strengths of interactions between species (3). Examining the long-term effects of extinctions on communities can only be accomplished by studying past ecosystems (4). The paleontological record and the remarkable historical record of species occurrences in Egypt document a biological community changing in the face of increasing aridification and human population densities (5). The timing and pattern of animal extinctions in Egypt are thus well suited to illuminate our understanding of how the structure and functioning of biotic communities are altered by changing climatic and anthropogenic impacts.

The Nile Valley north of Aswan is known for its intense heat, low rainfall, and relatively sparse vegetation. In fact, the last 2,750 km of the Nile is devoid of water-bearing tributaries and surrounded by desert with an average rainfall of 3.4 cm/y. The Egyptian landscape in the Late Pleistocene/early Holocene was very different; during the African Humid Period (AHP) (14,800–5,500 y B.P.), the region had a cooler, wetter climate driven by heavy monsoonal rains (5). These factors contributed to a diverse assemblage of mammals that bears a strong resemblance to communities in East Africa today.

Termination of the AHP was associated with increasingly weak summer monsoons (6) and the disappearance of many Egyptian species, including spotted hyenas, warthogs, zebra, wildebeest, and water buffalo (7–10), as well as the onset of dense human settlements in the region (11). A sharp increase in aridification

~5,000 y B.P. (5, 11) attended the fall of the Uruk Kingdom in Mesopotamia (5, 12), but it might have catalyzed the rise of the Egyptian Pharaonic state (12, 13). Another aridification pulse ~4,170 ± 50 y B.P. (5) coincided with the Egyptian First Intermediate Period (~4,140 y B.P.), an interval that is distinguished by failed flooding of the Nile (14) and rapid dynastic successions (15). Other potential aridity-induced political instabilities are evident at this time, including the collapse of the Akkadian empire (16) and the decline of urban centers in the Indus Valley (17). Finally, a third aridification pulse is evident in eastern Mediterranean sediments at ~3,000 y B.P. (5). This event is associated with widespread famines in Egypt and Syria (18, 19) and the end of the New Kingdom in Egypt (14) and the Ugarit Kingdom in Babylon (18).

The historical consequences of these aridification events are an enduring, and often contentious, topic of debate (14, 17, 20–22). At the same time, the historical ecology of Egyptian animal communities has been documented extensively (7, 23–25). These parallel efforts include descriptions of animal occurrences in paleontological, archeological, and historical records, as well as their artistic representations on tombs (26), knife blades (27), and funerary palettes (28), compiled by D. J. Osborn and J. Osbornová (8). Artistic representations of mammals are identifiable at the species taxonomic level (8, 27), with historical sources noting whether fauna were native or imported, or even domesticated (8). For example, Late Predynastic ceremonial palettes depict lions, wild dogs, and many species of ungulates including oryx, hartebeest, and giraffe (Fig. 1), none of which exist in Egypt today. Here, we combine these records of species occurrence with mathematical modeling to examine the patterns and consequences of extinctions during 6,000 y of Egyptian history (Fig. 2; see *Supporting Information, section I*, for detailed species occurrence information).

Significance

The composition of animal communities directly impacts the stability of ecosystems. Here, we use historical information of species extinctions in Egypt over 6,000 years to reconstruct predator–prey interactions and determine to what extent observed changes in species composition influence predictions of community stability. Our study reveals that the roles of species and the stability of the community have fundamentally changed throughout the Holocene, and provides compelling evidence that local dynamic stability is informative of species persistence over time.

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Fig. 1. Ancient Egyptian depictions of familiar predator–prey interactions. The (A) obverse and (B) reverse surfaces of a siltstone ceremonial palette accessioned (no. E.3924) in the Ashmolean Museum of Art and Archaeology, University of Oxford. The palette (known informally as the Ashmolean or two dog palette) was recovered from the main deposit at Hierakonpolis (~5,150 y B.P.). The object is surmounted and framed by two wild dogs (*Lycaon pictus*) clasp one another's paws. Other unambiguous species include ostrich, hartebeest, wildebeest, ibex, oryx, and giraffe. Some fictitious animals are also depicted, including serpent-necked panthers, or "serpopards", and a plausible griffin; these animals were excluded from our analysis. Photographs reproduced with permission (Copyright, Ashmolean Museum). (C) Line drawing of a mudstone ceremonial palette accessioned (no. EA20790) in the British Museum. The provenance of this Late Predynastic palette (known informally as the hunters' palette) is uncertain. The reliefs depict human hunters stalking and capturing lions, gazelles, hartebeest, and an ostrich with bows, spears, throwsticks, and lariat. For recent scholarship on, and interpretation of, these images, see Davis (57).

Patterns of Extinction

A total of 37 large-bodied (>4-kg) mammalian species are documented in Late Pleistocene/early Holocene Egypt, whereas only 8 remain today (24). Here, we focus on ungulates and their potential mammalian predators, as these animals are known to form a dynamically cohesive component of many food webs (3, 29–31), and binned their occurrences in the time periods shown in Fig. 2. To determine whether the extinction of species in the historical record could be predicted by random removal, we conducted randomized extinction simulations (5×10^5 replicates), where the number of extinctions at each time interval was conserved. Our analysis shows that changes in predator and prey richness—summarized by calculating the predator–prey ratio—are not predicted by random extinction trajectories until recent history (Fig. 3A). The ratio of predators to prey increased gradually from the Late Pleistocene to the end of the New Kingdom (part of the observed increase in the predator–prey ratio after 4,140 y B.P. is due to the appearance of

cheetah *Acinonyx jubatus*; Figs. 2 and 3A), followed by a decline from ~3,035 y B.P. to 100 y B.P.

To evaluate the effects of uncertainty in the timing of extinctions on the predator–prey ratio, we allowed the first and last occurrence of each species to vary probabilistically according to two different treatments: (i) the first/last occurrence could vary among the time bins directly before and after the recorded event; (ii) the first/last occurrence could vary among two time bins directly before and after the recorded event (illustrated in Fig. 2). To determine how uncertainty influenced the predator–prey ratio, we simulated the extinction trajectories of species over time, where the occurrence of each species was drawn randomly and independently according to each extinction probability treatment (5,000 replicates; Fig. 3A). This uncertainty introduces error in the timing of extinctions of ± 286 and ± 580 y (averaged across time bins), for treatments i and ii, respectively. Importantly, we find that this added uncertainty does not alter the qualitative nature of the predator–prey ratio over time.

The loss of large-bodied herbivores, such as elephants, giraffes, native camels, oryx, and two species of kob, characterizes the earliest documented extinctions in Egypt. Some of these extinctions could have been caused by competitive displacement; for instance, Churcher (7) suggested that wild asses (*Equus asinus*), which appeared in the early-mid Holocene, might have supplanted zebras (*Equus grevyi* and *Equus quagga*, the latter formerly *Equus burchelli*). Predator extinctions follow a similar pattern, with larger-bodied species disappearing earlier. Egyptian artisans depicted two distinct lion morphotypes (possibly subspecies) (32) before the Third Dynasty: a short-maned and a larger long-maned lion, which we treat separately. The long-maned lion was depicted until the end of the Second Dynasty (~4,645 y B.P.), and the short-maned lion until the end of the Twentieth Dynasty (~3,035 y B.P.); a span that excludes depictions of tame or imported lions). Compellingly, this latter date predates accounts of diminishing lion populations in classical antiquity. For example, lions reportedly attacked Xerxes and his consort in 2,430 y B.P., a time when lions were common in Greece (according to Herodotus, 2,434–2,375 y B.P.). A little over a century later (2,250 y B.P.), Aristotle reported that lions were rare (33).

The most dramatic shifts in the predator–prey ratio occurred ~5,050, 4,140, 3,520, 3,035, and 100 y B.P. (Fig. 3A). Although the direction of the shift at 100 y B.P. is prone to observational error, it is coincident with population growth and industrialization in Egypt (Fig. S1). Three of the remaining four shifts are contemporaneous with extreme environmental and historical events: (i) the aridification pulse associated with beginning of the Dynastic Period in Egypt (5, 12) (~5,000 y B.P.); (ii) the aridification pulse associated with the collapse of the Old Kingdom in Egypt (~4,170 \pm 50 y B.P.); (iii) the aridification pulse associated with the fall of the New Kingdom in Egypt (19) (~3,000 y B.P.).

Shifts in the predator–prey ratio reveal a long-term change in community structure: the reduction of herbivore richness beginning ~5,000 y B.P. followed by a decline in predator richness beginning ~3,035 y B.P. Although we cannot identify the causes of extinction at any single time interval, the co-occurring changes in climate, community composition, and human societies suggest three potential mechanisms that could have resulted in the observed patterns. First is the potential decline in herbivore richness due to human overkill followed by an indirect impact on predator richness. Egyptian peoples shifted from mobile pastoralism after the AHP to agriculture (12, 34), and subsistence hunting subsidized by agriculture (25, 35) may have increased overall mortality risks. Differences in species-specific traits and hunting preferences (cf. ref. 36) would then have contributed to shape patterns of extinction. Second, herbivore and carnivore richness may have been negatively impacted by bottom-up forcing due to climate-driven limitation in primary productivity. Third, resource or habitat competition with humans in the Nile floodplain, driven by an increased reliance on agriculture (34), and potentially exacerbated by decreased nutrient transport from species extinctions (35), might have resulted in

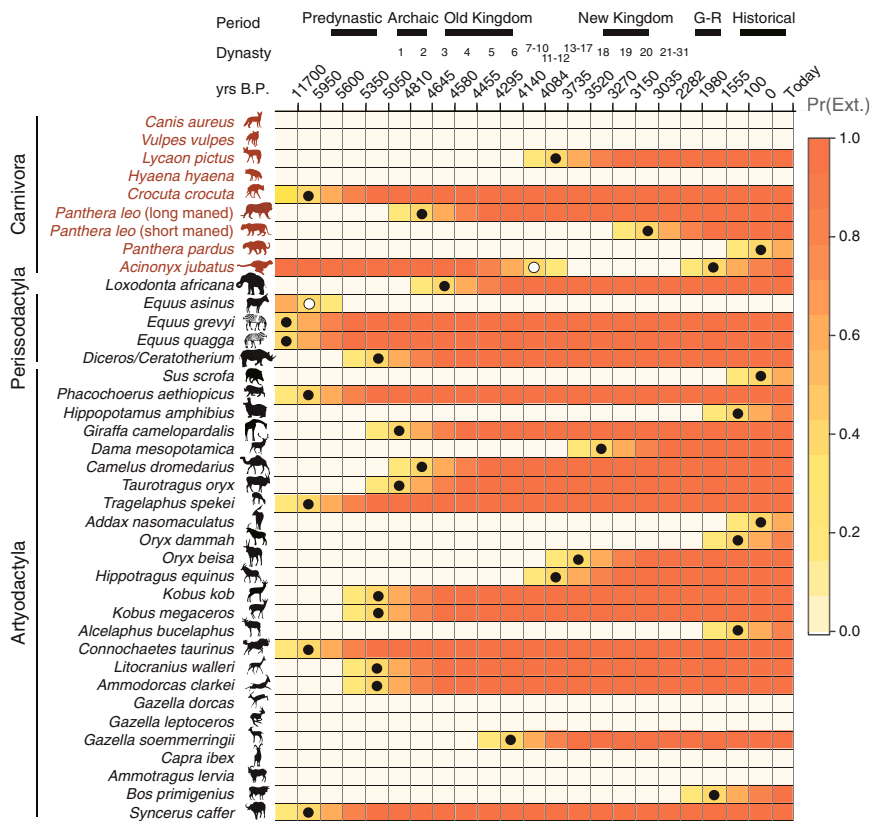


Fig. 2. The presence/absence of large-bodied mammalian species across six millennia of Egyptian history. All dates are in years before present, thus “years before 1950 A.D.,” such that we distinguish 0 y B.P. (1950 A.D.) from “today” (established as 2010 A.D.). The first time bin does not have a definitive starting date, generally representing the Late Pleistocene. The white circles denote the first time interval of a recorded species occurrence if it was not initially present; the black circles denote the last time interval of a recorded species occurrence if it is not extant. The color gradient is the probability that a given species is locally extinct for the treatment allowing first/last occupation to vary across two time bins before and after the recorded event. G-R, Greco-Roman.

declining herbivore richness, precipitating a cascading impact on the predator community.

The Dynamics of Collapse

As the composition of an ecosystem is altered, the potential dynamics of the community are bound to change (37). To understand how historical extinctions impacted the dynamics of Egyptian communities, we used predator–prey body mass ratios to calculate both the probability and strength of trophic interactions, thus reconstructing predator–prey interaction networks for each time bin (38) (*Materials and Methods* and *Supporting Information, sections II–IV*). We used generalized dynamical models to determine dynamic stability over time, thus requiring only basic assumptions of the functional relationships governing interspecific and intraspecific interactions between and among species (37, 39). Across all time bins, 2×10^5 predator–prey networks were constructed (for parameter values and ranges, see *Table S1*), thus accounting for potential variability in species interactions, interaction strengths, and intraspecific and interspecific functional responses (37). We then calculated the proportion of dynamically stable webs (PSW), the impact of a given species i 's presence on PSW, and the magnitude of species-specific responses to perturbations.

Because predator–prey interactions are a function of body size, the structure of the Egyptian trophic network is relatively robust to changes in species presence/absence over time (*Fig. S2*; cf. ref. 40). Despite the robustness of network structure, our results show that dynamic stability, measured as PSW, was highly sensitive to changes in the animal community, and reveal that extinctions in Egypt were inherently destabilizing (*Fig. 3B*). Moreover, the loss of species in the last 150 y had a disproportionately large impact

on PSW (*Fig. 3B*), which is a compelling indication that the effects of recent disturbances on animal communities may be more destabilizing relative to those before the modern era. Stability analyses of random food webs (41) have generally shown that the loss of species richness increases PSW (37, 42), fueling the diversity–stability debate (43). In contrast, our analyses combining generalized modeling with a realistic interaction network structure reveal that stability decreases with species loss, and this pattern is robust against uncertainty in the timing of both historical and recent extinctions (*Fig. 3B*).

In the modern Egyptian predator–prey network, there are a small number of crucial species (44) whose presence strongly and positively impacts stability, which is determined by calculating the difference in PSW (ΔPSW_i) for the system with and without each species i (2×10^8 replicates). Stabilizing species include gazelles, ibex, and Barbary sheep, all of which are smaller-bodied herbivores serving as important prey resources for the remaining predators (*Fig. 4A* and *Fig. S3*). Some of these species (e.g., *Gazella leptoceros*) are critically endangered (45). Although the impact of species i 's presence on PSW is correlated with body size (*Fig. S4*), as we observe the community earlier in time, the presence of all species has less impact on PSW (such that ΔPSW_i is closer to zero), suggesting that the historical community was more robust, presumably due to greater redundancy in prey species. Importantly, the decline in PSW essentially mirrors deviations in ΔPSW_i away from zero, meaning that earlier communities were more stable and less impacted by species removal, whereas recent communities are less stable and more impacted by species removal. Together, these findings indicate an increase in vulnerability over time (*Fig. S5*). We hypothesize that the vulnerability of many contemporary

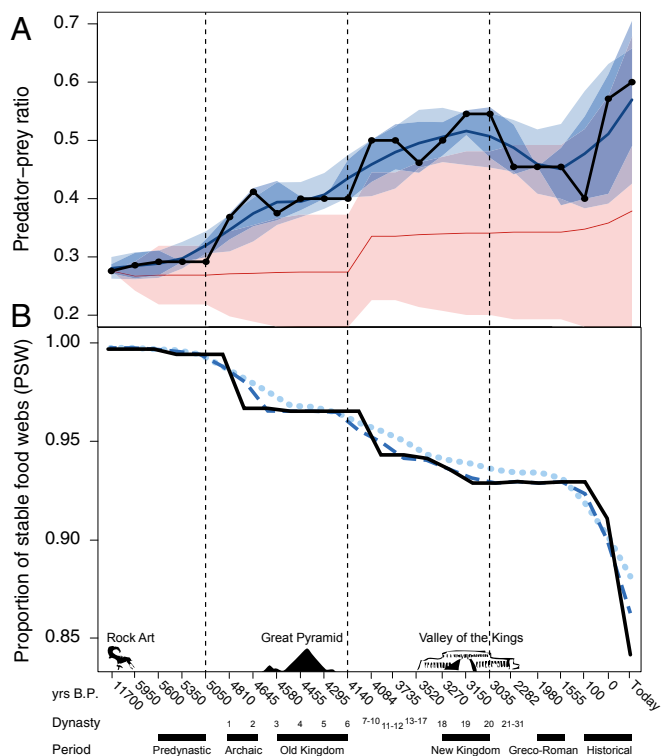


Fig. 3. Changes in the predator–prey ratio and dynamic stability of the Egyptian trophic network over time. (A) The predator–prey ratio is shown (black line) against simulations where extinction is treated probabilistically, incorporating error of 286 (dark blue polygon) and 580 (lighter blue polygon) years before and after first and last occurrences (the mean is denoted by the blue line). Random extinction trajectories are shown by the red line and polygon (mean and SD of 5×10^5 replicates, respectively). (B) Proportion of stable webs (2×10^5 replicates) for the Egyptian community (black), and with first and last appearances treated probabilistically, incorporating error of 286 (dark blue, dashed line) and 580 (lighter blue dotted line) years before and after the first and last occurrences. The vertical dashed lines denote the major climatic events at $\sim 5,050$, 4,170, and 3,035 y B.P.

animal communities (3) may be exacerbated by recent erosion of species richness, which our data suggest eliminates the functional redundancy of lower trophic-level species.

The primary productivity needed to support a diverse animal community is expected to have diminished as the Nile Valley became increasingly arid throughout the Holocene (14). Because changes in productivity can alter population-level responses to species interactions, we performed a sensitivity analysis to determine whether and to what extent changes in primary productivity influence estimates of PSW. We address changing habitat productivity by incorporating the following assumptions: (i) when productivity is high, the per-capita contribution of herbivores to population growth increases, such that the impact of herbivore density on growth is elevated; (ii) because prey are plentiful, the growth of predator populations is not limited by prey density (46). Conversely, when primary productivity decreases (as is assumed to have occurred over the Holocene), herbivore population growth becomes nutrient limited, such that changes in herbivore density have a smaller impact on population growth, whereas predator population growth becomes limited by herbivore density. This formalization allows us to explore how our results are impacted by changes in the functional relationships between population growth and its drivers due to changes in primary productivity at every time period by instituting the following constraints: as productivity decreases, the sensitivity of herbivore population growth to herbivore density (ϕ in the generalized modeling framework; *Supporting*

Information, section V) goes to 0, whereas the sensitivity of predator population growth to herbivore density ($\gamma = 1 - \phi$) goes to unity; for increases in productivity, this relationship is reversed. We find that increasing productivity is always destabilizing, which is expected in accordance with the well-known “paradox of enrichment” (47). Of more interest here is that lowering productivity does not have a qualitative impact on estimates of PSW (Fig. 4B), suggesting that changes in PSW over time were not solely driven by changes in productivity itself, but were chiefly influenced by changes in community composition and species interactions.

Predicting Persistence

Understanding the reciprocal feedbacks between a changing environment on the structure and functioning of ecosystems is

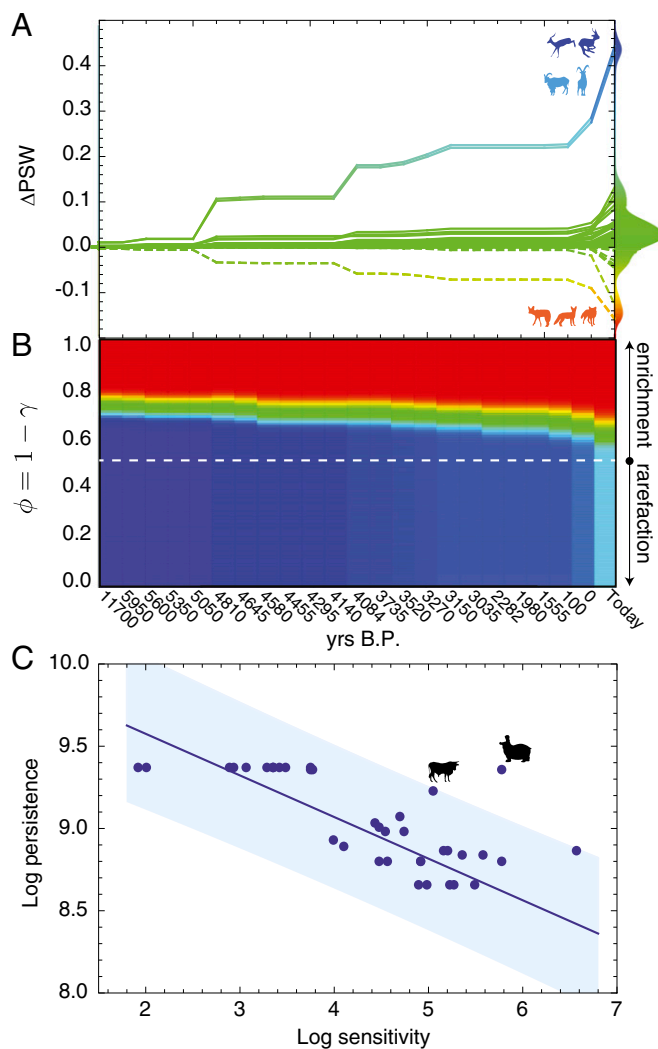


Fig. 4. (A) The mean change in PSW (ΔPSW) as a function of species presence over time. Predator presence destabilizes trophic network (stippled lines); prey presence stabilizes trophic networks (solid lines). Histograms on the y axes represent densities of ΔPSW values for the earliest and latest time intervals, and colors scale to the y axis. (B) PSW (colors scaled from red, $\text{PSW} = 0$, to blue, $\text{PSW} = 1$) as a function of the sensitivity of herbivore growth to changes in herbivore density (ϕ ; y axis) over time (x axis). The white stippled line denotes $\phi = 0.5$ used for the dynamic analysis (Table S1), such that $\phi > 0.5$ indicates nutrient enrichment (productivity increase), and $\phi < 0.5$ indicates nutrient rarefaction (productivity decrease). (C) Species sensitivity vs. persistence since the Pleistocene–Holocene transition (11.7 ky B.P.). Linear regression model: $R^2 = 0.36$, $p \ll 0.005$; blue shaded region is the 75% confidence interval.

a primary goal in modern ecological research (48). For instance, short-term environmental changes may be responsible for altering community structure in both limnetic invertebrate (40) and terrestrial vertebrate food webs (49), whereas shifting thermal baselines and mismatches in phenology have been observed to directly alter the composition of terrestrial communities (50, 51). Theoretical work suggests that climate warming may have a large impact on trophic chain length and top-down vs. bottom-up dynamics, where higher trophic species are predicted to be at greatest risk (52). However, to what extent the dynamical consequences of perturbed ecological communities impact species persistence is largely unknown, and this is partly due to a lack of knowledge regarding how animal assemblages and species interactions change over time (53).

Although we cannot ascribe causality to any single extinction event, because the persistence of each species over time is known, we can determine whether extinction is predictable. Perturbations are by definition disruptive, and their effects can be explored with respect to the system as a whole (PSW), or with respect to each species in the system. In general, we would assume that species strongly reactive to external perturbations would have lower persistence, thus being prone to extinction. Here, we determine whether the sensitivities of species to external perturbations can be used to predict persistence, defined as the period after the Pleistocene–Holocene transition (11.7 ky B.P.) of Egyptian occupation. We define the sensitivity of a species i (Se_i) (44) by the magnitude of its response to a press perturbation, introduced by altering the community steady state (54) (see [Supporting Information, section VI](#), for a formal derivation). Our results show that sensitivity is strongly predictive of persistence, and therefore extinction risk: species less sensitive to change are more likely to survive longer periods of time (Fig. 4C and Fig. S6). Of note are two outliers for which temporal persistence is greater than predicted by Se_i (silhouettes in Fig. 4C): hippopotamus (*Hippopotamus amphibius*), which rely primarily on river resources that are not included in the dynamic model, and wild cattle (*Bos primigenius*), potentially facilitated by association with domesticates (55). Our results confirm the generally accepted expectation of higher extinction risks for larger-bodied mammalian species (56) and indicate that measures derived from local stability analysis are predictive of these risks over millennial timescales.

The trajectory of extinctions over 6,000 y of Egyptian history is a window into the influence that both climatic and anthropogenic

impacts have on animal communities. The atypically strong effects that species extinctions have had on the stability of the contemporary Egyptian predator–prey network is due to the nonrandom but steady erosion of species richness over time. Our results directly fuel hypotheses on whether and to what extent cascading extinctions, changes in the sensitivity to perturbations, and the consequent decline of community stability as the result of both climate change and human impact, have contributed to the collapse of modern animal communities.

Materials and Methods

We compiled data on species occurrences from paleontological, archeological, and historical information spanning the last 6,000 y of Egyptian history. All dates are in years before present (y B.P.), thus “years before 1950 A.D.,” such that we distinguish 0 y B.P. (1950 A.D.) from “today” (established as 2010 A.D.). We used body mass ratios between predators and prey to determine the probability that a trophic link exists between species i and j [$\text{Pr}(\ell_{ij} = 1)$], where $\text{Pr}(\ell_{ij} = 1) = p/(1 + p)$, given $p = \exp\{a_1 + a_2 \log(\text{MR}) + a_3 \log^2(\text{MR})\}$, and MR is the log-transformed ratio of predator to prey biomass (38). We established this model on the Serengeti food web ($a_1 = 1.41$, $a_2 = 3.73$, and $a_3 = -1.87$), from which 74% of trophic links (both presence and absence) were predicted accurately. We capture the dynamics of an N species food web by N equations of the following form: $\dot{X}_i = S_i(X_i) + \eta_i F_i(X_1, \dots, X_N) - M_i(X_i) - \sum_{n=1}^N L_{n,i}(X_1, \dots, X_N)$, for $i = 1 \dots N$, where η_i is the transfer efficiency of predator growth from prey consumption; and S_i , F_i , M_i , and $L_{n,i}$ are unspecified functions that describe the growth of species i by primary production, the growth of species i by predation, the loss of species i due to natural mortality, and the loss of species i due to predation by species n , respectively. Local stability is computed by linearizing the nonlinear equation-system around the steady state in question. The result is the so-called Jacobian matrix that captures the system's response to perturbations in the vicinity of the steady state. For the generalized model, one formally computes the linearization for all feasible steady states (37). We thereby obtain a Jacobian matrix that captures the dynamical stability of every steady state in the whole class of models under consideration, as a function of a number of unknown, but directly interpretable ecological parameters. For additional details, see [Supporting Information, sections II–IV](#).

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Supporting Information

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I. Records of Species Origins and Extinctions in Egypt

We used data on species occurrences from paleontological, archeological, and historical records to analyze the impacts of species extinctions spanning the last 6,000 y of Egyptian history. All dates are in years before present (y B.P.), thus “years before 1950 A.D.,” such that we distinguish 0 y B.P. (1950 A.D.) from “today” (established as 2010 A.D.). Combining observations of animal occurrences in paleontological and archeological sites with depictions of these species in the art record, serves to increase the temporal resolution of community composition while enabling a better understanding of the timing of local extinctions across the Holocene.

Although these combined datasets are prone to biases affecting both the preservation of animal remains, and the artistic depiction of different species over time, we consider the earliest and latest occurrence of species in our records to be informative of the origination and extinction of species in Egypt. As such, we ignore temporary disappearances of species (i.e., “Lazarus” species), and assume that a species is present in Egypt after its first occurrence until its last occurrence. This “range-through” approach in reconstructing species’ occurrence is most prone to observation error with regard to the origination and extinction events, which we address by treating both origination and extinction probabilistically (see main text). Moreover, we address potential bias and error in our reconstruction of species occurrence in Egypt by evaluating the impact that species’ presence has on the percent of stable webs (PSW), as detailed in section IV.

Here, we provide detailed references regarding the information gathered to reconstruct local origination [first occurrence (FO)] and extinction [last occurrence (LO)] of each species in Egypt since the end of the Pleistocene. We note that if animal remains or evidence of occupation was documented for the Late Pleistocene or early-mid Holocene, such occurrences were binned together as “Late Pleistocene” or LP. Much of this information is detailed more explicitly by D. Osborn and J. Osbornová (1), on whose expertise in cataloging the occurrence of mammals in Egypt we have relied to a great extent in compiling this dataset.

Carnivora. *Canis aureus* (golden jackal).

FO: LP—Remains are first documented in the Late Pleistocene deposits of Wadi Halfa in South Sudan (2), as well as the early Holocene site of Dakhla Oasis in the Western Desert (3).

LO: Extant.

Vulpes vulpes (Egyptian fox).

FO: LP—Present in the Late Pleistocene at Wadi Halfa (2) and depicted in Predynastic rock drawings (4). *Vulpes vulpes* makes an occurrence in the Predynastic Hunters’ Palette (Fig. 1C).

LO: Extant.

Lycaon pictus (wild dog).

FO: LP—First depicted in Egypt in the Wadi Abu Subeira rock art, which is dated to 20–15 ky B.P. (5) and can also be observed in various Dynasty 1 palettes (6).

LO: 3,735 y B.P.—There is one known representation of *L. pictus* on the tomb of Ukh-hotep in Dynasty 12; however, all New Kingdom references list them as imports from Nubia (7).

Hyaena hyaena (striped hyena).

FO: LP—Remains are found in the Late Pleistocene deposits of Kom Ombo (8), are depicted in Predynastic rock drawings at Abu Agag (9).

LO: Extant.

Crocuta crocuta (spotted hyena).

FO: LP—Remains are found at Kom Ombo (8), the Paleolithic site of Helwan (10), and can be identified in an early-mid Holocene rock carving southwest of Aswan (9).

LO: 5,950 y B.P.—There is no evidence of occurrence in the Predynastic or Dynastic Periods.

Panthera leo (African lion).

FO: LP—Classified as two possible subspecies in Egyptian artwork: the larger-bodied, long-maned lion, and the smaller-bodied, short-maned lion. The earliest occurrence of lions in Egypt can be traced to burned Neolithic bones from Beni Salama (up to ~7,000 y B.P.) (11, 12), and given their African origin and expansion via the Isthmus of Suez (13), we assume that they were also present in the Late Pleistocene.

LO (long-maned): 4,645 y B.P.—The last depiction of the long-maned subspecies is from a granite statue at the end of the late Predynastic/early Dynastic (14, 15).

LO (short-maned): 3,035 y B.P.—The shorter-maned subspecies is thought to have remained in Egypt much longer: for example, the hunting of wild lions is depicted in multiple pharaonic tombs up to Amenophis III (Dynasty 18) (16). Tame lions are depicted into Dynasty 20 (17), whereas records of imported lions from Nubia are mentioned from Dynasty 19 onward (18).

Panthera pardus (leopard).

FO: LP—Remains are found at a Copper Age site in Maadi near Cairo (19) and are also found in the early Holocene South Galala Plateau cave in the Eastern Desert (20).

LO: 100 y B.P.—*Panthera pardus* has a historical distribution that includes oases in the Western Desert and the Sinai, and today is on the verge of extinction. We assume that it was ecologically extinct by the historical period.

Acinonyx jubatus (cheetah).

FO: 4,084 y B.P.—Representations in rock carvings are questionable (1), and the earliest Dynastic representation is of a cheetah sniffing a hedgehog in the Middle Kingdom site at Beni Hasan (21).

LO: 1,555 y B.P.—Late Dynastic depictions are of imports from the “Land of Punt” (18), and we assume ecological extinction by the beginning of the Greco-Roman Period. Occasional historical observations of cheetah have been noted, suggesting that there may be remnant populations in the Western Desert (22). The last confirmed sighting was of an individual shot by Bedouins in 1974 near el Maghra (23).

Proboscidea. *Loxodonta africana* (African elephant).

FO: LP—Remains are found at the early Holocene site of Dakhla Oasis (24, 25) and are also depicted in rock drawings in the Eastern Desert (26).

LO: 4,580 y B.P.—*Loxodonta africana* is estimated to have gone regionally extinct by the start of the Dynastic Period (27), although there was a substantial ivory trade facilitated via Nubia throughout the Dynastic Period (1).

Perissodactyla. *Equus asinus* (wild ass).

FO: 5,950 y B.P.—*Equus asinus* is thought to have entered Egypt from Sinai during the Paleolithic, possibly competitively displacing zebras (8). Although there may be a strong case for including *E. asinus* in the LP time bin (there are Late Paleolithic remains in shoreline deposits near Faiyum; ref. 28), here we assume that they arrive after the end of the Pleistocene.

LO: Extant.

***Equus grevyi* (Grevy's zebra) and *E. quagga* (formerly *E. burchelli*; common or plains zebra).**

FO and LO: LP—Remains are found in the late Pleistocene/early Holocene site of Dakhla Oasis (29, 30) but are not found or depicted afterward.

***Diceros/Ceratotherium* (black/white rhinoceros).**

FO: LP—Depicted in the early-mid Holocene rock drawings in the Eastern Desert (it is impossible to distinguish between black and white rhinoceroses) (4, 31).

LO: 5,050 y B.P.—Regionally extinct after the end of the African Humid Period (AHP) ~5,000 y B.P. (1).

Artiodactyla. *Sus scrofa* (wild boar).

FO: LP—Present in northeast Africa throughout the Late Pleistocene (32) and are depicted in rock drawings in the Late Pleistocene/early Holocene site of Dakhla Oasis (33).

LO: 0 y B.P.—*Sus scrofa* inhabited the reed beds and swamps of El Moghra Oasis and other parts of northern Egypt until the early 1900s (1).

***Phacochoerus aethiopicus* (warthog).**

FO: LP—Remains are found in the Late Pleistocene sites of Bir Sahara, Barqat el Shab Playa, and Dakhla Oasis (30, 34, 35).

LO: 5,950 y B.P.—There is no evidence of occupation in the Predynastic or Dynastic Periods.

***Hippopotamus amphibius* (hippopotamus).**

FO: LP—Originally inhabited the entire Nile Delta (1) and are often found in Early-Mid Holocene rock drawings (8).

LO: 100 y B.P.—*Hippopotamus amphibius* is known to have existed in northern Egypt into the 1800s (1).

***Giraffa camelopardalis* (giraffe).**

FO: LP—Remains are found at the early Holocene site of Gilf Kebir in southwestern Egypt (32). Depictions of hunting scenes involving *G. camelopardalis* are common throughout the Predynastic Period (4, 36) and were often carved into slates and ivory knife handles (6, 37).

LO: 4,810 y B.P.—*Giraffa camelopardalis* was regionally extinct by the Dynastic Period (1), after which they are depicted as imports or tributes from other regions.

***Dama mesopotamica* (dama deer).**

FO: LP—*Dama mesopotamica* crossed the Isthmus of Suez into Egypt during the Pleistocene (38). Pleistocene remains of these animals have been found south of El Badari and Wadi Halfa (39).

LO: 3,270 y B.P.—*Dama mesopotamica* are prominently depicted on a Dynasty 1 mace handle (40) and are found in hunting scenes until Dynasty 18 (1, 41, 42).

***Camelus dromedarius* (dromedary camel).**

FO: LP—Remains are found at the Holocene site of Gilf el Kebir in southwestern Egypt, as well as Pleistocene deposits near Dakhla Oasis (30).

LO: 4,645 y B.P.—The latest occurrence of wild *C. dromedarius* populations in Egypt is uncertain, but they likely were absent by the start of the early Dynastic Period (43).

***Taurotragus oryx* (giant eland).**

FO: LP—*Taurotragus oryx* occurs among the Quaternary fauna of Nubia (44), as well as the Quaternary deposits at Bir Tarfawi (34).

LO: 4,810 y B.P.—The only later occurrence of *T. oryx* is a representation on the Dynasty 1 mace handle from Selyala (45).

***Tragelaphus spekei* (sitatunga).**

FO: LP—Remains are found in archeological deposits in northern Egypt (46) and are associated with early Holocene sites in the Egyptian central valley (47).

LO: 5,950 y B.P.—There is no evidence of occupation in the Predynastic or Dynastic Periods.

***Addax nasomaculatus* (addax).**

FO: LP—Remains are found at the early Holocene site Gilf Kebir (32).

LO: 0 y B.P.—*A. nasomaculatus* is depicted often in rock carvings and illustrations throughout the Dynastic Period (48) but is thought to have been extinct in Egypt by the early 1900s (49).

***Oryx dammah* (scimitar oryx).**

FO: LP—There are no identified skeletal remains in Egypt (1), but they are depicted in rock drawings from the early Holocene (36) throughout the Dynastic Periods and into the Greco-Roman Era (26).

LO: 100 y B.P.—*Oryx dammah* lived throughout western Egypt until the mid-1800s (50) and may have gone extinct due to direct hunting (1).

***Oryx beisa* (beisa oryx).**

FO: LP—*Oryx beisa* are not present in Egyptian paleontological sites but are depicted in numerous rock drawings in the Eastern Desert (4), as well as on Predynastic palettes (Fig. 1). Here, we count them present in the earliest assemblages in Egypt, although there may be a case for setting their first occurrence during the Predynastic Period.

LO: 3,520 y B.P.—*Oryx beisa* is depicted in hunting scenes up to Dynasty 12 (21). Representations of *O. beisa* do occur after Dynasty 12 but in scenes depicting them as tributes from Nubia (18).

***Hippotragus equinus* (roan antelope).**

FO: LP—Remains are found in Late Pleistocene deposits in northern Sudan (51), are possibly depicted in rock drawings near Gebel el Silsila (4), although their earliest Dynastic reference is in Dynasty 5 (52).

LO: 3,735 y B.P.—*Hippotragus equinus* is last depicted in a hunting scene in the Dynasty 12 Beni Hasan Tomb of Baqt, whereas remains found after Dynasty 12 are associated with other imported fauna (such as elephants) and are thought to represent captive palace animals (53).

Kobus kob (kob) and Kobus megaceros (Nile lechwe).

FO: LP—Remains are found in Late Pleistocene deposits in southern Egypt (44) and Predynastic archeological sites in northern Egypt (46), respectively.

LO: 5,050 y B.P.—*Kobus megaceros* were regionally extinct by ~5,000 y B.P. (1).

Alcelaphus bucelaphus (hartebeest).

FO: LP—Present in many sites dating from the early Holocene to the late Predynastic Period (32), into the early Dynastic Period (25).

LO: 100 y B.P.—*Alcelaphus bucelaphus* were exterminated in Egypt by ~1850 A.D. due to extensive hunting (54).

Connochaetes taurinus (wildebeest).

FO: LP—Occupied Egypt until the Late Pleistocene (1), whereas the only known depiction is a carving on the reverse side of the Hierakonpolis palette (Fig. 1B) (6).

LO: 5,950 y B.P.—*Connochaetes taurinus* likely became regionally extinct during the AHP (1).

Litocranius walleri (gerenuk).

FO: LP—Present in numerous rock drawings during the early Holocene (4), into the late Predynastic (36), but are not known to be represented after the Predynastic Period.

LO: 5,050 y B.P.—*Litocranius walleri* are browsers requiring free water and are thus thought to have been pushed southward after the cessation of the AHP (1).

Ammodorcas clarkei (dibatag).

FO: LP—Found in rock drawings on the west bank of the Nile north of Aswan.

LO: 5,050 y B.P.—Assumed to have retreated southward in the late Predynastic Period (1). There are Dynastic representations of *A. clarkei*; however, they are generally illustrated as being offered in processions from adjacent regions (55).

Gazella dorcas (dorcac gazelle).

FO: LP—Remains were found in early Holocene archeological sites by Uerpmann (32), who commented that “no differences can yet be seen between the ancient and the present range of *G. dorcas* in NE Africa.”

LO: *Gazella dorcas* is extant in Egypt today and is present in much of its historical range (56).

Gazella leptoceros (slender-horned gazelle).

FO: LP—Remains are found in the late Pleistocene/early Holocene sites of Kom Ombo and Dakhla Oasis (3, 8).

LO: *Gazella leptoceros* is still extant in Egypt today but is on the verge of extinction (1, 56, 57).

Gazella soemmeringii (Soemmering's gazelle).

FO: LP—Not found known Egyptian fossil sites, potentially due to the difficulty in correctly identifying this species (1). Remains have been identified in mid-Holocene sediments in Libya (58), in addition to being represented in Egyptian rock drawings north of Silwa Bahari (4).

LO: 4,140 y B.P.—The last representations of *G. soemmeringii* are in Old Kingdom hunting scenes, e.g., at the Dynasty 5 Tomb of Sahure (38), and the Causeway of Unas (59).

Capra ibex (ibex).

FO: LP—Remains are found in Dakhla Oasis (3), are identifiable in rock drawings extending from the Late Pleistocene to the Greco-Roman Period (4).

LO: Extant.

Ammotragus lervia (Barbary goat).

FO: LP—*Ammotragus lervia* was a mid-Pleistocene migrant into Egypt (1) and is present in Late Pleistocene sediments at Kom Ombo (8, 60).

LO: Extant.

Bos primigenius (aurochs).

FO: LP—Remains are found in archaeological sites at Kom Ombo (8), and wild populations are thought to have inhabited North Africa since the mid-Pleistocene (61). The earliest depictions of *B. primigenius* are closely associated with floodplains, suggesting that it was dependent on standing water. Wild cattle were possibly domesticated by ~7,000 y B.P. (62), although there is considerable debate on the origin and timing of domestic cattle in North Africa (63).

LO: 1,555 y B.P.—Wild populations of *B. primigenius* extended into the Greco-Roman Period in northeast Africa (64).

Syncerus caffer (African buffalo).

FO: LP—Remains are known from late Pleistocene sediments at Kom Ombo (8), and early Holocene remains have been found at Dakhla Oasis (3, 29, 65).

LO: 5,950 y B.P.—There is no evidence of occupation in the Predynastic or Dynastic Periods.

II. Model Trophic Networks

We reconstructed predator–prey networks for each time period using a model that assumes interaction probabilities between predator and prey are a function of body mass ratios (66). All species occurring at each time period (Fig. 1 in the main text) were included in the networks, so that networks of different time periods potentially differ in the number of species and interactions. The probability that a trophic link exists between species i and j , $\Pr(\ell_{ij} = 1)$, is given as a function of predator and prey body mass (67), such that

$$\Pr(\ell_{ij} = 1) = p / (1 + p), \text{ given} \quad [S1]$$
$$p = \exp\{a_1 + a_2 \log(\text{MR}) + a_3 \log^2(\text{MR})\},$$

where MR is the log-transformed ratio of predator-to-prey biomass. The parameters of the model thus determine how interaction probability is linked to body mass relationships, such that assemblages with different body mass distributions may result in networks with different topologies even with similar model parameters. The constants $a_1 = 1.41$, $a_2 = 3.73$, and $a_3 = -1.87$ were parameterized from predator–prey relationships in the Serengeti, and predict 74% of both observed and unobserved trophic interactions. If body masses are not log-transformed, the constants are $a_1 = 2.51$, $a_2 = 0.79$, and $a_3 = -0.37$, which result in interaction networks with similar structures.

The relationships measured between predators and prey in the Serengeti community were used to parameterize our model trophic networks of the Egyptian community because the Egyptian mammalian assemblage at the end of the Pleistocene had a similar species composition and body mass distribution as that of the Serengeti today. We thus make explicit the assumption that species in Egypt were constrained by similar foraging limitations

as those that constrain species in the modern Serengeti, and this assumption is bound to result in networks with similar interaction structures.

We assessed network structure by computing the connectance $[C(t) = \ell(t)/(S_{\text{pred}}(t)S_{\text{prey}}(t))]$, where $\ell(t)$ is the number of realized trophic links, S_{pred} is predator richness, and S_{prey} is prey richness in time bin t , which measures the actual number of interactions relative to maximum number of possible interactions, and nestedness (NODF), which describes how interaction patterns overlap and varies between 0 (unnested) to 100 (completely nested) (68). The Serengeti network has a relatively high connectance and interactions are generally nested ($C = 0.52$; NODF = 73.8; ref. 69), such that the interactions of smaller predators form subsets within the interactions of larger predators. By comparison, the modeled Egyptian predator–prey networks at the end of the Pleistocene were structured similarly (mean \pm SD): $C = 0.55 \pm 0.02$; NODF = 80.89 ± 3.04 (Fig. S2). Because interactions are energetically bound as a function of predator and prey body size, the structure of the predator–prey network is relatively consistent throughout the Holocene until the recent, despite changes in species richness and the predator–prey ratio. We also used Eq. S1 to scale the strengths of interactions between predators and prey, assuming that if an interaction is more probable, a higher flow of biomass will characterize the trophic interaction. Variability in trophic interactions for all time intervals is thus captured by iterative sampling of trophic interactions in accordance with the calculated probabilities (section III).

III. Generalized Modeling of Trophic Network Dynamics

To model network dynamics, we used a generalized modeling framework established for multispecies food webs (70) (see ref. 71 for an ecological introduction to generalized modeling techniques and ref. 72 for mathematical proofs). Generalized modeling is a tool that permits the analysis of systems of equations where only the structure of equations, but not specific rate laws are known. In the present case, we capture the dynamics of an N species network by N equations of the form

$$\dot{X}_i = S_i(X_i) + \eta_i F_i(X_1, \dots, X_N) - M_i(X_i) - \sum_{n=1}^N L_{n,i}(X_1, \dots, X_N) \quad [\text{S2}]$$

for $i = 1..N$, where η_i is the transfer efficiency of predator growth from prey consumption; and S_i , F_i , M_i , and $L_{n,i}$ are unspecified functions that describe the growth of species i by primary production, the growth of species i by predation, the loss of species i due to natural mortality, and the loss of species i due to predation by species n , respectively. Local stability is computed by linearizing the nonlinear equation-system around the steady state in question. The result is the so-called Jacobian matrix that captures the system's response to perturbations in the vicinity of the steady state under consideration. For the generalized model, one formally computes the linearization for all feasible steady states (73). We thereby obtain a Jacobian matrix that captures the dynamical stability of every steady state in the whole class of models under consideration, as a function of a number of unknown, but directly interpretable ecological parameters. For the present model, the on-diagonal of the Jacobian matrix is as follows:

$$J_{ii|*} = \alpha_i \left\{ \hat{\rho}_i \phi_i + \rho_i (\gamma_i \chi_{ii} \lambda_i + \psi_i) - \hat{\sigma}_i \mu_i - \sigma_i \left(\sum_{k=1}^N \beta_{ki} \lambda_{ki} [(\gamma_k - 1) \chi_{ki} + 1] \right) \right\}, \quad [\text{S3}]$$

whereas the off-diagonal is as follows:

$$J_{ij|*} = \alpha_i \left\{ \rho_i \gamma_i \chi_{ij} \lambda_{ij} - \sigma_i \left(\beta_{ji} \psi_j + \sum_{k=1}^N \beta_{ki} \lambda_{kj} (\gamma_k - 1) \chi_{kj} \right) \right\}, \quad [\text{S4}]$$

where the parameters, as well as their assigned values or ranges, are as defined in Table S1. Although we do not prescribe the functional forms used in the model, the parameterization can be done in such a way that basic ecological insights (e.g., the effect of apparent competition) are taken into account. A detailed derivation of the Jacobian matrix from Eq. S2 using generalized modeling techniques is provided in refs. 70 and 73.

Here, we consider ensembles of many different steady states in different plausible predator–prey networks. These are generated by randomly sampling trophic interactions from pairwise interaction probabilities as well as parameter values that are substituted into the Jacobian matrix. For each time step, a food-web topology was first drawn randomly from the interaction probability matrix defined by the biomass ratios between each predator–prey pair (*Materials and Methods*). Other parameters appearing in the Jacobian were then drawn randomly from the distributions described in Table S1. For each such randomly generated parameter set, the stability of the corresponding network is then determined by numerical diagonalization of the Jacobian matrix. Mathematically, a dynamical system is stable if the real parts of all eigenvalues of the Jacobian are negative. To avoid numerical error associated with zero eigenvalues, we consider a system as stable if the real part of all eigenvalues was smaller than -10^{-6} .

Following the procedure described above, the stability of 2×10^5 food webs was thus determined for each time step. The proportion of stable webs, PSW, was then computed directly as the proportion of stable webs found in the respective ensemble. The PSW thus denotes the probability of randomly drawing a stable network given reasonable assumptions on the interactions in the community. It thus provides a measure of the structural robustness of a given community. With this number of simulation replicates, bootstrapped measurements of PSW error were found to be negligible.

IV. Change in PSW and the Effects of Extinction Bias

The preservation of animals in the fossil record is influenced by taphonomic processes, impacting the likelihood of recovery, and these processes are in part driven by the ecological and behavioral dynamics of species (74). Similarly, the representation of species in the Egyptian record of artistic works is also likely to be influenced by bias, where species that are particularly charismatic, or that played important roles in Egyptian hunting culture, may be more likely to be represented than others. In this section, we address two important considerations in dealing with uncertain species extinctions: (i) the potential impact of bias in the paleontological/historical record, and (ii) the effect that each species has on the stability of the Egyptian predator–prey network. To determine the extent that the presence of a given species influences system stability, we performed the above analysis both with and without the presence of each species at each time step, regardless of whether the species was extant or extinct in a given time bin. The metric ΔPSW_i for each species i is thus the difference between PSW when a given species is present and absent (Fig. S3). Accordingly, positive ΔPSW_i values indicate that the presence of species i had a positive impact on PSW (and is stabilizing), whereas negative ΔPSW_i values indicate that the presence of species i had a negative impact on PSW (and is destabilizing). Larger absolute values of ΔPSW_i indicate that species' presence has a larger effect on PSW.

Our results show that species influence system stability differently: in general, the presence of predators tends to destabilize the predator–prey network, and this destabilizing effect increases toward the recent. In contrast, the presence of smaller-bodied

herbivore species tends to stabilize the system (with a greater magnitude than the destabilizing effect of predators), which also increases toward the recent. Our calculation of Δ PSW thus addresses to what extent error/bias in records of species' occurrence may impact estimates of PSW, but also serves to evaluate the importance of different species to the stability of the system. We observe that the potential bias of species on PSW, alternatively viewed as the importance of species to system stability, is lower for older time bins. This is important for two reasons: (i) if it is assumed that older records of species occurrence are more prone to error, the bias that this error has on PSW is negligible, and (ii) the impact that individual species have on system stability has increased throughout the Holocene.

V. Accounting for Changes in Productivity over Time

To account for changes in primary productivity without expanding the dimensionality of our dynamic model, we modify our analysis with two basic assumptions: (i) when primary productivity is high, herbivore population growth is limited by herbivore density, whereas carnivore population growth becomes saturated; (ii) when primary productivity is low, herbivore growth is less limited by herbivore density but by the availability of nutrients in the environment, whereas carnivore growth becomes more limited by herbivore density (73). In the generalized modeling framework, these differential measures are accounted for in the Jacobian Matrix, and denoted as elasticities. The elasticity of herbivore growth with respect to herbivore density is $\phi_i = \partial s(x_i)/\partial x_i$, where $s(x_i)$ is the normalized growth function for herbivore i , whereas the elasticity of carnivore growth with respect to herbivore density is $\gamma_i = \partial f_i(t_i)/\partial t_i$, where f_i is the normalized growth function for predator i and t_i denotes the total herbivore biomass available to predator i (71, 73). Thus, if productivity is high, $\phi_i \rightarrow 1$, meaning that changes in herbivore density are matched by changes in herbivore growth, whereas $\gamma_i \rightarrow 0$, meaning that the predator population is saturated and that predator growth rates are not sensitive to changes in herbivore density. If productivity is low, $\phi_i \rightarrow 0$, meaning that changes in herbivore growth are insensitive in changes in herbivore density (because they are nutrient limited), whereas $\gamma_i \rightarrow 1$, meaning that changes in predator growth are proportional to changes in herbivore density.

Thus, we can simulate changing productivity by setting $\phi_i = 1 - \gamma_i$, and exploring how increases or decreases in ϕ_i impacts the stability

of the predator–prey network for each time bin. Our results show that, for increases in productivity at any time interval, there is a decrease in stability. This dynamic is the well-known “paradox of enrichment” (75), which is observed when standard Holling-type functions are used to capture density-dependent responses in food web models (76). However, the climate in Egypt has become increasingly arid throughout the Holocene, decreasing the primary productivity of the region. Incorporating declining productivity into our dynamic models, across all time bins, shows that there is no significant change to PSW. This suggests that our model results are robust to changes in primary productivity within the environment across the Holocene.

VI. Sensitivity to a Random Perturbation

We show that the theoretical sensitivity of each species to changes in the community steady state (Se_i) can be used to predict temporal persistence of species in the empirical Egyptian predator–prey network. Following the line of argumentation presented in ref. 77, the sensitivity is defined as follows:

$$Se_i = \log \left(\sum_k \frac{|v_i^{(k)}|}{|\lambda_k|} \right), \quad [S5]$$

where λ_k is the k th eigenvalue of the Jacobian matrix (λ_k^{-1} is the k th eigenvalue of the so-called impact matrix \mathbf{I} , where $\mathbf{I} = \mathbf{J}^{-1}$) and $v^{(k)}$ is the corresponding right eigenvector. This sensitivity quantifies the magnitude of the species' expected response to long-term changes (i.e., press perturbations) and thus provides a dynamic measure of the structural resilience of individual species.

Because sensitivity changed over time for each species, we used the sensitivity measurement for the time period immediately before its disappearance in our analysis. The sensitivity for a given species is thus a function of the community in which it interacted immediately before extinction, and this was deemed more instructive than measuring sensitivity with respect to a community that existed long before a species' disappearance. For species that still exist in the Egyptian mammal community, we used sensitivity calculated for the last time bin (such that sensitivity is determined as a function of the modern community).

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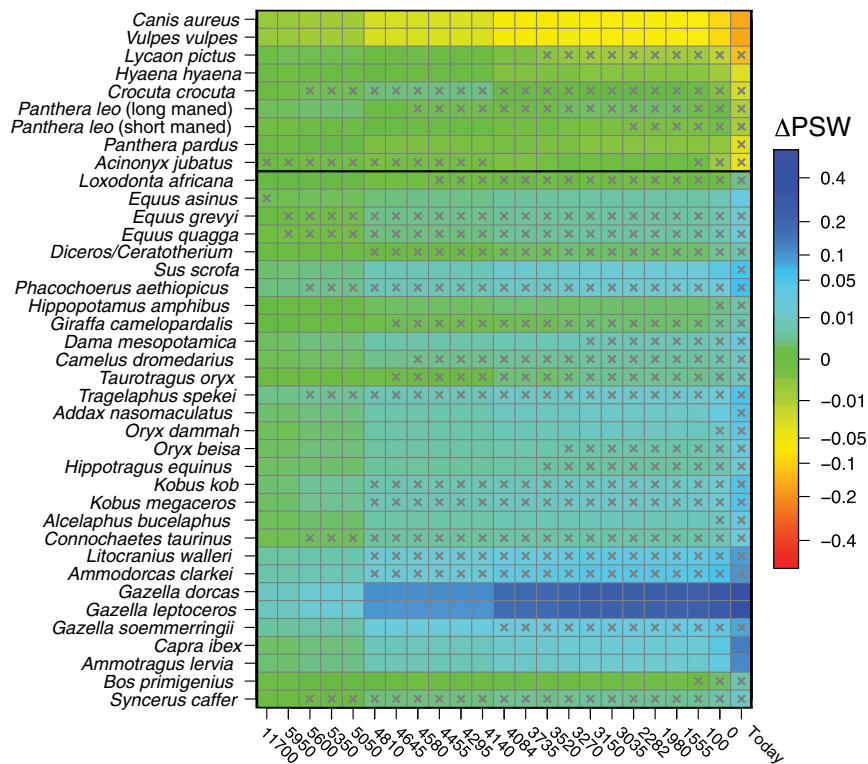


Fig. S3. The change in the proportion of stable webs (ΔPSW) as a function of species presence over time. Predator presence generally destabilizes trophic networks, whereas prey presence generally stabilizes trophic networks. An "x" symbol indicates that the species is locally extinct at a given time interval.

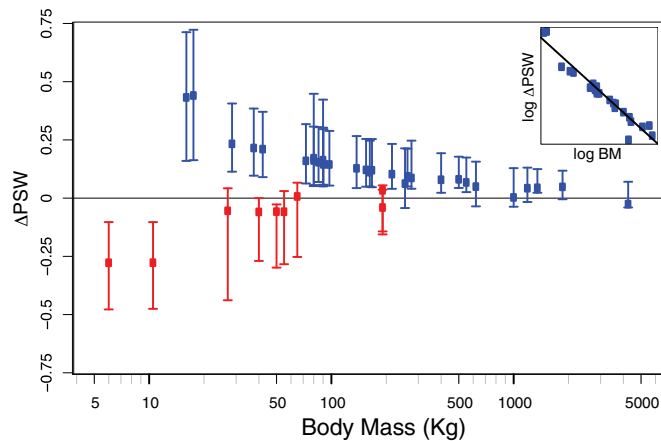


Fig. S4. The change in the proportion of stable webs (ΔPSW) as a function of species body mass. Body mass is closely related to the impact that each species has on PSW (inset: $R^2 = -0.97$). Smaller herbivores tend to be consumed by more predators, and their absence impacts the prey base of the network. In contrast, smaller carnivores tend to have disproportionately larger impacts on smaller herbivores, and their presence is generally destabilizing. Red indicates predator species, and blue indicates prey species.

