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Consequences of the Megafauna Extinction: Changes in Food Web Networks on the Edwards Plateau Across the Pleistocene–Holocene Transition

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ABSTRACT

Aims: Today, we are experiencing rapid biodiversity loss due to climate change and human impacts. Such biodiversity loss is not only harmful to the environment but can also alter the composition of communities and the interactions of their members. The late Pleistocene experienced a drastic loss of large-bodied mammals which resulted in significant changes in community structure due to changes in body size, diet, and species associations. However, the effect of climate change on species interactions and community structure across the Pleistocene–Holocene transition remains poorly understood.

Location: Edwards Plateau, Texas.

Time Period: Late Pleistocene–Holocene.

Major Taxa Studied: Terrestrial Mammals.

Methods: Using a robust data set on mammal species composition, stable isotopes, and body size, we constructed ecological networks for 16 time intervals across the last 22,000 years on the Edwards Plateau, Texas. We compared the structure and shifts in the food web over time using modularity and an index of node overlap and segregation.

Results: We found that node overlap and connectance increased while modularity decreased over time. Spearman-Rank correlation analyses indicate that changes in all network metrics were not driven by changes in species richness across time, nor were they driven by climate change. The degree of node overlap and connectance also shifted dramatically across the Pleistocene–Holocene transition and was significantly different from null model expectations in the Holocene but not in the Pleistocene.

Main Conclusions: These results suggest that the transition from a diverse and compartmentalised network to a network of less complexity with an overlap of interacting species may have been driven by other factors that altered the food web. This implies that the change in mammal food web structure of the Edwards Plateau was mainly a consequence of the megafauna extinctions and not coupled with climate change.

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1 | Introduction

The late Pleistocene (22,000–11,700 years) was a unique period where approximately 47% of large-bodied (megafauna) species went extinct globally (Barnosky et al. 2004; Smith et al. 2018). This extinction event especially impacted North America where ~76%–80% of megafauna species were lost within a short window at the terminal Pleistocene (Martin and Wright 1967; Martin and Klein 1989; Barnosky et al. 2004; Lyons, Smith, and Brown 2004; Smith et al. 2016). Several hypotheses have been proposed to explain the extinction including climate change (Graham and Grimm 1990; Graham et al. 1996; Graham and Lundelius 1984), human overhunting (Martin 1973, 1990), and disease (MacPhee and Marx 1997; Lyons, Smith, Wagner, et al. 2004). These hypotheses are still being debated, in part, because most fossil localities are not well-resolved enough to disentangle the potential drivers. Nonetheless, ongoing research suggests human impacts were a driving factor (Barnosky et al. 2004; Lyons, Smith, and Brown 2004; Lyons, Smith, Wagner, et al. 2004; Koch and Barnosky 2006; Smith et al. 2019).

Regardless of the mechanism, megafauna extinction likely had major consequences for the structure of ecological communities. Modern megafauna are ecosystem engineers who have an important role in structuring habitats and facilitating interactions between species (Janzen and Martin 1982; Owen-Smith 1988; Smith et al. 2016; Pires et al. 2020; Pires 2024). For example, they help maintain the diversity of plant species, often suppress woody regeneration, and promote nutrient cycling throughout the ecosystem (Owen-Smith 1988; Dublin et al. 1990; Bakker et al. 2006; Goheen et al. 2010, 2018; Doughty, Faurby, and Svenning 2016; Doughty, Roman, et al. 2016; Pires 2024). Large apex predators influence the abundance of herbivores, mesopredators, and other predators through top-down control over their ecosystem (Johnson 2009). Extinct megafauna likely played similar roles, suggesting their extinction may have heavily impacted ecosystems. Indeed, recent work reveals that the loss of megafauna species had cascading effects in communities such as shifting diets, changes in community assembly, and altering body size distributions (Turner 1992; Lyons, Smith, and Brown 2004; Lyons, Smith, Wagner, et al. 2004; Meloro et al. 2007; Raia et al. 2007; Lyons and Smith 2013; Smith et al. 2016, 2019, 2022, 2023; Tomé et al. 2020; Pires et al. 2020; Pires 2024). Their loss also led to significant changes in mammalian food webs and ecological networks that were less resilient to future extinctions, such as changes in links between species in food webs, stability and the community's ability to recover after megafauna loss (Fricke et al. 2022; Pires et al. 2015, 2020; Nenzén et al. 2014; Pires 2024).

Concurrently with the megafauna extinction, North America experienced climatic shifts, transitioning from a cool climate to a warmer climate that was punctuated by episodes such as the Younger Dryas cooling period (Alley 2000; Clark et al. 2012; IPCC 2014). Climate changes have the potential to alter the composition of communities and the species interactions within them by affecting the environment they inhabit (Lyons 2003, 2005; Blois et al. 2010; Smith et al. 2016; Tóth et al. 2019; Tomé et al. 2020). Alongside these climatic shifts, humans were present in North America perhaps as early as 23,000–21,000 years ago (Bennett et al. 2021; Pigati et al. 2023), although they were likely not widespread until >16,000 cal year BP (Surovell et al. 2022; Potter et al. 2022). Considering the environmental and ecological changes occurring during the megafauna extinction, the consequences of the extinction event may provide a baseline understanding of what may happen to future mammal communities if we lose our remaining megafauna.

Ecological networks, representations of the interactions between species within a community, provide an avenue to quantify ecological changes. Generally, we can quantify potential interactions based on a combination of body size, abundance, diet and other important traits of taxa in a community (Montoya et al. 2006; Meloro et al. 2007; Raia et al. 2007; Fortuna et al. 2010; Bascompte 2010; Delmas et al. 2019). In particular, food web networks have been widely used in ecological studies to examine predator–prey interactions, the structure of communities, ecosystem function, and more (Dunne et al. 2002a; Pascual and Dunne 2005; Montoya et al. 2006; Ings et al. 2009; Pires et al. 2020; Pires 2024). Fundamental structural properties of food web networks such as network size (i.e., species richness) and network connectance (i.e., proportion of species pairs that have trophic interactions) have important effects on function, such as robustness to species loss (Dunne et al. 2002b; Gilbert 2009). Another important structural property of food webs that has gained much attention is compartmentalization, which measures the degree that groups of species are more likely to interact with each other rather than with other individuals or groups in the food web (May 1972; Girvan and Newman 2002; Krause et al. 2003). The degree of compartmentalization of a food web has important impacts on the stability and dynamics of food webs (May 1972; Pimm 1979, 1980; Pimm and Lawton 1980; Yodzis 1982; Girvan and Newman 2002; Krause et al. 2003; Allesina and Pascual 2009; Rezende et al. 2009). Studies of compartmentalization in ecological networks have often analysed modularity, which measures the degree to which connections between nodes are clustered into discrete subunits (Newman and Girvan 2004; Guimerà et al. 2010). A complementary approach is to measure node overlap, or the degree to which species share interacting partners (Strona and Veech 2015; Strona et al. 2018). Examining the changes in the modularity and node overlap of mammal food web networks over time could shed light on how modern mammal communities differ from their ancient relatives as well as help elucidate factors related to the stability or instability of food web structure. Moreover, it could help predict how modern communities will respond to the ongoing challenges of global climate and anthropogenic change.

One approach to resolving the consequences of megafauna extinctions and climate change on the structure of ecological communities is to use sites with fossil records that have finely calibrated temporal resolution, although this is rare. Here, we employ the uniquely fine-scaled Hall's Cave and neighbouring cave sites' dataset to: (1) Understand how the structure of a North American mammalian food web has changed over the past 22,000 years, a time period spanning the megafauna extinction, (2) test the potential drivers of the changes in food webs, (3) determine whether and when the food web structure departs from expectations due to changes in the species assemblage, and (4) ask whether introduced herbivores that have naturalised populations in Texas have restored the food webs on the Edwards plateau. Specifically, we use an ecological network approach to measure the changes in the modularity, or compartmentalization, of the food web and ask whether the structural changes were driven by climate change or biodiversity loss.

2 | Data and Methods

2.1 | Study Site

Hall's Cave is located on the Edwards Plateau, Texas (Figure 1a). Modern vegetation of the region consists of woodland and savanna dominated by oak, junipers, and various tall and short grasses (Toomey III 1993; Joines 2011; Cordova and Johnson 2019; Tomé et al. 2020). Prior to deglaciation, the area around Hall's Cave was cooler and wetter and was dominated by pine, oak, and cool season grasses (Cordova and Johnson 2019). By the early Holocene, the site became warmer and more arid (Cordova and Johnson 2019). Hall's Cave has excellent preservation of the mammal community with a fossil record spanning the last 22,000 years (Toomey III 1993; Smith et al. 2016). In addition to mammals (Toomey III 1993; Smith et al. 2016; Hedberg et al. 2022; Tomé et al. 2020, 2022; Smith et al. 2022), studies of the site have ranged from paleoclimate reconstructions to opal phytoliths (Toomey III et al. 1993; Cooke et al. 2003; Joines 2011; Smith et al. 2016; Cordova and Johnson 2019). The record of flint and charcoal at the site indicates that humans were continuously present near Hall's Cave starting around ~15,500 years ago. The extinction at Hall's Cave occurred at the same time as the extinctions in the rest of North America (Smith et al. 2016), and is thus likely to be representative of the overall extinction event. Although not entirely coupled, the megafauna extinctions occurred alongside an overall increase in temperature at the site (e.g., Smith et al. 2016).

The Hall's Cave site has been well dated with 44 published dates across 3.5 m of stratigraphy excavated in 5 cm layers (Toomey III 1993; Supporting Information). Here, we reevaluated the calibrated age model from Tomé et al. (2020) based on these dates, removing three carbonate specimens (TMM 41229-1118, -1326, -1360) due to uncertainties in sample quality. The remaining 41 AMS ^{14}C measurements were calibrated to calendar ages (cal BP) using OxCal ver. 4.4.4 (Ramsey 1995, 2001, 2009, 2017) with the Northern Hemisphere atmospheric curve InCal20 (Reimer et al. 2020). We evaluated three potential age models (linear, split line and spline), as well as the original linear regression model from Tomé et al. (2020), using Akaike's information criterion (AIC). While all models found significant (p-value < 0.05) fit between stratigraphic depth and calendar age, the spline model was found to have the best fit (adjusted $r^2 = 0.98$) compared to the split line (adjusted $r^2 = 0.96$, 0.56, above or below a 213 cm depth respectively) and linear regression (adjusted $r^2 = 0.95$) models (Table S1). Using the mean calibrated radiocarbon ages (cal BP) and stratigraphic depth (cm), a smoothing spline was

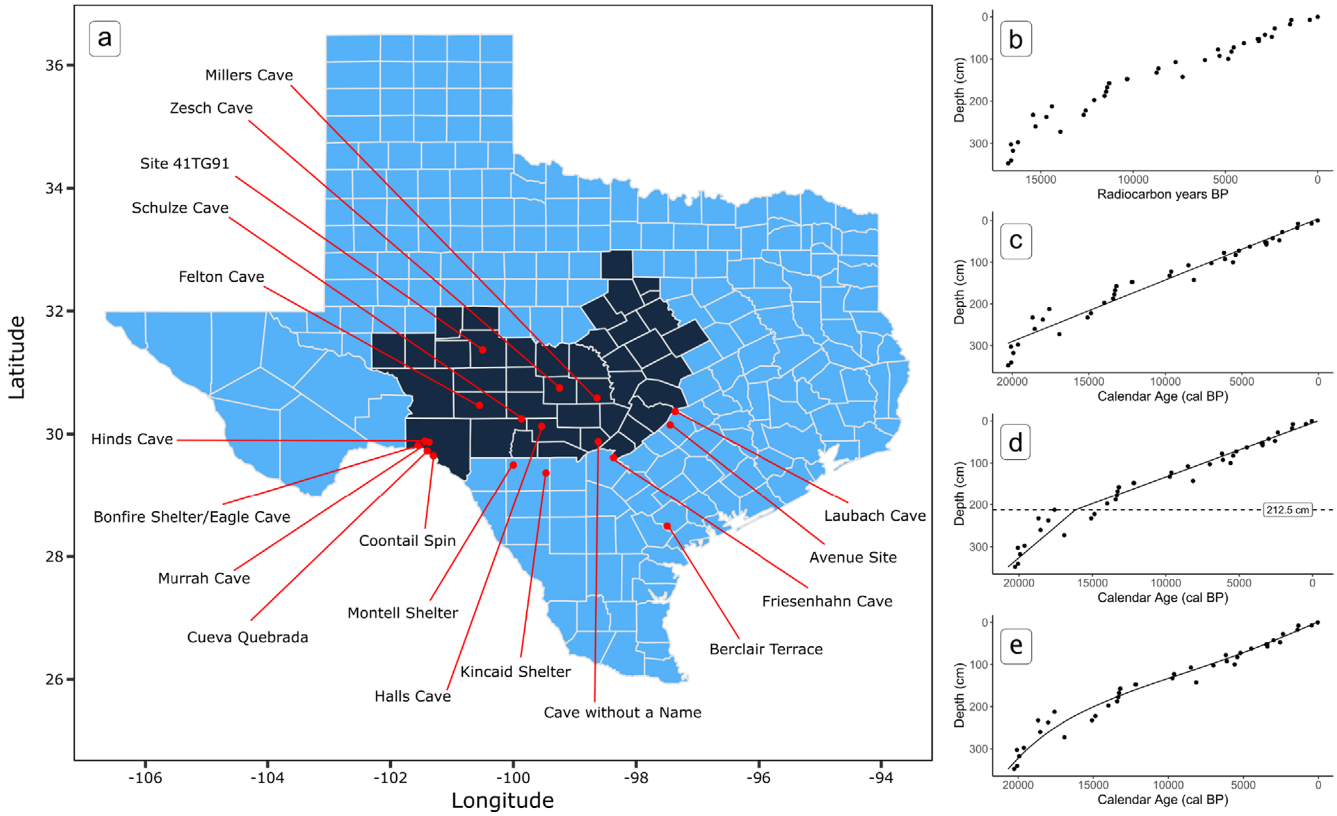

FIGURE 1 | Map of Hall's and Edwards Plateau Cave sites, radiocarbon dates, and tested age models. (a) The Edwards Plateau in dark blueorange and the fossiland fossil cave sites in redHall's Cave indicated in green. Age data from Hall's Cave stratigraphic record plotted as (b) unmodelled radiocarbon dates to depth (cm) and the three tested age models using calibrated calendar years before present: (c) linear, (d) split regression and (e) spline. Radiocarbon or Calendar Age is plotted on the x-axis, with stratigraphic depth on the y-axis, with oldest to youngest going left to right, and deepest to shallowest going down to up respectively.

modelled using the ss() function and estimated calendar ages for each 5 cm depth of the Hall's Cave stratigraphic record was calculated using the predict() function in the npreg R package (Helwig 2022) (Table S1; Figure 1b–e).

2.2 | Climate Data

We utilised downscaled and debiased paleoclimatic simulation data of the Community Climate System Model (CCSM3) developed by Liu et al. (2009). It is a unified dataset from climate simulations that spans the last 22,000 years in North America and provides daily estimates of climate variables (Lorenz et al. 2016). Similar to previous studies, the climate data for the region surrounding Hall's Cave was extracted in 500-year intervals (Tomé et al. 2020, 2022). Here, we averaged the climate data for each of 16 time intervals. Time intervals were designated to span important climatic or biotic events where possible, while also spanning generally consistent lengths of time. For example, our intervals include eight late Pleistocene and eight Holocene units across its 22,000-year span. The division separates not only the epochs, but purposely accounts for before and after the megafauna extinction. On average, the length of interval is between 1000 and 2000 years. Thus, we are comparing similar lengths of time across intervals. The most noticeable exception is the shorter second time interval (e.g., 1128–1458 ybp; Table S2), which had similar amounts of vertebrate remains compared to the first and third intervals, despite its shorter duration. Climate variables chosen included mean daily maximum temperature, standard deviation of the mean daily maximum temperature, mean daily minimum temperature, standard deviation of the mean daily minimum temperature and total monthly precipitation (Table S2).

2.3 | Food Web Networks

Species lists for each time period were taken from Smith et al. (2016) and Hedberg et al. (2022). These are presence/absence data and were constructed from Hall's Cave and other nearby cave sites on the Edwards Plateau (Figure 1a). The fossil record at Hall's Cave comes primarily from specimens that are washed in during flood events that happen regularly in the area (Toomey III 1993; Smith et al. 2016). As a result, the record at Hall's Cave is primarily a small mammal record. To get a complete picture of the mammal community at Hall's Cave, we used museum and literature records from nearby caves on the Edwards Plateau (Figure 1). For each species not found in Hall's Cave, the natal dispersal distance or home range size was calculated using the species average body mass and a guild-specific equation (Smith et al. 2016). For carnivores, maximum dispersal distance was:

$$D_c = 40.7M^{0.81} \tag{1}$$

where M is body mass in kg. For herbivores or omnivores, maximum dispersal distance was:

$$D_{h/o} = 3.31M^{0.65} \tag{2}$$

Equations for dispersal distance were taken from Sutherland et al. (2000). Home range was calculated using equations developed by Tucker et al. (2014). Home range for carnivores was:

$$\log \mathrm{HRc} = 1.19 \log M - 0.29 \tag{3}$$

and for herbivores or omnivores was:

$$\log \mathrm{HR}_{h/o} = 1.19 \log M - 1.47 \tag{4}$$

A species was included in our species list if the natal dispersal distance or home range was less than or equal to the straight line distance between Hall's Cave and the cave site that contained the species. Species were assigned to the appropriate time intervals based on age information from the level within the cave site where the species was found (Smith et al. 2016). The final time interval also includes introduced species on the Edwards Plateau (Hedberg et al. 2022). The species lists used here are based on the examination and identification of ~45,000 fossil specimens from cave sites across the Edwards Plateau. Thus, we are confident that this represents a robust list of the presence or absence of species from Hall's Cave across the last 22,000 years.

We constructed our food webs using a matrix of species likely to interact based on diet and body size (see Supporting Information). We used published body size and δ^{13}C and δ^{15}N stable isotopes data for specimens from Hall's Cave and the Edwards Plateau more generally (Smith et al. 2022; Tomé et al. 2020, 2022) to make dietary inferences for each species within the food web; when dietary data were not available for the Edwards Plateau, we used literature values (Wilman et al. 2014). δ^{13}C was used to infer whether a primary consumer was eating primarily C3 or C4 vegetation or whether they were a mixed feeder. Similarly, δ^{13}C indicated whether a secondary consumer was primarily eating browsers, grazers or mixed feeders (Smith et al. 2022; Gearty et al. unpublished manuscript). For example, we constrained prey choices for *Homotherium serum* based on the stable isotopic niche reported by Smith et al. (2022) for the Edwards Plateau. δ^{15}N indicated where in the trophic chain primary and secondary consumers fell and was used to differentiate apex and meso-predators. Following Carbone et al. (1999), we constrained maximum prey size to 1.19 times that of any predator greater or equal in mass to 21.5–25 kg, while predators under this cutoff were constrained to prey no larger than themselves. An exception of the predator/prey body size relationship was made for species likely to have used group hunting, such as wolves. Lastly, we removed carnivores and insectivore species as potential prey for other carnivores and omnivores, as such interactions are considered rarer and are not reflected in the isotopic values of Smith et al. (2022). Using the dietary and inferred scaling relationships, we created a food web network for each of the 16 time intervals at Hall's Cave and nearby cave sites. To form the food webs, we used the R package 'igraph' (Csardi and Nepusz 2006).

2.3.1 | Quantifying the Structure of Food Webs

We first measured changes in three network properties across time intervals: connectance (i.e., proportion of possible links that are realised), modularity, and node overlap (Strona and Veech 2015). Connectance describes the proportion of possible links that are realised, which has been shown to fundamentally affect food web function and robustness (Dunne et al. 2002b). Modularity quantifies how communities are partitioned into compartments of interacting species and has also been linked to food web stability

(Stouffer and Bascompte 2011). Node overlap is a measure of the degree to which species in a food web share interacting partners (Strona and Veech 2015). Both modularity and node overlap describe the degree to which the food web is compartmentalised into different clusters of interacting species. Importantly, these and many other network metrics may covary with connectance, as the degree to which nodes can be segregated or clustered into compartments is contingent on how well-connected the nodes are in the network. For example, a network in which all nodes are connected (i.e., connectance of 1) cannot contain separate compartments, and all nodes must overlap in their interacting partners. However, levels of modularity or node overlap can vary greatly in food webs with lower connectance, meaning that connectance sets limits on the levels of modularity and node overlap, but this relationship is nonlinear and complex (Fortuna et al. 2010).

We used two methods to measure the compartmentalization of the food web across time: (1) modularity using community detection with the whole food web, and (2) node overlap using a bipartite network of consumers and resources. As we show, the two approaches are complementary, with different strengths and weaknesses.

First, we measured the modularity of the whole food web using *the edge-betweenness community detection algorithm* (Newman and Girvan 2004). Briefly, this method identifies clusters, or 'node clusters' as partitions of the network that maximise the number of edges that link nodes within the same community and minimise the number of edges between communities. We used this algorithm because it is one of the few community detection algorithms that accommodates directed edges in a unimodal network (i.e., rather than a bipartite network: see below). A modularity value of 0 represents a network in which edges are random with respect to modules (i.e., there are no clear modules), and 1 represents a network in which all nodes in the same module are connected and there are no edges connecting nodes in different modules. This approach can be implemented on directed networks including primary producers. However, the drawback is that permutations of consumer-resource relationships on a directed network are complicated, making null hypothesis testing difficult.

As a complementary approach we took a second approach by converting the food web into bipartite networks of consumer-resource relationships. A bipartite network consists of two types of nodes (e.g., 'consumer' vs. 'resource'), with edges only connecting nodes of different types. Here, we created a simple consumer-resource network of only a predator eating prey while excluding primary resources. We assigned each omnivore as a 'consumer' or 'resource' based on its predator–prey ratio: an omnivore was considered a 'resource' if it had more predator species that consumed it than prey species that it consumed (e.g., *Peromyscus* mice), while an omnivore was considered a 'consumer' if it had fewer predator species than its prey species (e.g., bears). We then measured the node overlap and segregation (NOS) index, which measures the tendency of species to share or not share interacting partners and measures how much overlap there is between the pairs of interacting partners. The values of NOS range between −1 and 1, where −1 represents a network with complete segregation, 1 represents a network with maximum overlap (Strona and Veech 2015). We show here that NOS is strongly negatively correlated with modularity measured by edge-betweenness community detection described above, but the bipartite network approach allows us to use permutation-based statistical tests because it simplifies null model simulations (see below). We also measured changes in the connectance of the bipartite network at each time interval. Connectance ranges from 0 to 1, where 0 is a network with no edges, and 1 is a network in which all possible node combinations are connected.

2.4 | Statistical Analyses

2.4.1 | Null Model Testing of NOS and Connectance

Here, we are interested in determining how the observed structure of the food web may change due to changes in species composition across time. Therefore, we tested whether the observed NOS index and connectance of the bipartite network differed from what could have been expected if species composition were randomised. To do this, we first assembled a list of all species found in Hall's Cave and neighbouring sites on the Edwards Plateau during the entire sampling period (i.e., over the past 20,000+ years) and assigned each species as a 'consumer' or 'resource' using the same criteria as above (namely, 'consumers' consisted of carnivores and omnivores who had more prey species than predators). Then, for each time interval, we randomly selected consumers and resources from the total pool of species, matching the number of consumers and resources observed in that time interval. We then measured the NOS index and connectance of the resulting 'null' bipartite network. We repeated this procedure 10,000 times to generate a null distribution of the NOS index and connectance for each time interval. We generated p-values through a one-tailed permutation test, as the proportion of times the indices (NOS or connectance) of the null model equaled or exceeded the indices of the observed network at that time interval.

2.4.2 | Testing the Impact of Climate Change on Food Web Structure

Both food web structure and climate variables may be autocorrelated with time. To account for any temporal auto correlations, we took the first difference between time intervals in all variables. This successfully removed significant autocorrelation in all variables of interest (Figure S1). We used Spearman-rank correlations to understand how well correlated two variables are. In this case, we tested the relationship between the change in temperature, precipitation, and species richness to the change in modularity over time. Since we conducted multiple tests, we adjusted the p-values for false discovery rate (Benjamini and Yekutieli 2001).

3 | Results

3.1 | Changes in Edwards Plateau Food Web Structure From Pleistocene to Holocene

Network representations of the Edwards Plateau food webs organised in 16 time intervals over the Pleistocene and Holocene illustrate dramatic changes across the past 20,000 years (Figure 2). The network plots show changes in the structure of the ecological community that cannot be captured by metrics

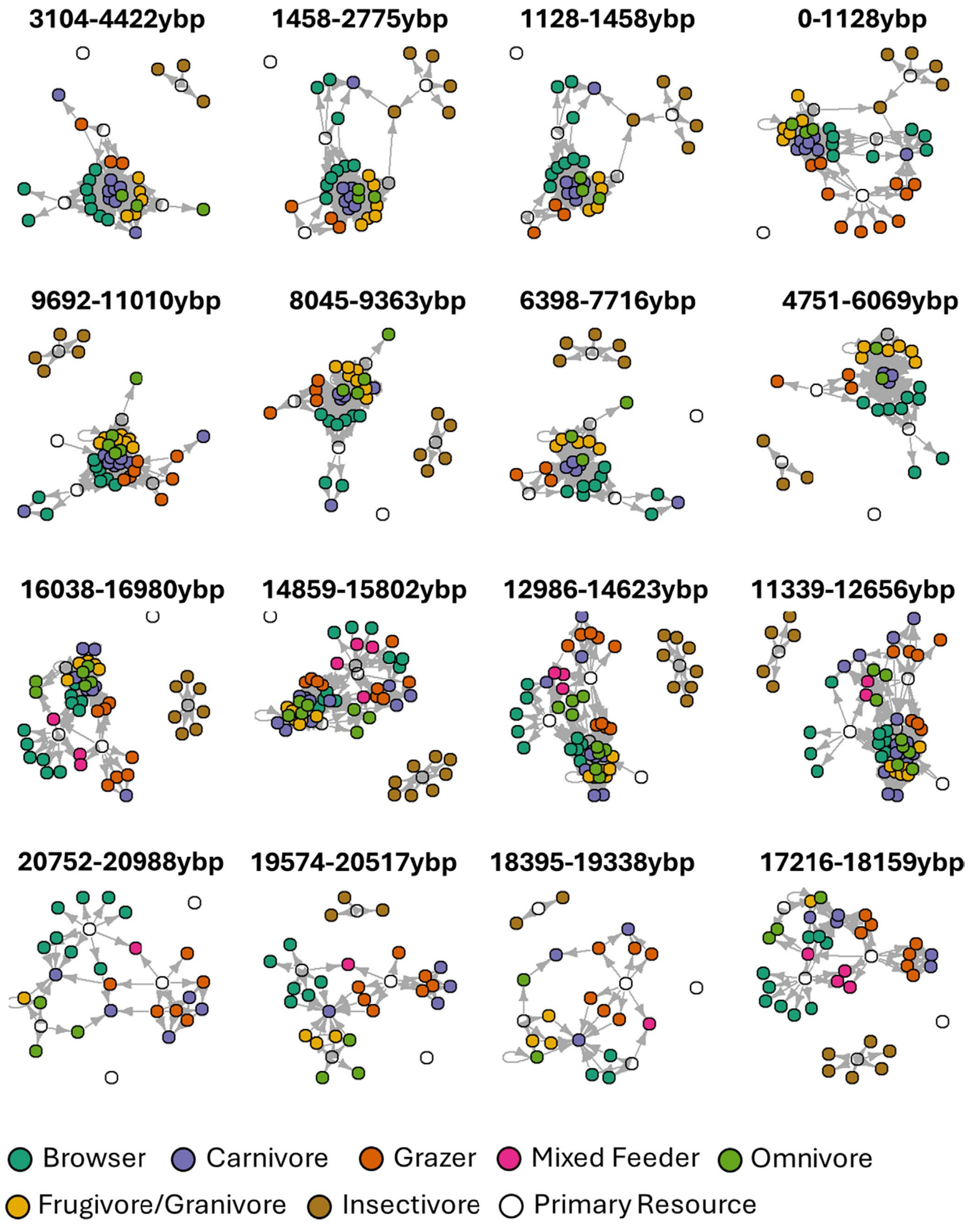

FIGURE 2 | Edwards plateau food web networks from the Pleistocene to Holocene. Time bins 1–9 = Holocene transition (Present–11,339), 10–16 = Pleistocene (12,986–20,988 years). Numbers denote the beginning and ending of each time interval. Nodes are colour coded by trophic groups indicated by the legend. The network plots use a force-directed layout, in which nodes simulate charged particles that are connected together by edges that simulate springs (Fruchterman and Reingold 1991). This is a popular network visualisation technique that arranges nodes in space based on their patterns of connections with each other.

of species diversity and connectance alone, such as the patterns of clustering of nodes based on shared resources and consumers. These clusters—or modules—are not defined solely by the trophic groups of their members, but rather by the patterns of shared consumers and resources, which change across time along with the turnover of species (Figure S2). These patterns are captured quantitatively through measurements of network properties such as connectance, modularity and the node overlap index (NOS). As expected, connectance is highly correlated with modularity (Spearman correlation: $\text{rho} = -0.74$, $p = 0.001$) and NOS ($\text{rho} = 0.86$, $p < 0.001$). Modularity and NOS are also highly negatively correlated ($\text{rho} = -0.69$, $p = 0.003$), which is also expected because they both measure how patterns of interactions are clustered among sets of species.

We found that the modularity of the network generally decreased from the Pleistocene to the Holocene, whereas the NOS and connectance both increased (Figure 3a–c). Modularity began to decrease ~18,000 years ago, was very low by the beginning of the Holocene and remained low throughout the Holocene before slightly increasing in the latest time interval (1128 years ago to present: Figure 3a). NOS and connectance follow a generally opposite pattern, beginning to increase at the Pleistocene–Holocene boundary, peaking 4751–6069 years ago, then decreasing to the present day (Figure 3b,c).

3.2 | Null Model Testing

Observed NOS indices were significantly higher than expected by chance for all the Holocene time intervals ($p < 0.025$) and the Pleistocene–Holocene transition ($p = 0.038$) except for the most recent time interval (Figure 3c: $p = 0.12$). In contrast, the observed NOS indices were not significantly different from expected for any of the Pleistocene time intervals (Figure 3a: $p > 0.27$ for all). Connectance deviates from values expected by chance after the transition into the Holocene ($p < 0.033$) except for the most recent time interval (Figure 3e: $p = 0.078$).

3.3 | Local Climate Associations With Food Web Modularity

To test associations between past climate change or species extinctions across time (Figure 3b,d,f) and network properties, we took the first difference between time intervals in all variables to remove significant temporal autocorrelations (Figure S1). We did not find significant relationships between temporal change in any climate variable and change in modularity, NOS, nor connectance (Table 1). We also did not find any correlation between changes in species richness and changes in modularity, NOS, or connectance (Table 1; Figures S4–S6).

4 | Discussion

Our results demonstrate significant changes in the Edwards Plateau cave sites' food web network structure during the Pleistocene–Holocene transition. Similar to findings for food web networks in South America across this time (Pires et al. 2020), we see a relatively sparsely connected, modular network with low levels of node overlap (measured by our NOS index) in the Pleistocene transform into a significantly more connected, less modular network with high levels of node overlap in the Holocene (Figure 3a,c,e). We used a null model approach for our metrics of the bipartite network (a simplified food web network without primary resources and animals assigned as 'consumers' and 'resources' based on the ratio of predators and prey they have) to show that connectance and the degree of node overlap were significantly higher than null expectations after the Pleistocene–Holocene transition (Figure 3c,e). These results are consistent with recent studies that have shown decreases in ecological network complexity at the Pleistocene–Holocene transition (Pires et al. 2020; Pires 2024; Fricke et al. 2022). Fricke et al. (2022) found that the reduction in the number of links between species after the megafauna extinction played a vital role in the lack of modern food web complexity. Modern food web networks have demonstrated similar responses in decreased modularity due to climate and anthropogenic change. Takemoto and Kajihara (2016) found that global warming and human impacts have caused decreased network modularity and an increase in nestedness for not only food webs, but also pollination and seed-dispersal networks. This suggested that increasing modularity enhances ecosystem stability and vice-versa. Interestingly, Pleistocene mammal food web networks were less stable than subsequent Holocene networks due, in part, to the size of the networks. Having more species connections or links between megafauna led to a less stable network with them being more vulnerable to environmental changes due to early human (Pires et al. 2015, 2020; Pires 2024) or climatic influences (Nenzén et al. 2014). Indeed, Pires (2024) suggests that the loss of modularity and resulting increase in stability may be a general pattern expected after the loss of megafauna. While this change is due, in part, to the direct loss of species, the indirect effects from the addition of a novel predator to the network (i.e., humans) on other network interactions are also important (Pires et al. 2020; Pires 2024).

Because of the dense sampling at this study site, we were able to analyse the changes across 16 time intervals—a finer-scale temporal analysis than has been attempted before (e.g., Nenzén et al. 2014), and we detected sequential change in network properties. We show that the shifts in modularity began around 18,000 years ago coincident with deglaciation (Clark et al. 2012) and the earliest evidence of humans at the site. Modularity reached its lowest levels two time intervals later, coincident with the start of mass megafauna extinction, and it remained low thereafter (Figure 3a). The dramatic shifts in food web structure we uncovered were not correlated with changes in species richness, precipitation or temperature across time intervals (Table 1; Figure S4). While the lack of correlation with these coarse-grained measures cannot rule out the effects of these factors on food web structure, our results point to other factors that may have driven changes in network structure over the past 22,000 years. One potential hypothesis relates to anthropogenic change in the region. The record of flint flakes indicates that the earliest evidence of humans at Hall's Cave occurred ~18,000 years ago and by ~15,500 years ago humans were continuously present at the site. Shortly after, by ~11,000–11,500 years, most megafauna at the site were extinct (Smith et al. 2016, 2022). Just after this transition, we see low species richness without much recovery as the richness in the

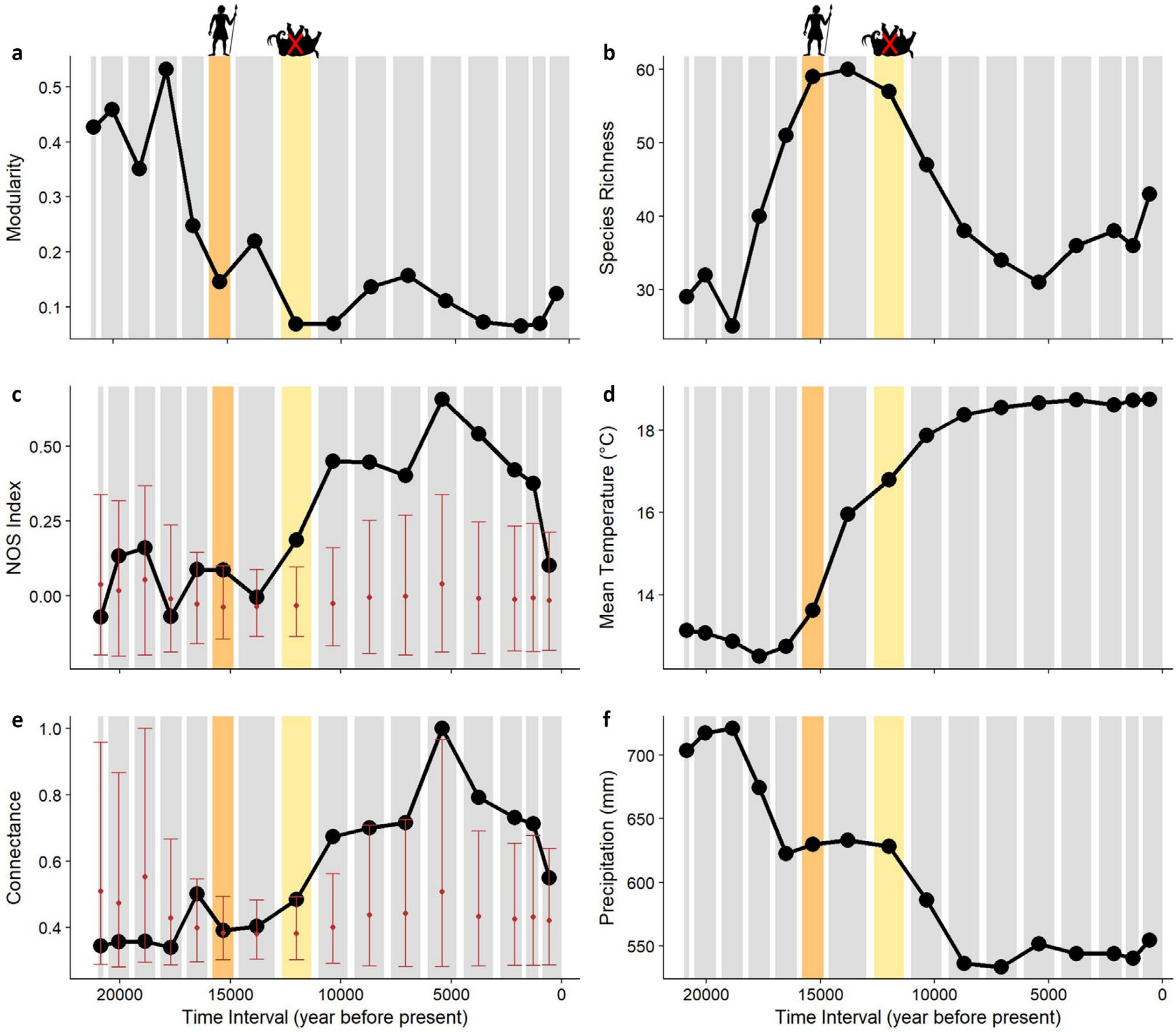

FIGURE 3 | Network metrics, climate variables, and species richness on the Edwards Plateau over 20,000 years. The width of the grey and yellow bars represent the length of a time interval. The orange bar represents the start of continuous human occupation in the region. The yellow bar indicates the transition from the Pleistocene to the Holocene and is the extinction interval. (a) Modularity over time. (b) Species richness over time. (c) Observed NOS deviates (black line) from values expected by chance (red dots and error bars represent mean and 95% confidence interval of NOS values from null model) only after the transition into the Holocene except for the most recent time interval. (d) Average maximum temperature of the region over time. (e) Connectance deviates (black line) from values expected by chance after the transition into the Holocene except for the most recent time interval. (f) Annual precipitation of the region over time. NOS and connectance have an inverse relationship with modularity. When modularity declines, NOS and connectance increases and vice-versa.

Pleistocene (Figure 3b). Thus, it is plausible that anthropogenic changes in species composition, that is, the specific types of taxa that went extinct, rather than the number of species, could have been a major driver for changes in the food web structure.

Past research has demonstrated that loss of key guilds during the megafaunal extinction event led to large shifts in ecosystems, and this specific pattern of species loss may be related to the shifts in food web structure that we detected. For example, megaherbivores (e.g., *Mammut americanum*, *Mammuthus* sp., *Bison latifrons*, *Bison antiquus*) influenced the abundance of C3 and C4 plant vegetation (Owen-Smith 1988; Bakker et al. 2006; Goheen et al. 2010, 2018; Doughty, Faurby, and Svenning 2016; Doughty, Roman, et al. 2016). Apex predators (e.g., *Smilodon fatalis*, *Homotherium serum*, *Panthera leo atrox*, *Canis dirus*) were likely controlling the abundance of the prey and other predators and preventing overgrazing/over predation (Johnson 2009). Indeed, loss of the apex felid guild resulted in a classic case of meso-carnivore release in the extant felids (Smith et al. 2022). Thus, the consequences of megafauna extinctions were the loss of important species (e.g., ecosystem engineers) in the community that led to a less diverse and less complex food web network structure. Similarly, an examination of the functional diversity of Hall's Cave and neighbouring cave sites over time found that extinct megafauna were functionally unique and entire regions of functional space were lost as a result of the extinction

TABLE 1 | Spearman-rank correlations between the first differences of climate variables and species richness against network metrics.

	Δ Modularity		**Δ Connectance**		**Δ NOS**	
Variable	**rho**	***p***	**rho**	***p***	**rho**	***p***
Δ Average temperature	−0.107	0.995	0.429	0.264	0.371	0.404
Δ Precipitation	−0.004	0.995	−0.225	0.489	0.036	0.903
Δ Max temperature	−0.150	0.995	0.479	0.256	0.393	0.404
Δ Max temperature SD	−0.054	0.995	−0.354	0.274	−0.139	0.725
Δ Min temperature	−0.054	0.995	0.161	0.567	0.229	0.719
Δ Min temperature SD	0.007	0.995	−0.368	0.274	−0.146	0.725
Δ Species richness	0.038	0.995	−0.520	0.256	−0.461	0.404

Note: p values are adjusted using false discovery rate (Benjamini and Yekutieli 2001).

(Hedberg et al. 2022). Thus, we hypothesise that some aspects of the species composition that changed after the arrival of humans in North America were more important than overall species richness or climate factors in structuring the food web. However, there are many potential combinations of species that could have been lost or gained to cause large changes in network structure, and testing this hypothesis will require data on the change in food web structure and species composition from multiple communities.

There have been many efforts to restore structure to face biodiversity loss due to these global effects, such as rewilding of species back into communities. Rewilding efforts have occurred around the world such as rewilding extirpated species in Europe (Pereira and Navarro 2015), and rewilding of African mammals in Texas environments (Schmidly and Bradley 2016). Multiple species have been introduced to private lands in the Texas hill country, where the Edwards Plateau is located, for big game hunting. Several of these species have naturalised including Blackbuck antelope (*Antilope cervicapra*), axis deer (*Axis axis*), cattle (*Bos taurus*), horse (*Equus caballus*), sika deer (*Cervus nippon*), fallow deer (*Dama dama*), sheep (*Ovis aries*), the oryx (*Oryx dammah*), and the wild boar (*Sus scrofa*) (Hedberg et al. 2022) (Figure S3). In addition, the Edwards Plateau Holocene community includes introduced species from ~1128 years ago, showing early rewilding of species brought in with early humans (e.g., *Canis familiaris*) (see Supporting Information). The introduced species filled in the space previously occupied by the extinct megafauna and have been shown to partially restore the lost functional diversity of the Edwards Plateau community (Hedberg et al. 2022). Moreover, their presence does provide partial restoration of the overlap in modularity and the NOS index in the most recent time interval. The network in the most recent time interval has an increased number of discrete clusters that include two separate clusters with links to the mountain lion (Figure S3). One is a previously existing cluster that has expanded to include the sika deer. Most of the other introduced herbivores are now in a new cluster with bison and pronghorn. Although the values for connectance and the NOS index in the most recent time interval are not different from expected given our null model, the changes in modularity do not reach the levels they attained prior to the extinction (Figure 3a, last time interval). This is likely because their predators were not introduced and they are not the preferred prey of extant predators in the area. Without the restoration of predator–prey interactions, the missing links and modularity of the Edwards Plateau food web cannot be restored. Our results and others (e.g., Hedberg et al. 2022) suggest that rewilding (Josh Donlan et al. 2006) with only herbivores restores some, but not all, of the lost ecosystem function. These results have implications for modern rewilding efforts that mainly focus on rewilding with still extant, but locally extirpated large herbivores. Although plant biodiversity increases and ecosystem function improves with the restoration of these herbivores (Bakker and Svenning 2018; Svenning et al. 2024), the resulting food webs are likely still incomplete. Management of these ecosystems will need to account for the missing predators and the ecosystem services they provide.

5 | Conclusions

We find that the extinction of the megafauna at the terminal Pleistocene had significant effects on the food web of the mammal community on the Edwards Plateau, TX. Modularity of the food web network decreased dramatically, while connectance and node overlap increased. These findings suggest that the food web collapsed after the extinction, changing from a network with several clusters to one with only a few clusters. Moreover, we find that these changes cannot be explained by simple changes in temperature, precipitation or species richness. Instead it is likely that the changes are a result of which species were lost and the ways in which those species were integrated into the food web. Our work documenting the shifts in a mammalian food web across the past 22,000 years has important implications for modern food webs. The earth is currently experiencing rapid diversity loss because of global climate change and anthropogenic impacts (Barnosky et al. 2011; Dirzo et al. 2014; Ceballos et al. 2017; Habell et al. 2019). While we are not yet in a mass extinction, local and global extirpations of species have altered community structure in many ways (Takemoto and Kajihara 2016; Gilarranz et al. 2016; Hedberg et al. 2022). In particular, the loss of large bodied mammalian apex consumers leads to trophic cascades and highly altered ecosystems (Estes et al. 2011; Malhi et al. 2016; Doughty, Faurby, and Svenning 2016; Doughty, Roman, et al. 2016; Smith et al. 2023). Moreover, rewilding efforts that restore still extant, but locally extirpated species lead to increases in plant diversity and may be restoring lost ecosystem function (Svenning et al. 2024). Our data demonstrate that rewilding efforts may help rebuild structure of food web networks; however, they cannot restore lost ecosystem function completely when only herbivores are introduced. This study highlights the importance of not only understanding the impact of extinctions on ecosystems, but also the effect megafauna has within those ecosystems. This understanding of the consequences of the megafauna extinctions changing the structure of food web networks may contribute to future studies on the effects of megafauna decline and biodiversity loss.

Author Contributions

S.K.L., D.S., and Q.A.S. conceived of the study. S.K.L., C.P.T., and F.A.S. contributed data on stable isotopes of mammals from Hall's Cave and the data on the species composition of mammals at Hall's Cave through time. S.K.L., C.P.T., and W.G. developed the table of inferences of species interactions. Q.A.S. and D.S. performed the statistical analyses and drafted the figures. Q.A.S. drafted the manuscript with input from D.S. and S.K.L. All authors helped revise the manuscript and gave final approval for submission. D.S. and S.K.L. jointly supervised the study.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code have been included as Supporting Information and publicly available on Zenodo at: https://doi.org/10.5281/zenodo.16621465.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** geb70113-sup-0001-DataS1.docx.