# Modern Lessons from Ancient Food Webs

*From the Cambrian Burgess Shale to ancient Egypt, food webs share surprising structural attributes. When redundancy is lost, the threat of extinction grows.*

Justin D. Yeakel and Jennifer A. Dunne

About 10,000 years ago, one could have mistaken the Egyptian landscape for that of East Africa today. Instead of vast arid deserts, the region north of Aswan held enough annual precipitation to support large herbivores that are strongly tied to standing bodies of water, including zebra, elephant, and rhinoceros. Lions, wild dogs, giraffes, and wildebeest filled out the savanna-woodland landscape, while the earliest pyramids were still thousands of years in the future. This was Egypt during the African Humid Period, which ended roughly 5,500 years ago, when the moisture supplied to equatorial Africa by seasonal monsoons declined, resulting in an increasingly arid climate.

It was just after the African Humid Period that urban centers began to develop around the Nile Valley. As humans shifted to agriculture and population densities grew, the local animal community became increasingly marginalized. The cumulative evidence of mammalian species present in Egypt before the end of the African Humid Period, taking into account paleontological and archeological observations, reveals 37 larger-bodied species occupying the region. Of those 37, only 8 remain today. This massive loss of biodiversity likely resulted from a combination of factors: habitat loss, hunting, and local and regional climate change.

Reconstructing how extinctions throughout the Holocene affected the patterns of feeding interactions between and among species (food web structure) and changes in species' abundance over time (dynamics) of the Egyptian mammal community is providing insight into how this ecosystem unraveled in the face of both climatic and human-induced pressures. But the observed community collapse in Egypt is just a small piece of a much larger story that describes the rise and fall of animal communities over the last 540 million years of multicellular life on Earth.

As with the analysis of ancient Egyptian ecosystems, a central goal in ecology is to understand how animal and plant communities arise, change, and respond to disturbances both large and small. To that end, ecologists have adopted new tools designed to investigate ecological networks and help us uncover and understand past extinctions and their community-level consequences in the hopes of predicting those in the future. To do so, we compare reconstructions of past ecological networks, such as food webs, to modern biological communities in an effort to identify similar drivers of change.

Analysis of the structure and function of modern and paleontological ecosystems falls within the bounds of complex systems science, a burgeoning suite of research topics that unite many aspects of mathematical, physical, and biological sciences. As researchers at the Santa Fe Institute in New Mexico—a not-for-profit organization centered around the study of complex adaptive systems—we think that our understanding of the underlying organization of natural systems is more complete when we unite the detailed but temporally limited knowledge of modern ecological systems with the wealth of information obtained from historical and paleontological contexts.

Recent investigations into the structure and dynamics of past and contemporary food webs has shown that there is a certain fixedness in the patterns of species interactions, independent of species identity, habitat, and time. However, this fixed structure appears to be sensitive to external disturbances, in particular large-scale events such as mass extinctions. The structural features common to food webs, as well as their sensitivity to disturbances, are relevant to our ability to predict (and perhaps engineer) the fate of modern biological systems. Integrating contemporary ecology with observations of the past will provide key insights into the future risks and uncertainties facing the multitude of species with which we share the planet.

### Food Webs in Deep Time

The behaviors of all evolutionarily successful organisms are constrained by two major dictates: They must pass down their genetic material, and they must acquire the necessary energy to do so. Plants and other organisms that can make their own food generate their own energy; herbivores, carnivores, and omnivores must find, capture, and consume their food to acquire energy. In a community of many species, the sum total of the patterns of interactions that characterize these processes can appear to be a chaotic tangle. In fact, they comprise a highly organized network of who eats whom.

*Justin D. Yeakel is an Omidyar Postdoctoral Fellow at the Santa Fe Institute. Jennifer A. Dunne is a professor and the Vice President for Science at the Santa Fe Institute. E-mail for Dr. Yeakel: jdyeakel@gmail.com.*

Griffith Institute/University of Oxford

**Depictions of animals, such as this hunting scene from one side of King Tutankhamun's Painted Box, built more than 3,000 years ago, document the mammal community of ancient Egypt over time. Piecing together ancient food webs can help us understand their fundamental properties.**

Determining how these communities function requires not only knowing which species are present and when, but how they interact. In a relatively recent development, ecological researchers are now borrowing tools from graph theory and nonlinear dynamics, analyzing the structure of ecological communities as networks, with nodes representing species or groups of similar species and links representing a type of interaction. For example, food webs are ecological networks where links represent a flow of biomass between two species, and the patterns of these feeding interactions determine the structure of the community.

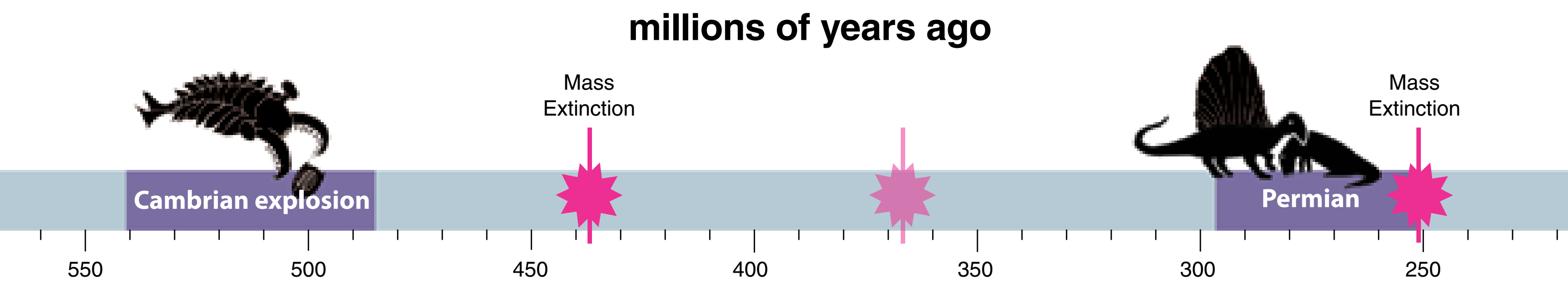
This nonrandom organization is in part responsible for the dynamics of the system: how long the system is expected to persist, whether it is sensitive to external disturbances, and to what extent it can recover after a disturbance has ended. In addition to a large and growing body of work on contemporary ecological networks, uncovering the structure of paleontological or historical communities provides a means to understand how they evolve and change over long periods of time, and to gauge how they respond to known large-scale changes in the environment.

Much like other kinds of real-world networks including social groups and power grids, research on ecological networks such as food webs shows that they have nonrandom structure. This property implies that there are underlying forces that constrain interactions between species, much as there are underlying—though different—forces constraining the formation of friendships in social networks or transmission lines in power grids. More surprising, food webs, independent of locality, habitat, and species composition, appear to share a number of regularities in their organization. For instance, the distribution of feeding links across species (the *degree distribution*, which characterizes the relative abundance of specialist or generalist feeders) is similar across food webs, such that most species are quite specialized and a very few are highly general feeders.

Because food-web structure is systematically sensitive to the numbers of species and links represented in the system, when this scale dependence is accounted for, the remarkable regularity of the degree distribution is uncovered. In this case, the general pattern across food webs only emerges when counts of feeding links for each consumer are normalized (divided by the average number of links per species in its food web).

The remarkable similarity of the structure of modern food webs gives rise to a tantalizing question: Have food webs always been this way? In other words, is the fundamental structure of food webs fixed? If food webs have an underlying structure that is maintained across different ecosystems over evolutionary time, there may be fundamental rules driving ecological interactions independent of species, habitat, or community. If some underlying mechanism guiding community structure exists, they might respond similarly to large perturbations. In this case, such knowledge could directly inform management of contemporary ecosystems in the wake of current or future perturbations.

To address these questions, one must look into the fossil record, and the Cambrian-era Burgess Shale fauna is about as far back in time as preservation allows for ecosystem-level analysis. The Burgess Shale was formed more than a half a billion years ago,




when a muddy embankment collapsed on a shallow sea community that now lies interred in the Canadian Rockies. The species in this ecosystem were shelled or plated invertebrates that crawled and swam along the shores of the Panthallasic Ocean, and have been a subject of intense study for much of the 20th century. Stephen Jay Gould remarked of the fossils in his book on the Burgess Shale, *Wonderful Life*: "They are grubby little creatures of a sea floor 530 million years old, but we greet them with awe because they are the Old Ones, and they are trying to tell us something."

The Burgess Shale fossils, which are remarkably well preserved, give a surprising amount of evidence about species' morphologies, evolutionary relationships, and ecological roles. As such, this ancient assemblage provides an exciting opportunity to test the notion of fixedness in the structure of food webs.

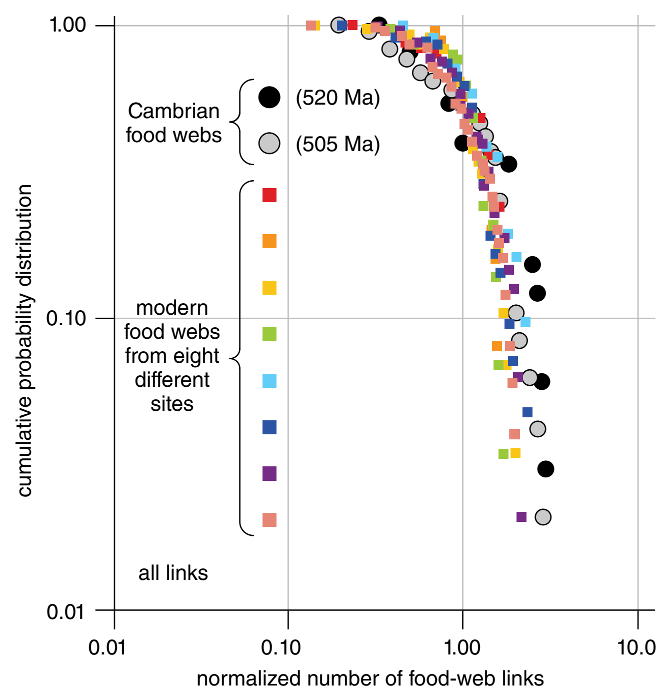
Reconstructing the feeding interactions of the Burgess Shale is no easy task, particularly with species whose strange morphologies inspire names such as *Anomalocaris* and *Hallucigenia*. However, it turns out that there are many ways to infer feeding from the Burgess fossils, for example from fossilized gut contents, from the matching of mouthparts to bite marks, and from constraints of body size. Many of the inferred feeding links can be assigned with relatively low uncertainty, and analyses of the resulting food web can account for how sensitive the assessment of structure is to whether low-certainty links are included or excluded.

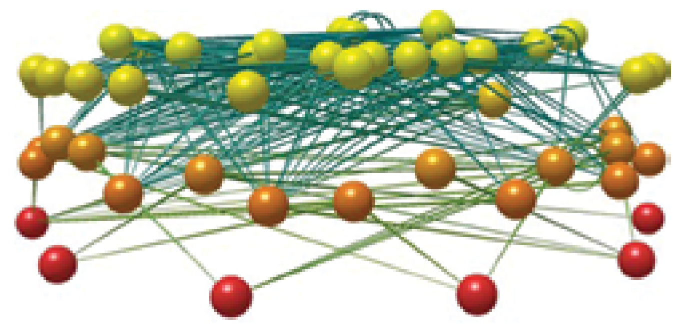
Although many Burgess lineages were evolutionary dead ends, and taxa giving rise to modern lineages looked different from their descendants, the patterns of feeding interactions are surprisingly similar to those of today. For example, food webs for both the Burgess Shale and an earlier Cambrian community in China (the Chengjiang Shale) had normalized degree distributions indistinguishable from modern ecosystems (*see figure below*).

The implications of this structural durability are profound. First, it suggests that the forces shaping the overall structure of species interactions in communities emerged early in the history of multicellular life. Second, it implies that the structure of food webs is largely independent of the identity and history of their component species. Third, it implies that the core food-web structure of ecological systems is—in the long run—relatively resilient to large-scale perturbations to the biosphere.

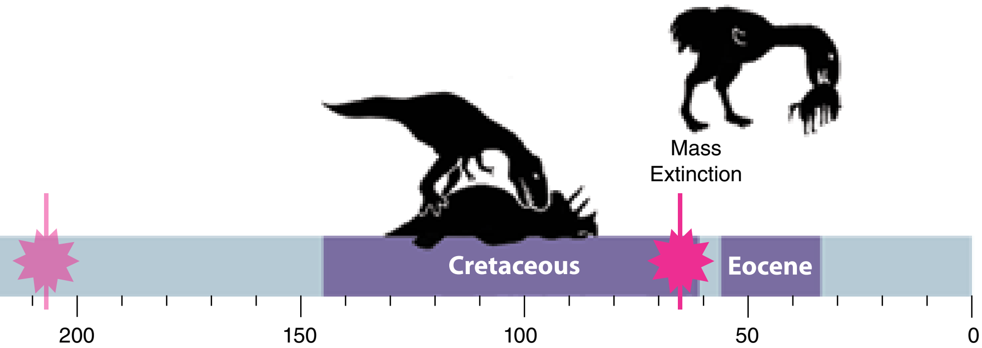
**Predicting Extinctions**

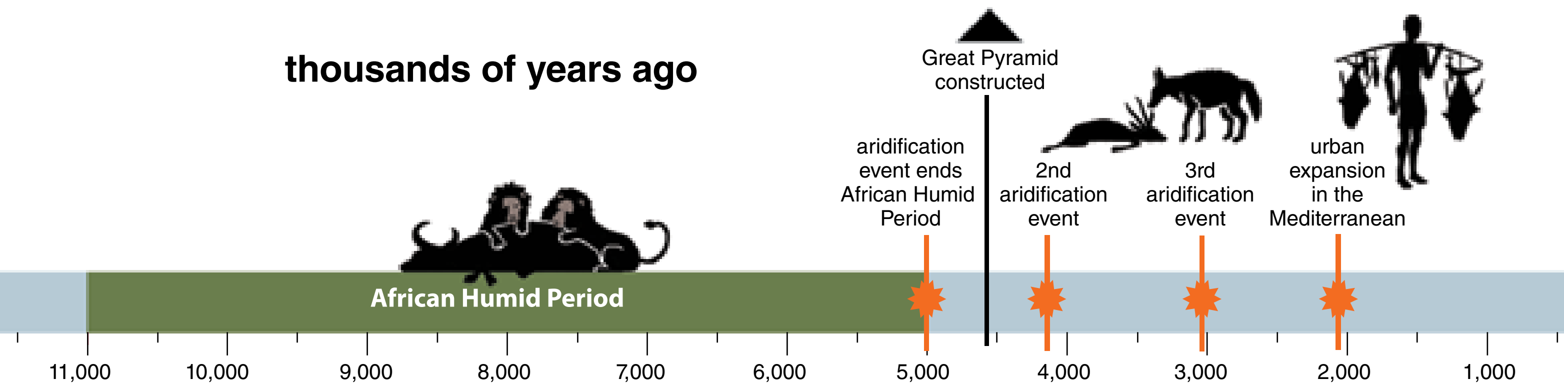
To what extent global perturbations disrupt ecological communities, and how these systems contract or reassemble after a perturbation, are topics that have important implications for modern ecosystems. For example, the end-Permian mass extinction (251 million years ago) marks the largest die-off in Earth's history, resulting in the extinction of 70 percent of terrestrial vertebrates and 96 percent of marine species. The early Triassic communities that emerged immediately after this extinction differed substantially from those in the Permian, having a greater diversity of amphibian versus amniote species.



**Food webs, such as the one from the Cambrian Burgess Shale shown above, are made up of nodes (spheres, representing species or groups of species) and links (green lines, representing who eats whom). Yellow spheres show top predators, whereas red spheres represent primary producers and decomposers. Food webs across geological time share remarkable structural similarities. The probability distribution at left shows the prevalence of the number of links across the nodes in a network, normalized by the size of the network. The graph shows that nodes with a large number of feeding links (those toward the right side of the x-axis) are rare. The shape of this curve portrays deep information about a network's structure, and the fact that all of these food webs across geological time have similar cumulative link distributions is incredible. Figures adapted from J. A. Dunne, et al., 2008.**




**Mass extinctions at the end of the Permian and Cretaceous, respectively (*left*), and the aridifications in ancient Egypt (*below*), disrupted food webs. These networks are more susceptible to extinction cascades after such large-scale events. After the mass extinctions, the food webs eventually recovered over millions of years—with new sets of species. Across time, food-web structure appears to be predictable.**

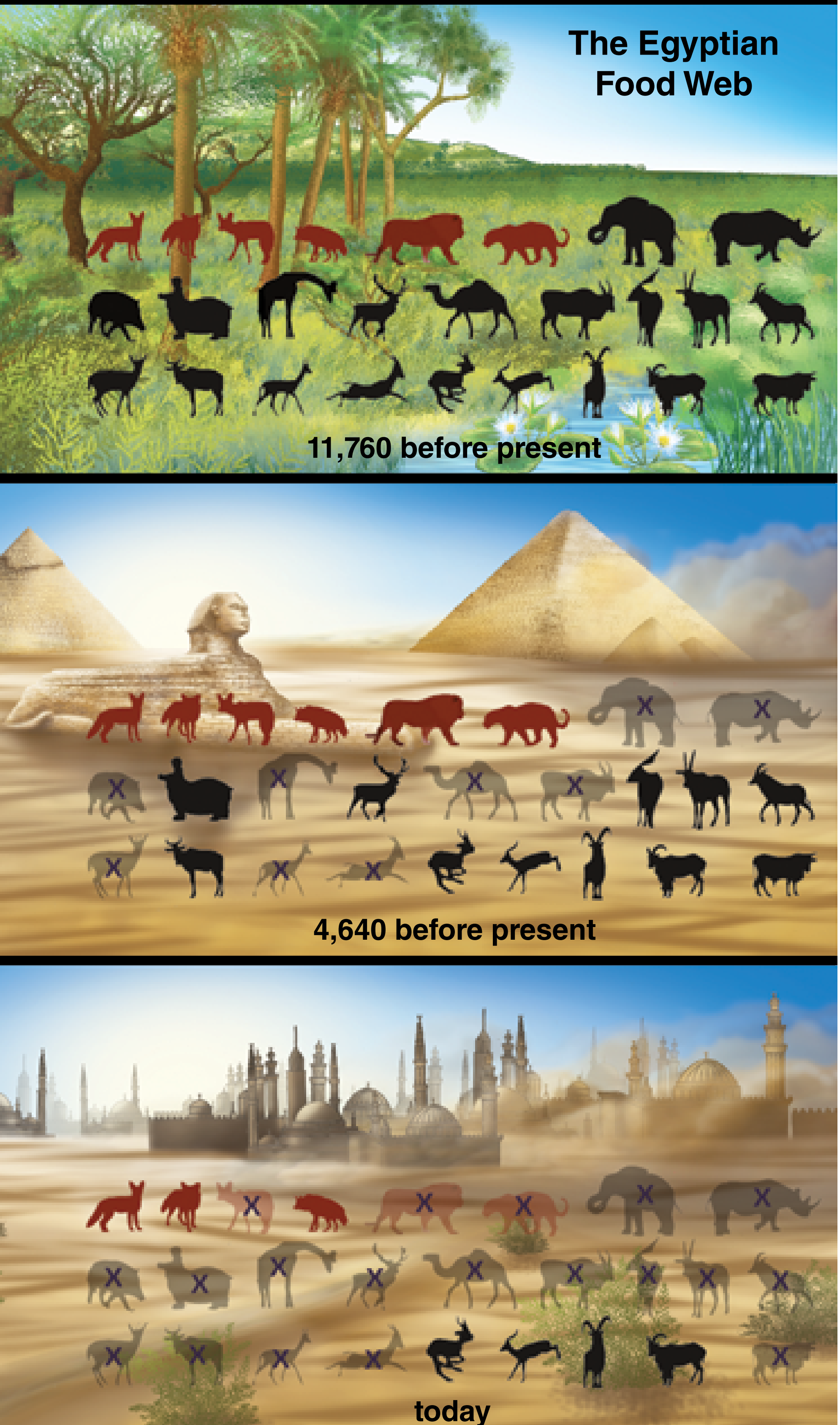
A second mass extinction that famously occurred 66 million years ago (the Cretaceous-Paleogene extinction) was likely initiated by an asteroid impact and resulted in the disappearance of nonavian dinosaurs, thus setting the stage for mammalian diversification. Prior to this extinction event, during the end-Cretaceous, was a large shift in dinosaur species composition, which may have left these systems vulnerable to the asteroid impact. Recent analyses led by Peter Roopnarine of the California Academy of Sciences and Jonathan Mitchell of University of Chicago, respectively, have shown that both post-perturbation communities (the Triassic following the Permian, and the end-Cretaceous) exhibited shifts in feeding interactions between surviving species that resulted in a restructured food web.

Such changes to food-web structure offer a way to study and measure altered ecosystem functioning, which can be estimated by calculating community robustness, the resistance of a system to change in the face of an imposed perturbation. Communities that absorb perturbations and remain relatively unaltered are considered robust, whereas those that are reactive and prone to reorganization or contraction are not. Accordingly, if the structure of the community is known, and given some basic assumptions regarding the dynamics that regulate how populations change over time, one can then determine the proportion of species that are likely to lose all of their food sources following a simulated disturbance that results in one or more primary extinctions. Food webs with a lower proportion of secondary extinctions based on these simulated disturbances are generally expected to be more robust than those with a higher proportion, because they are expected to be more resistant to extinction cascades.

Simulations of perturbations initiated at the base of the community straddling the end-Permian demonstrated that robustness was lower in the post-perturbation Triassic versus the pre-perturbation Permian. Similarly, the restructuring of end-Cretaceous communities led to a decline in robustness immediately before the Cretaceous-Paleogene extinction event, potentially creating the conditions for the mass extinction that followed. Although extreme perturbations tend to lead to subsequent domino-effect extinctions as the base of the food web is eroded, the patterns of interactions in pre-perturbation communities appear to be more resistant to the effects of smaller disruptions. This observation suggests that ecosystems in the Permian and mid-Cretaceous were more robust, whereas the structural organization of early Triassic and late Cretaceous communities was more easily unraveled. These restructured communities were likely fragile, such that successive environmental changes posed much greater risks to surviving species. The structure of food webs following large disturbances appears to increase the likelihood of additional extinctions, yet food web structure appears remarkably stable over large periods of time. Somehow biological communities must recover these structural attributes after disruptions—but how, and how quickly?

Events after the Cretaceous-Paleogene extinction offer clues. The disappearance of nonavian dinosaurs made room for the diversification of mammals, many species of which increased in body size, perhaps filling similar ecological roles as their extinct saurian cousins. The Eocene (56 to 33.9 million years ago) marked a pinnacle of mammalian evolution, witnessing the diversification of hooved mammals, carnivores, and early primates, among others. The Eocene mammalian community evidently was a direct recipient of the ecological space cleared by the events occurring before and during the Cretaceous–Paleogene extinction, but did this leave a lasting imprint on food-web structure?

Recent analysis of food webs for a 48-million-year-old small maar lake and the surrounding paratropical forest (now located in Germany) indicate that—in the long run—it did not. The food-web structure of these Messel Shale ecosystems (comprising 700 lake and forest taxa, thereby exceeding the resolution of extant food web data sets)




**The mammalian food web of Egypt lost its redundancy as the climate became more arid and human population densities increased. Most notably midsized herbivores—such as gazelles that link to the most carnivores—declined. Mammal species remaining in the food web today (*bottom panel*) are much more susceptible to disturbance than those in the rich assemblage of the African Humid Period (*top*). Some species are lumped with congeners here.**

revealed unambiguous similarities with modern ecosystems. This finding suggests that the structuring of food-web relationships observed within modern animal communities—also evident in the Cambrian—unfolded at least 18 million years after the asteroid impact.

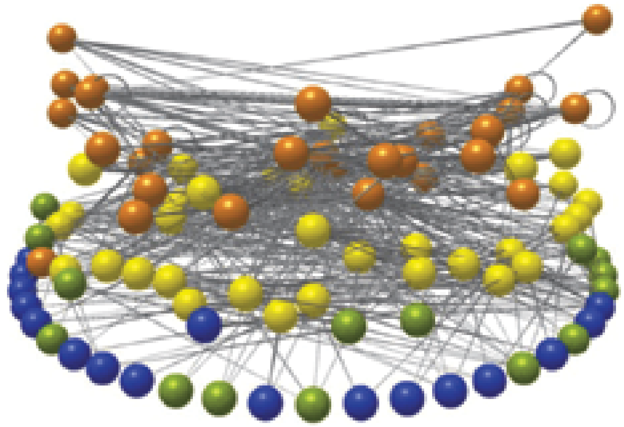
Despite a sensitivity to disturbance, the structural features common to both modern and paleontological food webs have survived five major and many minor extinction events. This structural reemergence points to consistent ecological mechanisms constraining interactions between species, despite the major evolutionary, environmental, and climatic transitions distinguishing the last half-billion years of Earth's history.

### Humans in Ancient Food Webs

There is increasing convincing evidence that we are currently nearing the brink of a sixth mass extinction, resulting from human impacts related to climate change, land-use changes, and other anthropogenic drivers of extinctions. If it is assumed that all threatened species go extinct within a century, and that such an extinction rate is maintained, it is expected that 75 percent of species will become extinct in about 250 to 500 years. Understanding the effects of large-scale disturbances on the structure and functioning of ecosystems thus requires higher resolution observations of biological communities over more recent timescales. In this case, we shift our focus from the fossil record to the historical record.

During the past 50,000 years, a combination of natural climatological and human-induced changes have shaped animal communities. The latter have become particularly significant in the last 15,000 years, as populations have migrated into unpeopled continents and islands, invading existing food webs. In some cases, hunter-gatherers may have migrated into ecosystems without significantly altering long-term food-web organization, as suggested by research from the eastern Aleutian Islands in the North Pacific.

In Beringia—a region including the Yukon, Alaska, northeastern Siberia, and the landmass now located on the seafloor of the Bering Strait—humans may have moved into ecosystems that had already been significantly reorganized by the Last Glacial Maximum, a large climatic perturbation that occurred near the end of the Late Pleistocene. In other cases, humans may have played a strong role in restructuring the ecosystem, evidenced by, for instance, changing interactions between seed dispersers and seed-bearing plants in the Pantanal, Brazil. Where humans settled into dense and expanding agricultural societies, the potential for effects on food-web structure, robustness, and functioning were high.



**The Eocene Messel Shale food webs, such as this one reconstructed from fossils in a small maar lake, show unequivocal similarities with modern ecosystems. Species are arranged along the vertical axis from primary producers (*bottom*) to higher order consumers (*top*), with color indicating types of organisms: vertebrates (*orange*), invertebrates (*yellow*), bacteria and fungi (*blue*), and plants and phytoplankton (*green*). From J. A. Dunne, et al., 2014.**

Ancient Egypt is one of the most extreme transitions to dense urban settlements in the historical period and is unusually well documented, making it a powerful case study of such effects, especially during a period of concurrent climatic change. The region around the Nile floodplain primarily supported nomadic pastoralists until the end of the African Humid Period 5,500 years ago. Permanent agricultural societies emerged soon after, perhaps in response to a landscape that was becoming increasingly arid. It was during the latter half of the Holocene (5,000 to 6,000 years ago), as the density of human populations increased and the landscape became dominated by desert-adapted flora, the historical animal community—comprising 37 larger-bodied mammals—was diminished to its current state of 8 species.

Unlike the extinction events of the deep past, the collapse of the Egyptian animal community was witnessed by settled human populations, with artisans who recorded what they saw in rock, stone tablets, ivory knives, and tomb walls. Although artistic recordings of animals served many purposes—from religious iconography to fanciful decorations—many depictions are of animals in ecological contexts. The incredible temporal resolution of these historical observations offers an unprecedented account of an animal community declining in response to human influences and a changing climate.

Researchers rarely glimpse transitional states in nature as they are seen in the Egyptian data. In the body of artistic work, depictions of species disappear at different times, likely as a consequence of local extirpation. Combining those data with evidence of species occupation in the fossil record permits a detailed reconstruction of how the community composition changed.

For example, the African elephant is present in early Holocene fossil deposits and is even depicted in rock engravings credited to Predynastic nomads, but it is not found or depicted in a local context afterward. The dama deer, thought to have migrated across the Isthmus of Suez during the Pleistocene, is found in contemporanious fossil deposits in Egypt and is depicted on mace handles and in hunting scenes until the 18th Dynasty (circa 3,270 years ago). Carnivores, including leopards, cheetah, wild dogs, spotted hyenas, and possibly two subspecies of lions, were ancient inhabitants of Egypt, but today are all locally extinct, having disappeared at different times during the past 6,000 years.

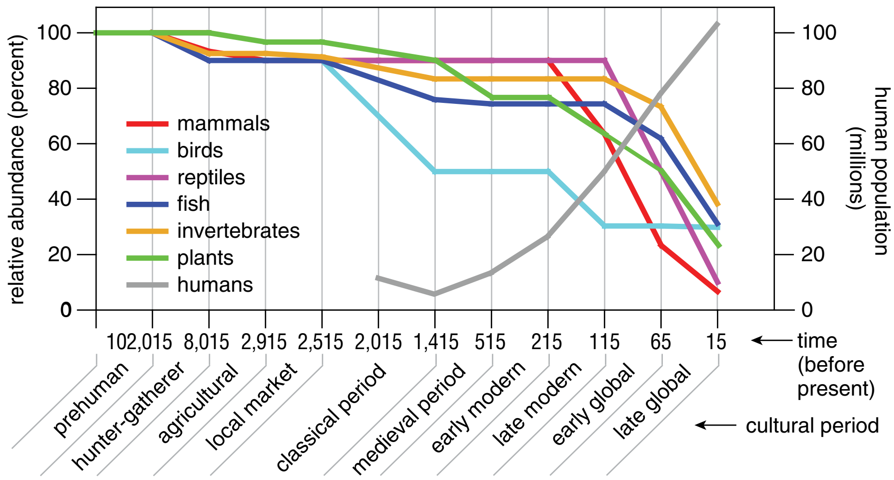
The rise of urban societies in Egypt occurred in an environment with a rich assemblage of mammalian species. Over the same time frame, there were three well-documented aridification events, each occurring over a relatively short period, that have been associated with major political disruptions and famines: The first, about 5,050 years ago, marked the beginning of the Egyptian Pharaonic state; the second, circa 4,140 years before present, was linked to the end of the Old Kingdom; and the third, about 3,035 years ago, marked the end of the New Kingdom as well as widespread famine in Egypt and Syria. The expansion of agricultural settlements and human densities in Egypt and a general shift toward aridity—itself marked by three significant climatic pulses—are well suited for examining how the structure and dynamics of animal communities were influenced by the cumulative effects of these events.

Ashmolean Museum, University of Oxford

**This siltstone ceremonial palette excavated from the ancient Upper Egypt city of Hierakonpolis is about 5,150 years old and shows predator-prey interactions in Egypt at that time. Framed by two wild dogs clasping paws, ostrich, hartebeest, wildebeest, ibex, oryx, and giraffe are depicted (as are several fictitious animals such as serpent-necked panthers).**

## Dynamics of Extinction

In the absence of highly resolved and comprehensive food-web data, one simple way to characterize the structure of a community is to compare the ratio of predator to prey species. This property has been shown to be relatively stable for long periods of time in the marine paleontological record, with intermittent shifts to new values. On the much shorter timescale considered here, the ratio of predators to




**The food webs of the Adriatic Sea became less diverse, less robust, and more unstable as human densities increased, especially after the rise of the Roman Empire a little over 2,000 years ago. Adapted from H. K. Lotze, et al., 2010.**

prey in the Egyptian community clearly shifted. It first increased (relatively more herbivores went locally extinct) from the end of the Pleistocene until approximately 3,035 years before present, and then decreased until 150 years ago (relatively more carnivores went locally extinct), and has since increased.

These shifts are too dramatic to be explained by random extinctions, indicating that there were different pressures on carnivores and herbivores over time. Three of the four largest shifts in the predator-prey ratio coincide with the notable aridification pulses at 5,050, 4,140, and 3,035 years before present, although it is not yet clear what caused the differential extinctions.

Earlier, we identified robustness as an important property of network dynamics, measured by imposing an extinction on a community and quantifying the ensuing effects. We now rephrase this general idea in terms of assessing the effects of applying a small perturbation to the sizes of populations within a community and assessing the resulting effects, rather than simulating the loss of any particular species as a whole.

If the system returns to its prior state after a simulated perturbation, it is considered *dynamically stable*, and if it does not, it is considered *dynamically unstable*. Dynamically stable communities are more likely to persist because they are assumed to be less reactive to changes in population size levied by external disturbances.

Quantifying dynamic stability of the Egyptian community over time revealed a surprising pattern. At the end of the Pleistocene, a period representing the height of mammalian species richness in Egypt, the food web was highly stable, meaning that the system was generally robust to perturbations. Throughout the Holocene, as the community faced a growing number of extinctions that altered its size, composition, and patterns of interaction, its dynamic stability declined steadily until a precipitous drop over the last 150 years. This change in stability was insensitive to variability in food web interactions and to potential error in the timing of extinctions.

The picture that emerges is straightforward: As the animal community in Egypt suffered accumulating extinctions (due to climate change, human influences, or both), its ability to absorb external impacts eroded—particularly in the last 150 years—leaving behind a fragile ecosystem that is a shadow of its historical state.

Although the ultimate causes of the Egyptian extinctions cannot be determined based on their observed trajectories, the cause of the decline in stability is more apparent: The system lost its redundancy. Food web interactions among larger-bodied mammals are, to a large extent, governed by body-size limitations: Smaller predators generally consume smaller prey, whereas larger predators can consume a larger range of prey body sizes. Accordingly, medium-size animals such as gazelle are vital components of a functioning food web, because they form the prey base of the system.

In Egypt during the African Humid Period, such animals were diverse and included gerenuk, sitatunga, ibex, Barbary sheep, and several species of gazelle, among others. Of those species, only four remain today, some of which (such as the rhim gazelle) are on the verge of extinction. Indeed, simulations of extinctions of the remaining herbivores predict a much larger impact on stability than the extinction of any one species historically. What was once a redundant guild of herbivores has today been reduced to a few species, the loss of which has a heightened influence on the stability of the animal community.

As paleobiologists examine an increasing number of food webs before and after game-changing perturbations, we find commonalities. Similar to analyses of the early Triassic and late-Cretaceous post-perturbation food webs, the mammalian community in Egypt appears to have become fragile after the trials of the Holocene. The loss of a few key species today may have a much larger effect on the community than at any time in the recent past. Changes to community functioning and dynamics in response to increasing human pressures can be seen in other impacted ecosystems as well, revealing that anthropogenic disturbances can alter food webs with lasting consequences.

The Adriatic Sea, 1,200 miles northwest of the Nile Valley, is one of the more productive basins in the Mediterranean. As in Egypt, human populations have been present along the shores of the Adriatic for nearly 100,000 years, and urban centers developed about 2,700 years ago. An abundance of paleontological and archeological sites in the region, as well as an incredible array of historical records pertaining to local natural history, permits reconstruction of both the occurrence and approximate abundances of species inhabiting marine and estuarine habitats throughout the Late Pleistocene and Early Holocene in the Adriatic.

Even more so than in Egypt, the cumulative evidence of species abundance in the Adriatic paints an alarming picture of human impacts on regional populations. Although humans have hunted and fished for resources in the Adriatic for tens of thousands of years, there is no evidence to suggest human-induced depletion of natural resources until the beginning of the Roman Empire. At that time, species' abundances declined precipitously, then recovered, and then fell again during and after the Middle Ages.

Although analyses of the Egyptian and Adriatic systems examined different food webs, some similarities emerge. First, both suffered from simplification of the food web. In Egypt, this simplification was dramatic, resulting in the local extinction of species. In the Adriatic Basin, although few species were completely extirpated, the abundances of many animals declined drastically—the majority being species near the top of the food web. These changes can be directly linked to overexploitation by human populations. Hence, the Adriatic food web suffered a decline in connectance, meaning that the average number of feeding interactions per species declined over time. This, in turn, led to a reduction in robustness as defined by the percentage of secondary extinctions following an initial perturbation.

The message seems clear: The nature of human-induced impacts on animal communities is qualitatively different today than in the distant past, likely due to the efficiency with which large human populations extract resources from the environment, as well as the degraded condition of contemporary animal communities compared to their historical state. We must take these differences into consideration, particularly if we hope to develop a framework for predicting how communities will change in the future.

**A Bridge to Somewhere**

A recent survey of bridges in the United States revealed that 3 percent (or about 18,000) were deemed fracture critical, meaning that the failure of a single component could lead to failure of the entire structure. As with a bridge, the stability of a food web is determined by the presence and functioning of its component parts. As bridges may collapse when enough components fail, large perturbations appear to lower the robustness of food webs and may require evolutionary time to recover, whereas accumulating extinctions appear to increase the likelihood of dynamic instability. However, the comparison of food webs with bridges is not a perfect one. A bridge that fails ceases to be a bridge; a food web that is unstable remains a food web, though one that is less diverse than its ancestral state.

The imperfection of the bridge analogy points to an important ecological truism: Biological communities are not fracture critical—they will exist as long as there is life. However, they will certainly change, and it is evident that our expanding human reach will continue to introduce new challenges. From a perspective of self-preservation, biological diversity is the raw material from which agriculture, medicine, and all natural resources—including the air that we breathe—derive. Maintaining intact communities of interacting species harbors this diversity, and is thus a requirement for the survival of human societies. So, the question is not whether the bridge will fail, but whether the bridge goes anywhere we would like to go.

**The loss of a few key species today may have a much larger effect on the community than at any time in the past.**

From the invertebrate-dominated Cambrian-era Burgess Shale, to the diverse mammalian faunas of the Eocene, to the desert-adapted communities of Egypt following the African Humid Period, there is an underlying thread that unites the patterns of interactions between species and their responses to disturbance, spanning half a billion years of complex life on Earth. This startling observation not only suggests that there exist fundamental rules determining how biological communities organize, but that disruptions to these systems from external events such as climate change may be predictable.

Understanding the similarities that unite modern and ancient food webs is an ongoing area of intense research, and stands to illuminate the principles that dictate how communities both assemble and unravel. Such knowledge may also aid conservation efforts by enabling identification of species that might have an unexpectedly large influence on ecosystem function. If such a predictive understanding of community dynamics is discovered and acted upon, we might avoid the potentially multimillion-year timescales generally associated with the recovery of food webs in the fossil record.

The ability to predict which species or which communities are most susceptible to current and future disturbances lies at the intersection of ecology and conservation, though the answers are elusive and whether such an understanding is possible is still an open question. Despite this lack of surety, what is clear is that incorporating lessons from the past is of vital importance if we are to maintain the current diversity of the natural world in the face of an uncertain future.

**Bibliography**

Barnosky, A. D., et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471:51–57.

Dunne, J. A. , C. C. Labandeira, and R. J. Williams. 2014. Highly resolved early Eocene food webs show development of modern trophic structure after the end-Cretaceous extinction. *Proceedings of the Royal Society B* 281:20133280.

Dunne, J. A., R. J. Williams, N. D. Martinez, R. A. Wood, and D. H. Erwin. 2008. Compilation and network analyses of Cambrian food webs. *PLoS Biology* 6:e102.

Lotze, H. K., M. Coll, and J. A. Dunne. 2010. Historical changes in marine resources, food-web structure and ecosystem functioning in the Adriatic Sea, Mediterranean. *Ecosystems* 14:198–222.

Maschner, H. D. G., et al. 2009. An introduction to the biocomplexity of Sanak Island, Western Gulf of Alaska. *Pacific Science* 63:673–709.

Mitchell, J. S., P. D. Roopnarine, and K. D. Angielczyk. 2012. Late Cretaceous restructuring of terrestrial communities facilitated the end-Cretaceous mass extinction in North America. *Proceedings of the National Academy of Sciences of the U.S.A.* 109:18857–18861.

Pires, M., et al. 2014. Reconstructing past ecological networks: the reconfiguration of seed-dispersal interactions after megafaunal extinction. *Oecologia* 175:1247–1256.

Roopnarine, P., K. Angielczyk, S. Wang, and R. Hertog. 2007. Trophic network models explain instability of Early Triassic terrestrial communities. *Proceedings of the Royal Society B* 274:2077–2086.

Yeakel, J. D., P. R. Guimarães Jr, H. Bocherens, and P. L. Koch. 2013. The impact of climate change on the structure of Pleistocene food webs across the mammoth steppe. *Proceedings of the Royal Society B* 280:20130239.

Yeakel, J. D., et al. 2014. Collapse of an ecological network in Ancient Egypt. *Proceedings of the National Academy of Sciences of the U.S.A.* 111:14472–14477.

For relevant Web links, consult this issue of *American Scientist Online:*

http://www.americanscientist.org/issues/id.114/past.aspx