FAUNAL DECLINE

Collapse of terrestrial mammal food webs since the Late Pleistocene

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Food webs influence ecosystem diversity and functioning. Contemporary defaunation has reduced food web complexity, but simplification caused by past defaunation is difficult to reconstruct given the sparse paleorecord of predator-prey interactions. We identified changes to terrestrial mammal food webs globally over the past ~130,000 years using extinct and extant mammal traits, geographic ranges, observed predator-prey interactions, and deep learning models. Food webs underwent steep regional declines in complexity through loss of food web links after the arrival and expansion of human populations. We estimate that defaunation has caused a 53% decline in food web links globally. Although extinctions explain much of this effect, range losses for extant species degraded food webs to a similar extent, highlighting the potential for food web restoration via extant species recovery.

Human activities have caused global extinction or local extirpation of many animal species (*1*). Habitat loss, direct exploitation, invasive species, and other global change drivers have contributed to recent defaunation (*2*), which in turn has caused cascading impacts on biodiversity and ecosystem functioning through disruption of food webs (*1*, *3*, *4*). Yet defaunation, and the potential for food web disruption, is not only a contemporary phenomenon. Declines in species diversity since the last interglacial period (~130,000 years ago) are well known for groups such as terrestrial mammals (*5*, *6*). Although there are persistent discussions on the relative roles of humans, climate, and their interactions as drivers of these extinctions, the spatiotemporal pattern of declines strongly suggests a major human role (*5*, *7–9*). The past, and ongoing, selective loss of large-bodied mammals has caused a marked downsizing of mammal assemblages relative to the preceding 30 million years (*7*). The strong ecological effects of human-induced food web disruption observed in recent decades (*10*) raise questions regarding the global magnitude and timing of food web changes that have resulted from extinctions, local extirpation, and species introductions throughout human history and prehistory. However, evidence of species-specific predator-prey interactions has seldom been preserved in the fossil record (*11*), and the scarcity of fossil evidence has prevented direct quantification of past defaunation's effects on food webs.

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When direct observations are unavailable, researchers can construct food webs by modeling predator-prey interactions; ecologists commonly use two approaches. First, trait-matching models examine how an ecologically relevant trait of predator or prey species relates to observed interactions. Body mass is recognized as a key trait, and the ratio of predator to prey body mass is a central determinant of food web interactions (*12–14*). By fitting a model using interaction observations and body mass ratios, researchers can estimate interactions given masses of candidate predator and prey species (*15–18*). Second, phylogenetic models rely on closely related species preying on, or being preyed on by, other sets of closely related species. Using observed interactions from the field or literature, researchers may estimate that a predator that is known to prey on one member of a genus would also prey on another member of the genus (*19*, *20*). A third approach, which extends the trait-matching approach to multiple traits and complex relationships among them, uses machine learning algorithms trained on observed interactions to predict interactions among candidate species on the basis of their traits (*21*). For each of the three approaches, researchers use a simplifying assumption that species have similar interaction determinants over space and time. This allows researchers to predict food webs given any scenario of species composition, which can include reconstructing food webs that likely occurred under past species composition, generating current food webs in regions where food webs have not been recorded directly, and forecasting future food webs under altered species composition. Most existing applications have reconstructed food webs over time at regional scales using body mass data (*15*, *17*, *22*).

Here, we provide a global reconstruction of terrestrial mammal food webs by modeling predator-prey interactions through a synthesis of data on observed interactions and species traits. Although food webs involving only mammals represent just a portion of the food web encompassing all species, a spatiotemporal reconstruction of mammal food webs is possible because of the strong fossil record and data on modern predator-prey interactions available for this group (*23*). We assembled a global database encompassing >17,000 unique predator-prey records for co-occurring pairs of extant mammal species from the scientific literature and existing databases of predator-prey interactions (*24*, *25*). We used a synthesis of trait databases (*26*) covering extant and extinct mammals to characterize each species based on variables related to morphology, life history, and ecology (*27*). To assess the ability to predict predator-prey interactions globally using each of the approaches described above, we built a model using 75% of the records and tested its predictive performance on the 25% of records withheld (table S1). The deep learning model strongly outperformed the commonly applied approaches that are based on body mass ratio or genus-level information; when fitted using the full dataset, it achieved 90% accuracy [area under curve (AUC) = 0.93; kappa = 0.52; true skill statistic (TSS) = 0.69].

To illustrate how the deep learning model can be used to reconstruct food webs, Fig. 1 demonstrates, for several locations, food webs generated under alternate scenarios of mammal species composition. The two scenarios shown here represent extant species' current ranges or ranges of both extant and extinct mammals as they would occur today in the absence of human-linked extinction, local extirpation, or introduction from the Late Pleistocene to the present day (*6*). The range reconstructions leverage historical records and fossil evidence to model ranges while accounting for range shifts due to climatic changes since the Late Pleistocene (*27*). Comparisons among species composition scenarios allow us to assess how defaunation at sites worldwide has led to the simplification of food webs.

Having developed the capacity to generate food webs given alternate scenarios of species composition, we sought to quantify how extinctions have affected food webs over time and to assess food web resilience to extinction. We used estimates of extinction dates from the fossil record (*5*) and focused on species extinction at regional scales because detailed temporal estimates of range changes are unavailable for most species. Figure 2 shows change over time, averaged within each region, in two basic measures of food web complexity: the number of species participating in a food web, and the number of food web links (*28*). To examine whether a reduction in the number of species present led to a decline in food web properties different from that expected by chance, we compared observed changes in food web complexity to a null model in which the same

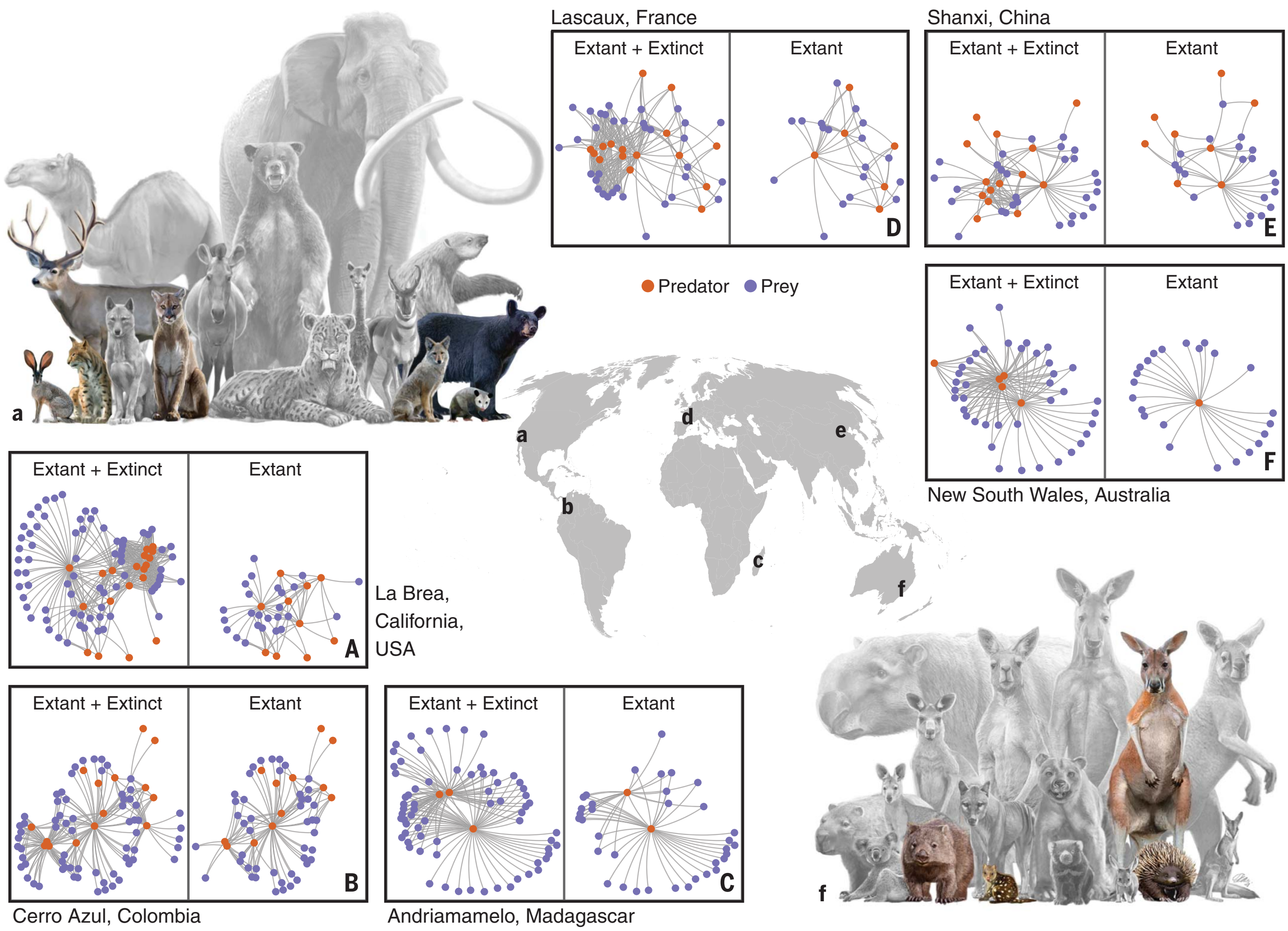

Fig. 1. Comparing terrestrial mammal food webs under current species composition and under species composition unaffected by extinction, local extirpation, and introduction. Lowercase letters correspond to locations on the map and illustrations of species composition, with color showing species that are extant at the site and grayscale indicating species that are extirpated or extinct.

number of extinctions was simulated, but in which the identities of mammal extinctions were randomized. This allowed us to distinguish between two alternatives regarding the resilience of food webs. If food webs have been resilient under extinction pressure either as a result of trophic redundancy (*29*) or because extinction is less likely for highly interactive species, then food web complexity would decline less than what would be expected by chance under random extinction. Alternatively, disproportionately greater extinction of highly interactive or functionally distinct species (*30*) would cause greater declines than expected by chance, indicating food web collapse (*31*). Thus, although food webs would be expected to decline to some extent given reduced species richness, the null model allows us to evaluate quantitatively whether observed food webs exhibit resilience (i.e., declining statistically less than the null model as reflected by nonoverlapping confidence intervals), a proportionate decline (i.e., declining as expected by chance), or food web collapse (i.e., declining more than expected by chance). Note that the food webs include only species that interact with at least one other mammal species; thus, the number of species participating in a food web may decline faster than the number of species present if a species that is present no longer participates in the mammal food web (e.g., a species no longer co-occurs with its mammalian predator).

We found that in most cases, the observed declines in each region either started to be statistically more severe than the null expectation, or became more severe still, after the arrival of *Homo sapiens* (*8*) or European colonization (Fig. 2). Notably, the two regions occupied by hominins prior to *Homo sapiens* (Africa and Eurasia) exhibited the smallest-magnitude declines, and these declines differed little from the null expectation until industrialization. One potential explanation for the relative resilience of African and Eurasian food webs compared to other regions may be more gradual coevolution among hominins and other mammals in these regions (*32*). Comparing observed extinctions to the null model, we estimate that food webs globally have lost 57% more links and 60% more species than would be expected by chance. Extinct species on average interacted with more species than did extant species (fig. S1A; $F_{1,4001} = 180$, $P \ll 0.0001$), and their loss has contributed to mammal food web collapse.

We next sought to understand how contemporary food webs have been shaped by past extinctions and range changes. We compared food webs constructed under alternate scenarios of species composition to determine the cumulative effects of extinction and range changes. To isolate the effect of extinction, we compared food webs composed of only extant species to food webs composed of both extant and now-extinct mammals. In both cases, we generated food webs as though all species filled their natural ranges (*27*), with ranges unaffected by range loss or anthropogenic species introductions (*6*). The largest declines

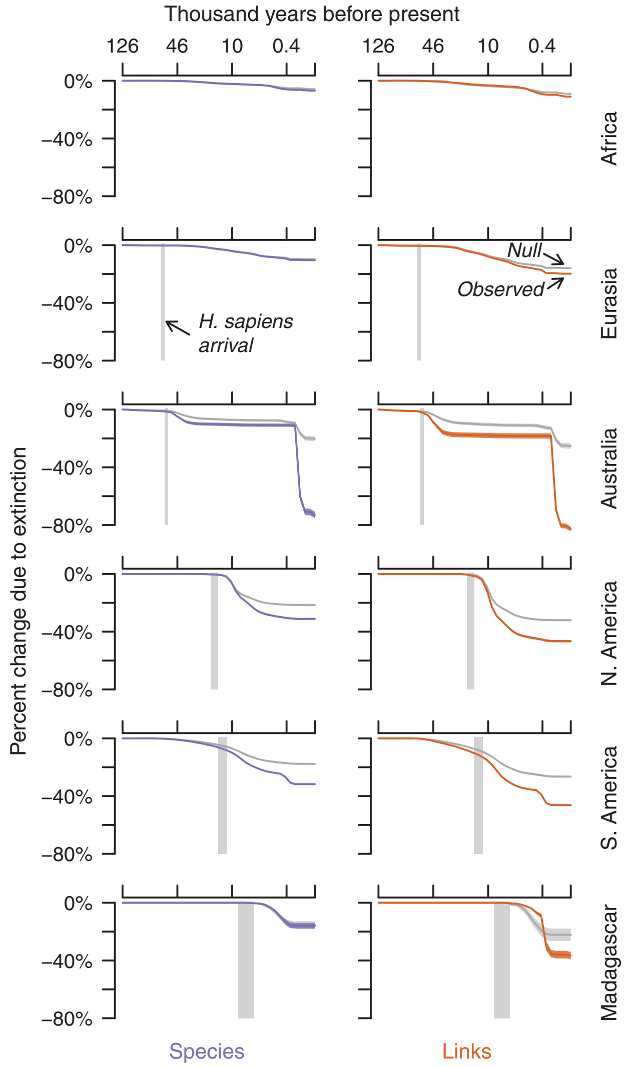

Fig. 2. Change due to extinction over the past 130,000 years in the number of participating species and links in reconstructed terrestrial mammal food webs. Lines show average percent change, and confidence intervals indicate ±1.96 standard errors, with null model results shown in gray.

in species and links due to extinction alone were in the Americas, Australia, and Madagascar (Fig. 3, A and B). In these areas, the concomitant decline in links per species indicates that extinct species were disproportionately important for food web complexity (Fig. 3A and fig. S1A). Attempts to fully restore food webs in these areas would require replacements by functionally equivalent species native to other regions (*33*). At the region scale, extinctions have caused average declines of 7% to 73% in the number of participating species and average declines of 11% to 83% in food web links (Fig. 3B). Globally, we estimate that extinctions alone have caused a 20% decline in the number of species participating in terrestrial mammal food webs and a 29% reduction in food web links.

To assess the net effects of species range changes on food web complexity, we compared food webs consisting of extant species in their current ranges to food webs constructed for extant species as though their ranges were unaffected by local extirpation or anthropogenic species introduction (*6*). We found that further losses were widespread, also greatly affecting areas whose food webs were less affected by extinctions, including Africa and southern Eurasia (Fig. 3). Relative declines due to range changes, considering extant species only, were 7% to 76% across regions in the number of participating species and 13% to 82% in food web links (Fig. 3A), amounting to a further 20% global decline in participating species and 35% in links. Declines in links per species due to range changes indicate that species that experienced distributional contractions were disproportionately interactive within their former ranges (Fig. 3A and fig. S1B; $F_{1,3765}$ = 114.5, $P \ll 0.0001$). When cumulative effects of extinctions and range changes were combined at the region scale and compared against the scenario where both extinct and extant species filled their natural ranges, average declines in participating species ranged from 27% to 94% and in links from 45% to 97% (Fig. 3B). At the global scale, we estimate that late-Quaternary defaunation has resulted in mammal food webs on average consisting of 35% fewer species and 53% fewer links.

Lastly, we considered how the potential future extinction of endangered mammals would affect food webs globally. Relative to current species composition, the largest further losses in the number of participating species and the number of food web links would occur in areas including the Arctic and tropical and subtropical regions of Africa and Asia (Fig. 3A). In most areas where food webs are threatened by species loss, endangered species extinction would decrease the number of links per species (Fig. 3A). In other words, endangered species are central to preserving food web complexity in such areas. Exceptions include equatorial central Africa and parts of southeast Asia, where endangered species extinction would reduce the number of species and food web links but would not substantially alter links per species. Generally, endangered species interact more broadly than extant nonendangered species (fig. S1C; $F_{1,3765}$ = 19.0, $P \ll 0.0001$), indicating their greater structural importance within food webs. Across regions, endangered species extinction would cause 10% to 67% further reductions in participating species and 15% to 80% in links beyond that incurred by existing defaunation (Fig. 3A), amounting to a further 14% global reduction in participating species and 21% reduction in food web links.

Our reconstruction of terrestrial mammal food webs allowed us to estimate the global magnitude of mammal food web collapse since the Late Pleistocene. We found that although only ~6% of terrestrial mammal species have gone extinct since the Late Pleistocene (*6*), more than half of mammal food web links have disappeared. Although much of the global food web simplification has resulted from extinctions that occurred centuries to millennia ago, range contractions in surviving species explain a similar magnitude of simplification. Controlled and natural experiments show that food web complexity supports ecosystem resilience and functioning (*10*, *34*, *35*), and ecological network simplification reduces ecosystem functioning (*36*). We found that the species most affected by defaunation are among the strongest contributors to food web complexity. Recovering food web complexity could be achieved with natural recolonization (*37*) and reintroduction (*38*, *39*) of native mammals to their historic ranges, or with non-native functional analogs where necessary and appropriate (*33*, *39*). Critical roles played by species affected by range contractions and recognized as endangered further underscore the need for their conservation to sustain food webs, as well as the strong potential for the restoration of food webs in the Anthropocene through recovery of these species to their historic ranges (*40*).

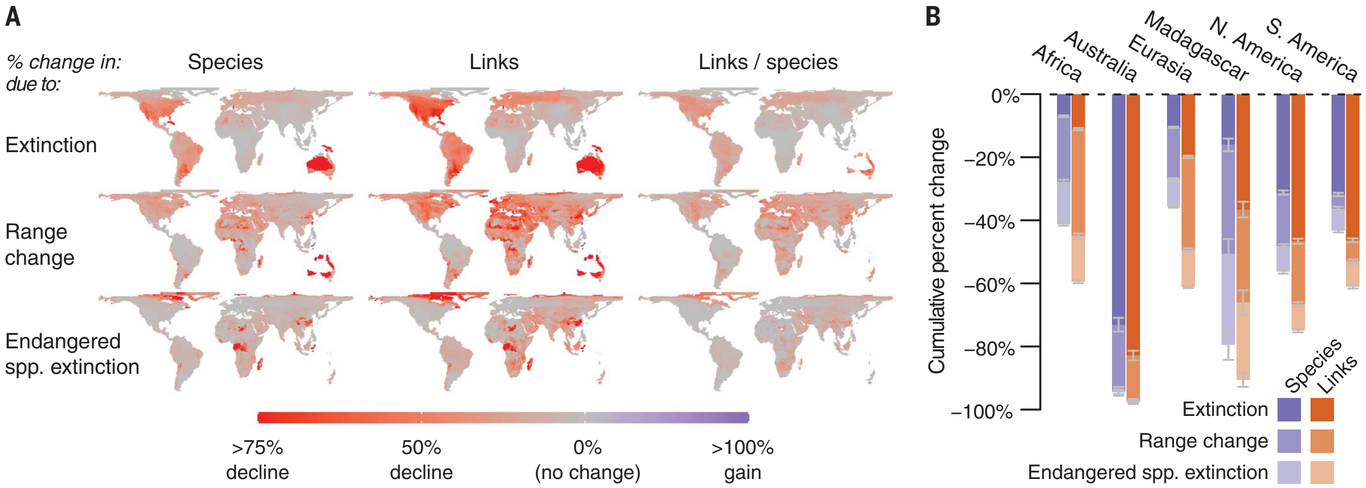

Fig. 3. Attributing change in food webs to extinction and range changes and assessing threats due to species endangerment. (**A**) Color scale indicates relative percent change in the number of participating species, number of links, and links per species due to extinction, the further percent change due to current range losses and species introductions, and the percent change relative to current species composition under potential future extinction of endangered species. Note that relative percent change values can sum to >100%. (**B**) Region-level absolute percent changes, with ±1.96 standard error bars in gray, presented relative to food webs under species composition unaffected by extinction or range changes.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abn4012
Materials and Methods
Supplementary Text
Figs. S1 to S3
Table S1
References (*42*–*73*)

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Depauperate webs
In the last 50 years, 60% of animal populations have been pushed to extinction. Although already tragic, such losses also have profound impacts on the ecological integrity of biological systems. Fricke *et al*. looked across mammalian communities globally over the past 130,000 years and found that more than half of the links, or connections, within these communities have been lost (see the Perspective by O'Gorman). This loss is due to extinction of species but also to a reduction in the ranges of extant species because the total numbers of individuals within a species have also declined. Such losses could have profound impact on the long-term persistence and function of ecosystems. —SNV

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