

RESEARCH ARTICLE

The hidden legacy of megafaunal extinction: Loss of functional diversity and resilience over the Late Quaternary at Hall's Cave

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Abstract

Aim: Functional traits mediate the interactions of species among themselves and with their environment, providing a link between diversity and ecosystem function. Crucially, the loss of biodiversity can jeopardize the functionality of ecosystems. Much focus is on predicting the impacts of current and future species loss; however, modern ecosystems have undergone biodiversity decline throughout the Late Quaternary, starting with the Pleistocene megafaunal extinctions. Thus, the fossil record offers the opportunity to investigate the long-term legacy of biodiversity erosion and how this is affecting modern ecosystems in a cumulative manner. We aimed to investigate changes in functional diversity and redundancy of a local mammal community at Hall's Cave, a site with a continuous record from 21,000 years ago to the present. Additionally, we included several common introduced species in the modern community to test whether they restore some lost ecological function.

Location: Central Texas.

Time period: Late Pleistocene to Present.

Major taxa studied: Mammals.

Methods: We used eight functional traits (mass, diet, arboreality, cursoriality, soil disturbance, group size, activity period and migration habit), which, collectively, describe the ecological role of a species and its influence on ecosystem processes, to construct a multidimensional functional space. The functional richness, range and distribution of the Hall's Cave community and the degree of functional redundancy were characterized statistically over time.

Results: We found that declines in functional diversity were greater than expected given the decrease in species richness, implying that lost taxa contributed higher than average distinct ecological function. Functional distances between the remaining species increased through time, leading to reduced functional redundancy in younger communities. However, recently introduced taxa increased functional diversity to levels similar to those in the Holocene and partly restored the functional space occupied by Late Pleistocene fauna.

Main conclusions: Our local-scale analysis demonstrates how prolonged biodiversity erosion not only leads to functionally depauperate communities, but, crucially, lowers ecological resilience to future disturbance.

KEYWORDS

biodiversity, conservation, functional diversity, Late Quaternary, megafauna, palaeoecology

1 | INTRODUCTION

We are currently facing widespread species extinction and population declines on every continent (Barnosky et al., 2011; Ceballos et al., 2017; Dirzo et al., 2014). Critically, the erosion of biodiversity over time can jeopardize or eliminate integral ecosystem processes (Cardinale et al., 2012; Hooper et al., 2012). The relationship between biodiversity and ecosystem function, rather than being reflective solely of species richness, is underpinned by the diversity of ecological roles represented in an ecosystem (Cadotte et al., 2011; Díaz et al., 2007; Gagic et al., 2015; Mouillot et al., 2011). Functional traits offer an avenue to characterize and estimate the ecological role of a species. Functional diversity, which quantifies the value, range and relative abundance of functional traits in a given community (Díaz et al., 2007), therefore represents a link between faunal composition and ecosystem processes. Unlike taxonomic diversity, the unique functional contribution of each species varies based on overlap with surrounding fauna (Mouillot et al., 2013). In a community supporting many species with similar ecological roles, functional redundancy is high, and a decrease in species richness may have little effect on ecosystem function. The opposite occurs, however, in a community with low redundancy and many functionally distinct members. Functional redundancy, therefore, increases the ecological resilience of a community by providing a buffer against loss of function following disturbance (Fonseca & Ganade, 2001; Petchey & Gaston, 2009; Pimiento et al., 2020; Walker, 1995). Consequently, species richness and functional diversity, although related, are often decoupled during periods of biodiversity decline (Boyer & Jetz, 2014; Petchey & Gaston, 2009).

Characterizing the true impact of the current biodiversity crisis is challenging because some of the direct or indirect effects of species loss can take decades to centuries to play out. However, anthropogenically mediated biodiversity decline is not only a recent phenomenon; there is emerging consensus that humans played a significant role in extinctions over the Late Quaternary, including the Terminal Pleistocene megafaunal extinction in North America c. 11.5 ka (Barnosky et al., 2011; Lyons et al., 2004; Smith et al., 2018). These extinction events were characterized by extreme size selectivity; large-bodied mammals across the globe became extinct, including all those > 600 kg in North America (Lyons et al., 2004; Smith et al., 2018). Furthermore, the status of remaining large-bodied vertebrates has become more perilous over time, as populations increasingly experience extirpations and range contraction (Estes et al., 2011; Laliberte & Ripple, 2004; Turvey & Fritz, 2011). Recent work characterizes them as “on the brink” of biological annihilation (Ceballos et al., 2020), underscoring the pressing need to gain a better understanding of their ecological impact. By focusing on the Late Quaternary fossil record, we can examine the long-term legacy

of the megafaunal extinction and subsequent climate- and human-mediated turnover during the Holocene and Historic era. Moreover, modern ecosystems, even those considered pristine and largely unaffected by human influence, are remnants of a diverse Pleistocene fauna. Thus, consideration of this broader temporal context is crucial for understanding the status of current biodiversity.

Consequently, scientists have begun to characterize Late Pleistocene and Holocene communities in terms of functional diversity (Davis, 2017; Lundgren et al., 2020; Ordonez & Svenning, 2017). For example, a continental-scale analysis of North American large mammals demonstrated that functional diversity loss was within the expected range given the decline in species richness over the megafaunal extinction (Davis, 2017). However, the extinction was highly selective based on certain traits (e.g., body size), which in turn led to a shift in the functional composition of the continental assemblage (Davis, 2017). This broad-scale analysis was highly informative on how the continental mammalian biota shifted in functional space, yet it did not capture how individual communities were affected over this interval. Communities are structured by varying processes across scales; local assemblages may be structured by competition and/or habitat filtering, whereas regional- and continental-scale assemblages may be more reflective of evolutionary history and biogeographical factors (Brown & Nicoletto, 1991; Hawkins et al., 2012). This variation in community assembly processes with scale can result in distinct differences in functional composition (Belmaker & Jetz, 2013), especially given that large-bodied fauna make up a larger proportion of an assemblage at local versus continental scales (Brown & Nicoletto, 1991). Thus, examining the effects of this global phenomenon at the local scale will yield unique and necessary insights into the ramifications of megafaunal extinction.

Here, we examine shifts in functional diversity in a terrestrial mammal community in the Edward's Plateau of Texas from the Late Pleistocene to the present. We focus on a local community centred around Hall's Cave, whose diverse and abundant faunal record includes micro- to mega-mammals, from 5 g shrews to > 10 ton mammoth. The well-defined stratigraphy of the site extends from c. 21 ka to the present, encompassing the Terminal Pleistocene megafaunal extinction, climatic shifts during the Holocene, and escalating human impacts on the environment through the present. This site is uniquely suited to exploration of the dynamics of a single community over a broad temporal window, bridging the local spatial scale with the temporal insights of the fossil record. Hence, the results of our analysis can advance our understanding of how major biodiversity loss over the Late Quaternary altered local-scale mammalian functional diversity in North America. Furthermore, we explore the ramifications of long-term biodiversity erosion on modern ecosystems and its implications for conservation.

TABLE 1 Descriptive information and functional diversity metrics for temporal communities at Hall's Cave

Temporal community	Dates	SR	Turnover	FVol	FRic	FDis	FDiv	FEve
Terminal Pleistocene	21,000–11,700 BP	69	NA	0.0196	0.0380	0.2317	0.8471	0.9722
Early Holocene	11,700–8200 BP	49	30	0.0159	0.0273	0.1952	0.8178	0.9700
Middle Holocene	8200–4200 BP	44	5	0.0155	0.0266	0.1954	0.8147	0.9703
Late Holocene	4200 BP to 1850 CE	43	9	0.0150	0.0263	0.1926	0.8116	0.9695
Historic	1850–1950 CE	35	9	0.0128	0.0142	0.1788	0.8217	0.9718
Modern	1950 CE to present	33	2	0.0121	0.0122	0.1725	0.8162	0.9735

Note: Turnover refers to the total difference in species compared with the previous temporal community.

Abbreviations: FDis, functional dispersion; FDiv, functional divergence; FEve, functional evenness; FRic, functional richness; FVol, functional volume; NA, not applicable; SR, species richness.

Specifically, we addressed the following questions:

1. How has functional diversity changed over time in response to changes in species richness and composition? Greater than expected decline in functional diversity could indicate that the species lost were functionally distinct and might have contributed ecological function that is not readily replaced by the remaining fauna.
2. How has the functional composition of the community shifted? The influence of biodiversity on ecosystem processes is determined by the underlying trait distributions; how were these altered by extinction and climate-driven turnover over the Pleistocene and Holocene?
3. Has the degree of functional redundancy of the community varied over time? Loss of species could influence the ecological resilience of the community by reducing or eliminating redundancy of ecological roles and functional processes. Moreover, changes in functional redundancy might not occur uniformly across the community if specific areas of functional space become more or less occupied and functional overlap among individual species shifts.
4. To what extent do introduced species in the modern community replace ecological function and resilience lost over time? In addition to common mammalian livestock and commensal species, Texas is home to many species of large-bodied exotic herbivores. Originally introduced as game animals, many have naturalized and might now occupy the vacated ecological roles of extinct or extirpated species.

faunal list was based on the study by Smith, Tomé, et al. (2016), with revisions to reflect changes in mammal taxonomy and additional species newly identified from the site (for details, see Supporting Information Appendix; Table S1). Mammals ranging in size from shrew to bison have been recovered directly in the Hall's Cave fossil record; however, inclusion of nearby sites allowed the complete characterization of the local community. Note that analysis of any single palaeontological site is highly unlikely to include all mammals within a local community because of taphonomic biases, in addition to the reduced likelihood of preservation of the largest mammals owing to lower density on the landscape (see Supporting Information Appendix). Thus, as has been done previously, taxa from other sites were included if either the natal dispersal distance or the average home range overlapped with Hall's Cave (Smith, Tomé, et al., 2016; Toomey, 1994; Toomey et al., 1993). Most fauna were identified to the species level, but this was not always possible. In such cases, potential species were grouped under a genus-level identification (Supporting Information Appendix; Table S2).

Faunal occurrences were split into the following six distinct temporal communities: the Terminal Pleistocene (TP) from 21,000 to 11,700 BP; the Early Holocene (EH) from 11,700 to 8200 BP; the Middle Holocene (MH) from 8300 to 4200 BP; the Late Holocene (LH) from 4200 to 1850 CE; Historic (Hist) from 1850 to 1950 CE; and Modern (Mod) from 1950 CE to the present (Table 1). Time bins were divided by major ecological, climatic or historical events to represent ecologically relevant periods, and therefore do not necessarily encompass the same amount of time (see Supporting Information Appendix).

2 | MATERIALS AND METHODS

2.1 | Site description

Our analysis centres around Hall's Cave, an exceptionally well-preserved fossil site located on the Edward's Plateau in Texas. Well-defined horizontal layers deposited from repeated flooding show minimal bioturbation and have been described chronologically using an age model developed from 44 published Accelerator Mass Spectrometry ¹⁴C measurements from the site (Tomé et al., 2020). We included a total of 79 taxa representing the native terrestrial mammalian fauna from the Terminal Pleistocene to the present. The

2.2 | Ecological traits

Functional traits can be split into two broad and often overlapping categories: response traits that describe the adaptations of a species to its biotic and abiotic environment; and effect traits that describe the effect of a species on ecosystem processes (Lavorel & Garnier, 2002; Suding et al., 2008). Implicit in our analysis is the assumption that the included functional traits are effect traits that characterize the ecological role of a species and key aspects of their influence on ecosystem function. Accordingly, we chose the following ecologically relevant traits: (1) body mass; (2) diet; (3) arboreality;

(4) cursoriality; (5) soil disturbance; (6) activity period; (7) social group size; and (8) migration habit (Supporting Information Table S3). Justification for each trait and an explanation of their linkage to ecosystem processes can be found in the Supporting Information (Appendix).

Diet was split into percentage components of browse, graze, fruit/grain, vertebrates and invertebrates. For modern species, dietary percentages were estimated from published studies using gut contents or similar methods quantifying specific components of the diet (Supporting Information Table S1). Studies from populations in Texas were preferred, followed by regions with habitat similar to that found on the Edward's Plateau. If multiple relevant studies were found for a single species, average values of each component were calculated. For extinct species, dietary percentages were estimated primarily based on stable isotope values from Hall's Cave specimens (Smith, F. A., Villaseñor, A., Elliott Smith, E. A., Tomé, C. P., Lyons, S. K. & Newsome, S. D., unpublished observations) and augmented with additional published isotope data when necessary (for details, see the Supporting Information Appendix). For herbivorous and omnivorous taxa, in particular, we considered additional published sources of evidence when determining dietary components, including dental microwear texture analysis, morphology, and comparison with modern analogues. All sources used to determine diet are listed in the Supporting Information (Table S1). We recognize that representing diet by percentage components does not capture the intraspecific and even intra-individual variability that exists in diet, especially given the temporal extent of our study. Furthermore, there are high levels of uncertainty about the diet of some extinct taxa, in addition to some less-studied modern taxa. Thus, each individual percentage component does not fully represent the dietary breadth of any species and may be biased toward modern populations and/or a few sampled individuals. Despite this shortcoming, the general character of various diets will be reflected by these estimations (i.e., insect-dominated omnivore vs. granivore-foolivore, etc.) in addition to genuine interspecific variation that is otherwise omitted by broad dietary categories.

Body mass (in grams) was obtained from MOM v.4.1 (Smith, Lyons, et al., 2003), a global database of Late Quaternary mammal body masses, and \log_{10} -transformed because of substantial variation in size among taxa. Arboreality, cursoriality and soil disturbance were treated as ordinal variables ranked from one to four, with four the highest level. Soil disturbance incorporates the level of fossoriality in addition to other behaviours that affect biopedturbation, such as rutting, wallowing, and digging for food. We defined activity period as a categorical variable with four classifications: diurnal, nocturnal, crepuscular and arrhythmic. Social group size refers to the average number of individuals in conspecific groups cooperatively sharing space and/or resources, not including groups of a mother and offspring. We estimated social group size as a continuous variable; this too was \log_{10} -transformed because of high variance among taxa. Finally, migration habit was treated as a binary variable representing migratory (one) and non-migratory (zero) taxa.

We gathered trait data for all taxa from peer-reviewed literature sources (Supporting Information Table S1). Further details of how trait values were determined are described in the Supporting Information Appendix. For fossil taxa, direct behaviours cannot be observed. Consequently, traits were estimated based on ecological inferences from peer-reviewed literature sources using a variety of approaches, including stable isotopes, morphology, biomechanical reconstruction and comparison to modern analogues. We recognize that there is uncertainty in assigning trait values, particularly behavioural traits, to extinct taxa, which might bias our results. Specifically, the reliance on modern analogues and the inherent assumption of similarity between closely related species, although common in palaeoecological studies, may have resulted in characterizing extinct taxa as more functionally similar to their modern counterparts than they were. Thus, our measures of functional richness and dispersion are likely to be conservative. Sensitivity tests removing each trait individually produced qualitatively similar results (Supporting Information Appendix Figure S1; Table S4), suggesting that no single trait is driving overall trends.

For taxa evaluated at the generic level where several potential species were present, we used an average of the trait values for these species (Supporting Information Table S2). In all cases, individual species within the genus were functionally similar; hence, the average values are characteristic of the functional role of any potential member (see Supporting Information Appendix).

2.3 | Data analysis

All data analysis was performed in R (v.4.0.5). To compute functional similarity among taxa, we first calculated pairwise distances between species across all traits using Gower's distance (Gower, 1971). We weighted traits to reflect their ecological importance by giving body mass a weight of one, diet components a weight of one-fifth, and arboreality, cursoriality, soil disturbance, activity period, social group size and migratory habit weights of one-sixth, respectively. This resulted in body mass, collective diet and all other ecological traits combined having equal weights. For direct assessment of the influence of our weighting scheme on our analyses, we conducted a series of sensitivity tests; these all produced qualitatively similar results (Supporting Information Appendix Figure S2; Tables S5 and S6). We constructed a functional dendrogram from the Gower's distance matrix to visualize functional relatedness among taxa, following the methods of Petchey and Gaston (2002b) and using unweighted pair-group method using arithmetic averages (UPGMA) clustering (Supporting Information Appendix Figures S3 and S4). The tree is generated in a similar manner to phylogenetic dendrograms; however, branch lengths represent functional as opposed to genetic dissimilarity.

We then constructed multidimensional functional space using principal coordinates analysis (PCoA) of the Gower's distance matrix using the *dbFD* function in the "FD" package (Laliberté et al., 2015). This function calculates maximum trait range (FRic), functional

evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) (Laliberte & Legendre, 2010; Villéger et al., 2008) based on the position of taxa in functional trait space for each temporal community. FRic is calculated by measuring the volume of the minimum convex hull enclosing all taxa; this metric is highly sensitive to outliers and therefore represents the maximum range of traits represented by a community (Legras et al., 2018). FEve measures the regularity of spacing among taxa and can range from zero to one, with one representing perfectly even spacing along trait axes (Villéger et al., 2008). FDis and FDiv represent the average distance to the centroid and the evenness of distances from the centroid, respectively (Laliberte & Legendre, 2010; Villéger et al., 2008). In short, they describe the spread and symmetry of species in functional space. We constrained all calculations of functional diversity metrics to the first four PCoA axes, which account for 71% of the total variation among species.

We calculated an additional measure of functional richness for each temporal community using n -dimensional kernel hypervolumes (Blonder, 2018; Blonder et al., 2014), referred to here as FVol. This method is increasingly used in functional diversity analyses (e.g., Lamanna et al., 2014; Mammola & Cardoso, 2020) and measures geometries in multidimensional space using kernel density estimation around observations (Blonder et al., 2014, 2018). Unlike FRic, FVol is not sensitive to outliers and accounts for the density of observations within the volume as opposed to only the vertices; hence, it is more representative of functional richness (Legras et al., 2018). All hypervolumes were generated using the “hypervolume” package (Blonder et al., 2014) using the first four principal coordinate axes to remain consistent with other metrics (for details, see Supporting Information Appendix). To quantify how the temporal communities shifted in functional space, we calculated dissimilarity between hypervolumes using the “BAT” package (Cardoso et al., 2015; Mammola & Cardoso, 2020). Functional dissimilarity was decomposed into two components: Difference in volume (β_{diff}) and difference in position (β_{rep}).

Functional diversity is expected to change over periods of extinction and species turnover, and intuitively, measures of functional richness are highly correlated with species richness (Petchey & Gaston, 2002a; Villéger et al., 2008). We generated a null model to examine how changes in functional diversity at Hall's Cave compare with the expected loss, given the decline in species richness over time. The number of species and turnover between time bins was identical to the real scenario; however, the species in each bin were selected randomly from the general pool. We simulated the null model 1,000 times and measured FRic, FEve, FDis, FDiv and FVol for each simulation. The median, 50%, and 95% confidence intervals for each null functional diversity metric were compared with the values at Hall's Cave. To assess the severity of changes between bins, the net difference in each functional diversity metric (Δ_{obs}) was compared with that of the null model (Δ_{null}) using Z-scores: $Z = [(\Delta_{obs}) - \text{mean}(\Delta_{null})]/SD(\Delta_{null})$. We considered Z-scores with an absolute value > 1.96 to be significant, because this indicates a value beyond of 95% of the null distribution.

Functional redundancy reflects the amount of overlap in functional traits among species in an ecosystem. This metric can be assessed at an individual level by quantifying the rarity of the combination of traits of a species within the community, or at a community level by assessing how closely packed species are in functional space. We measured the functional rarity of each species by calculating functional distinctiveness, which is the average functional distance between a species and the rest of the community, and uniqueness, which is the distance to their nearest functional neighbour (Violle et al., 2017). Distances were measured via the Euclidean distance in the first four dimensions of functional space, consistent with other metrics. A shorter distance indicates higher functional overlap, or redundancy, between neighbours. We compared the distribution of functional distinctiveness and uniqueness values among temporal communities to assess broad shifts in community functional redundancy over time.

Community-wide mean trait values, or CWMs, were used to assess shifts in community composition over time at Hall's Cave (Boyer & Jetz, 2014; Laliberte & Legendre, 2010). For numerical traits, CWMs represent the mean value for all species included in the community. For ordinal or categorical traits, CWM values are the proportion of taxa in each level or category. We calculated a weighted average from the proportions in each level of the ordinal traits (cursoriality, arboreality and soil disturbance) to represent each by a single value. A value closer to one indicates a greater prevalence of fauna with high scores in a given ordinal trait. Given that activity period is categorical, we could not condense this trait to a single value representing the distribution across all categories, and each category is represented by a separate proportion. To assess which aspects of functional composition shifted in a non-random manner through time, we compared observed CWMs from each temporal community with the distribution of CWMs from the null model using Z-scores. Null CWM distributions represent the expected range of trait values in the absence of any community structuring processes or extinction selectivity; hence, significant deviations ($|Z| > 1.96$) can indicate how these processes have affected the distribution of traits in the community.

We evaluated multivariate similarity in functional composition among temporal communities using a PCoA on CWM values (Laliberte & Legendre, 2010). Given that all values represent numerical averages, even those on ordinal or categorical traits, a Euclidean distance matrix was calculated between temporal communities and used to build PCoA axes. Each activity period category value was weighted to one-quarter to give it collectively equal weight to the other traits. The position of each temporal community was compared, in order to assess qualitatively how trait distributions changed over time and identify similar community-level trait distributions.

To analyse the extent to which introduced species replaced lost ecological function in the modern community, we included five of the most common exotic herbivores found in the vicinity of Hall's Cave: Blackbuck antelope (*Antelope cervicapra*), axis deer (*Axis axis*), sika deer (*Cervus nippon*), fallow deer (*Dama dama*) and scimitar-horned oryx (*Oryx dammah*). Although all are known to have

populations on private ranches, *Antelope cervicapra*, *Axis axis*, *Cervus nippon* and *Dama dama* also have wild populations on the Edward's Plateau (Schmidly & Bradley, 2016). In addition to exotic species, we included seven common mammalian livestock and commensal species not otherwise native to central Texas (listed in Supporting Information Appendix; Table S1). We recalculated all functional diversity metrics and community weighted mean trait values for the Modern + introduced community and compared them with previous temporal communities at Hall's Cave.

3 | RESULTS AND DISCUSSION

3.1 | Changes in functional diversity

Functional diversity was dramatically altered over the Late Quaternary at Hall's Cave (Table 1). Unsurprisingly, the most severe declines occurred following the megafaunal extinction separating the Terminal Pleistocene and Early Holocene temporal communities (Figure 1; Supporting Information Appendix Figures S5–S7). Both functional richness (FVol) and maximum functional range (FRic) declined significantly more than expected given the decline in species richness (Figure 2a,b). Although the values of both fall just inside the expected range in the Early Holocene, the reduction from the Terminal Pleistocene community, indicated by the slope, is significantly steep for both metrics (FVol $Z = -2.15$; FRic $Z = -2.55$; Supporting Information Table S7). Fauna that went extinct in the

Terminal Pleistocene were largely clustered in several distinct regions of functional space (all associated with large body size) as opposed to randomly dispersed throughout (Figure 1). This resulted in a substantial reduction (but not entire elimination) of the area of functional space once populated by the diverse large carnivore and herbivore assemblages of the Pleistocene. This truncation of functional space is reflected in the significant drop in functional dispersion (FDIs; $Z = -6.30$; Figure 2c). This metric signifies the spread of the community from the centroid; hence, a steep decline suggests that extinct species consistently had more extreme trait values and sat in the outer portions of occupied functional space. Furthermore, functional divergence (FDiv) declined from a relatively high value in the Terminal Pleistocene to the lower 25th percentile of null values in the Early Holocene ($Z = -1.76$; Figure 2d; Table 1), indicating a reduction in symmetry around the centroid. Functional divergence and dispersion are independent of species richness, meaning that the pronounced declines following the extinction reflect substantial changes to the distribution of the community resulting from the loss of taxa concentrated in specific regions of functional space.

The transition from the Late Holocene to Historic temporal communities was accompanied by another severe decline in functional richness and dispersion. This contrasts with the preceding period over the Holocene, which was relatively stable in functional diversity despite some climatically driven turnover in species (Smith, Tomé, et al., 2016) (Table 1; Figure 2). At the onset of the Historic period, nine species were extirpated from the Hall's Cave community, including several remaining large-bodied mammals, such as *Bison*

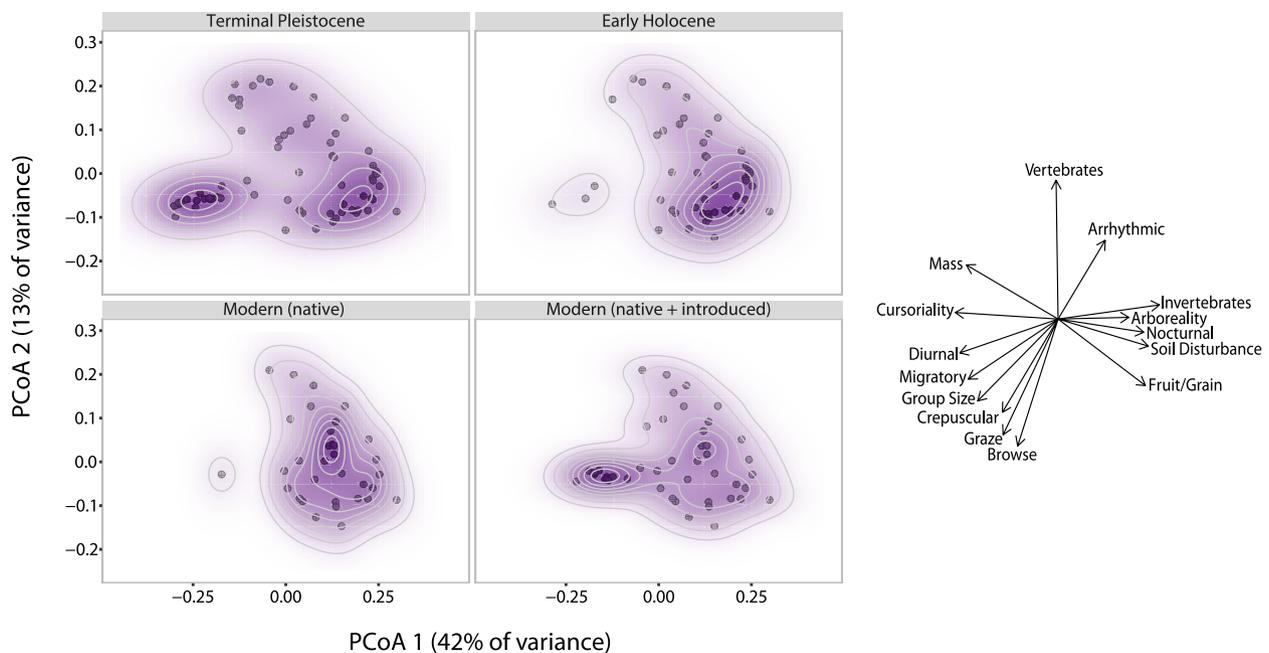


FIGURE 1 Functional trait space of select temporal communities at Hall's Cave visualized on principal coordinates analysis (PCoA) axes 1 and 2 (55% of variance; for plots of additional temporal communities and axes, see Supplementary Information Appendix; Figures S5–S7). Arrows on the right indicate how traits load onto each axis, with PCoA 1 primarily reflecting mass ($r = -.921$), invertebrate consumption ($r = .996$) and migration habit ($r = -.901$) and PCoA 2 primarily reflecting vertebrate consumption ($r = .999$) and browse ($r = -.914$) or graze ($r = -.833$) consumption. Each point represents a species, and fill colour represents their density in functional space

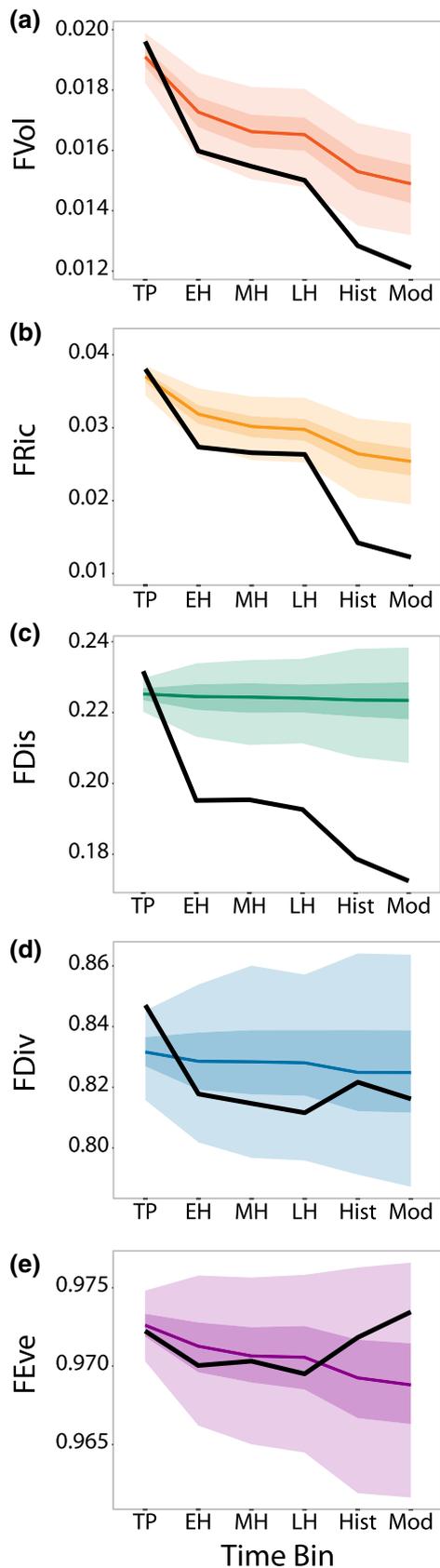


FIGURE 2 Functional diversity metrics at Hall's Cave over time. Black lines represent empirical values; coloured lines represent median values from null model simulations. Shading around coloured lines indicates the 50% confidence interval (darker) and 95% confidence interval (lighter) of null model values. (a) Functional volume (FVol). (b) Functional richness (FRic). (c) Functional dispersion (FDis). (d) Functional divergence (FDiv). (e) Functional evenness (FEve). Abbreviations: EH, Early Holocene; Hist, Historic; LH, Late Holocene; MH, Middle Holocene; Mod, Modern; TP, Terminal Pleistocene

Cave record (Figure 2a,b). Here, the decline in FRic was even more deviant from the null expectation ($Z = -4.35$) than the decline following the Terminal Pleistocene extinction. In contrast, the change in FVol, although large, was not significant ($Z = -.81$). This discrepancy reflects the loss of several remaining large-bodied mammals, which greatly reduced the functional range of the community but had a smaller effect on overall functional volume because the density of this region of functional space was already diminished by the extinction filter. This transition was also accompanied by another significant decline in functional dispersion ($Z = -2.80$; Figure 2c) as species in more distant regions of functional space continued to disappear from the community. However, both functional divergence (FDiv; Figure 2d) and evenness (FEve; Figure 2e) increased, suggesting that the distribution of surviving taxa became more symmetrical around the centre of gravity and evenly distributed in the remaining functional space.

The sustained declines in functional richness, range and dispersion over time resulted in a severely functionally depauperate modern mammal community. Loss of functional diversity exceeded that of random species loss, suggesting a fundamental decoupling of functional diversity and species richness over the Late Quaternary; that is, what species were lost mattered much more than simply the number of species lost. Previous work at the continental scale had found that functional diversity loss following the Terminal Pleistocene extinction was largely indistinguishable from random species loss of the same magnitude (Davis, 2017). Interestingly, this discrepancy might indicate that large-bodied mammals make up a larger proportion of functional diversity at the local scale compared with either regional- or continental-scale assemblages. Furthermore, some ecosystem processes might be reduced or even absent compared with the Late Pleistocene baseline community.

3.2 | Shifts in functional composition

The consequences of functional diversity loss on ecosystem function largely depend on the areas of functional space that were most affected. The reduction in measures of both functional richness and dispersion over time represents a truncation of functional space and, consequently, a major shift in the underlying trait distribution in the community. Specifically, the functional composition of the Early Holocene community was significantly lower in mean mass

bison, *Antilocapra americana* and *Panthera onca*. After this transition, functional richness (FVol) and functional range (FRic) both dropped below the envelope of expected values for the first time in the Hall's

($Z = -5.55$), social group size ($Z = -2.58$), diurnal activity ($Z = -4.94$) and migratory behaviour ($Z = -3.83$) than expected; life-history traits generally associated with large-bodied herbivores (Figure 3; Supporting Information Table S8). Invertebrate consumption and soil disturbance exhibited higher than expected prevalence ($Z = 1.98$ and 2.39 , respectively), undoubtedly because the assemblage was weighted toward small-bodied, omnivorous survivors. Graze and browse consumption also showed a distinct decline, whereas fruit/grain consumption increased in prevalence (Figure 3; Supporting Information Table S8).

These changes in the underlying trait distributions reflect a fundamental shift in energy flow through primary consumers, which can impact the floral composition and vegetation structure. Modern studies have demonstrated that exclusion or extirpation of large-bodied mammalian herbivores quickly cedes woody encroachment in open habitats and increased tree cover on the order of years to decades (Asner et al., 2009; Bakker et al., 2016). Indeed, the Hall's Cave pollen record during the Early Holocene documents an increase in the abundance of trees (Cordova & Johnson, 2019). However, this period also experienced climatic warming following the Younger Dryas and changes in regional precipitation, making the potential impacts of climate versus faunal assemblage shifts difficult to disentangle (Cordova & Johnson, 2019).

The Holocene epoch at Hall's Cave was characterized by climatically driven turnover of mostly small- to medium-sized mammals (Graham et al., 1996; Lundelius, 1967; Toomey, 1993). As

some cool- and/or moist-adapted species shifted north and east over the late Holocene (e.g., *Sorex cinereus*, *Blarina carolinensis*; Lundelius, 1967), other species immigrated into central Texas from the south as the local environment became more suitable (e.g., *Dasyurus novemcinctus*; Humphrey, 1974). Although immigrating and emigrating species were not necessarily functional replacements, climatically driven turnover throughout the Holocene was not driving major shifts in functional composition at Hall's Cave (Figure 3). The three Holocene temporal communities demonstrated highly similar CWM trait values, indicating consistency in overall functional composition over this period. Although our analysis did not quantify the abundance of species through time, surviving small-bodied mammals at Hall's Cave and other sites might have increased in abundance in response to the loss of megafauna (e.g., Blois et al., 2010), potentially making their impact on ecosystem function more pronounced.

The loss of large-bodied taxa through both the Historic and Modern periods once again resulted in major changes in the functional composition at Hall's Cave. Shifts in the underlying trait distribution between the Holocene, Historic and Modern communities exhibited a similar direction to those observed between the Terminal Pleistocene and Early Holocene transition, although with even stronger prevalence of fruit/grain consumption ($Z = 2.72$) and relatively high arboreality ($Z = 2.64$) (Figure 3; Supporting Information Table S8). Previous studies have demonstrated that large-bodied animals have an oversized impact on their local environment and provide ecological functions not readily replicated by smaller fauna,

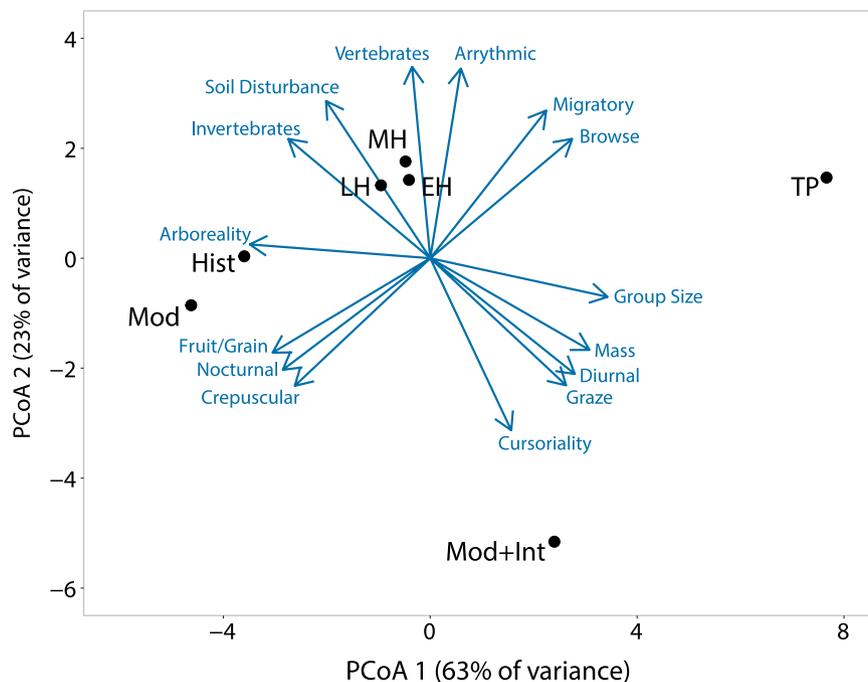


FIGURE 3 Principal coordinates plot showing functional composition of each temporal community at Hall's Cave represented by community-wide mean (CWM) values for each trait. Differences in the position of each community indicate variation in the underlying trait distributions. Arrows indicate how traits load onto first two principal coordinates analysis (PCoA) axes (86% of variance), with PCoA 1 primarily reflecting arboreality ($r = -.997$), group size ($r = .979$) and mass ($r = .879$) and PCoA 2 primarily reflecting vertebrate consumption ($r = .995$), arrhythmic activity ($r = .986$) and cursoriality ($r = -.894$). Abbreviations: EH, Early Holocene; Hist, Historic; LH, Late Holocene; MH, Middle Holocene; Mod, Modern (native only); Mod + Int: Modern (native + introduced); TP, Terminal Pleistocene

including nutrient and seed dispersal over large ranges, prevention of woody growth encroachment, and even timing and duration of spring green-up in some plants (Doughty et al., 2016; Geremia et al., 2019; Johnson, 2009). The shift in trait distribution over time at Hall's Cave, specifically the significant decline in grazing, migratory habit, group size and body size [strongly influencing home range size (Harestad & Bunnell, 1979)] suggests that these ecological functions could have been eroded over time.

3.3 | Change in functional redundancy

The severe decline in functional richness and dispersion following the Terminal Pleistocene megafaunal extinction suggests that species lost provided ecological function that was relatively distinct compared with the community as a whole (Mouillot et al., 2013; Violle et al., 2017). Indeed, extinct taxa demonstrated significantly higher functional distinctiveness than those that survived into the Early Holocene (Student's unpaired t -test, $p = .008$; Figure 4a). Of the top ten most distinctive taxa in the Terminal Pleistocene, seven are extinct megafauna, including *Mammut americanum*, *Mammuthus columbi*, *Bison antiquus* and *Camelops hesternus* (Supporting Information Table S9). Consequently, the mean functional distinctiveness of the Early Holocene community was far lower than that in the Terminal Pleistocene, and it continued to decrease over time (Figure 4b). This signal indicates that species in the outer areas of functional space were consistently lost from the community, resulting in a much more functionally similar modern community with lower functional breadth.

Functional redundancy can be thought of as a measure of ecological resilience; that is, the buffer maintained by a community or ecosystem against the loss of ecological function following extinction or other disturbances (Walker, 1995). A second key dimension of functional redundancy is functional uniqueness, or the amount of overlap between a species and its nearest functional neighbour, measured as pairwise nearest taxon distance (NTD). Importantly, a species can have high functional distinctiveness without being functionally unique. For example, *Bison antiquus* and *Bison bison* had some of the highest functional distinctiveness scores, but one of the lowest pairwise functional distances, suggesting that these taxa were functionally redundant with each other, whilst having a relatively rare combination of traits compared with the overall community. The same is true for some groups of small mammals, such as shrews, which occupy a distinct area of functional space from the greater community but all exhibit high functional similarity (Supporting Information Tables S9 and S10). Thus, the distribution of nearest neighbour distances can indicate how closely packed species are within functional space, whereas the distribution of functional distinctiveness values describes the overall spread.

In comparison to the Terminal Pleistocene community, we found a slight decrease in the number of relatively short NTDs and an increase in far NTDs in the Early Holocene community, although the median distances are statistically indistinguishable (Wilcoxon-Mann-Whitney test, $p = .405$; Figure 5a). This non-significant shift in functional uniqueness contrasts with the marked decline in functional distinctiveness over this same interval. Despite their relative functional rarity in comparison to the community as a whole, many megafauna were not particularly unique and overlapped

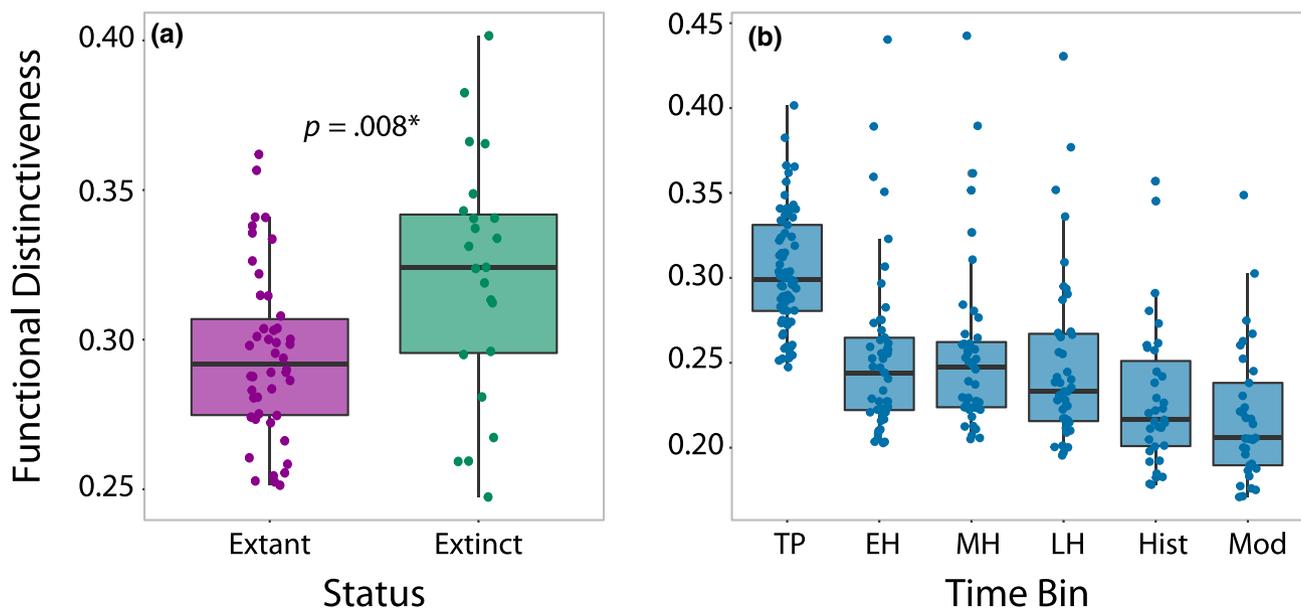


FIGURE 4 (a) Functional distinctiveness values between extant and extinct taxa from the Terminal Pleistocene community. The p -value from Student's unpaired t -test comparing group means indicates that extinct species were significantly more distinct than those that survived. (b) Distribution of functional distinctiveness values of all taxa from each temporal community, showing a decrease in average distinctiveness over time. Abbreviations: EH, Early Holocene; Hist, Historic; LH, Late Holocene; MH, Middle Holocene; Mod, Modern; TP, Terminal Pleistocene

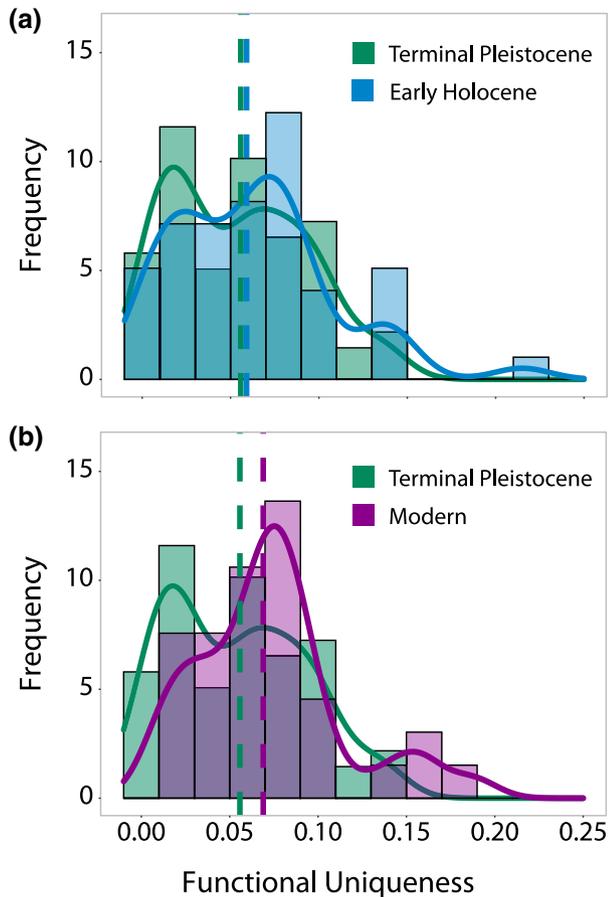


FIGURE 5 Distribution of functional uniqueness values for taxa in (a) Terminal Pleistocene versus Early Holocene community, and (b) Terminal Pleistocene versus native Modern community. Functional uniqueness is measured as the pairwise nearest taxon distance (NTD) in functional space; greater distance indicates higher functional uniqueness. Continuous coloured lines show the density function of distance frequencies for each temporal community; dashed lines indicate the median distance. The distribution of nearest neighbour distances in the Early Holocene is statistically indistinguishable from that in the Terminal Pleistocene (Wilcoxon–Mann–Whitney test, $p = .405$). Distances in the Modern are shifted to the right, with a significantly higher median value compared with the Terminal Pleistocene (Wilcoxon–Mann–Whitney test, $p = .045$)

functionally with other megafauna. Instead, the most unique species in the Terminal Pleistocene were small- and medium-sized mammals, such as *Cynomys ludovicianus* and *Taxidea taxus* (Supporting Information Table S10). Furthermore, because species targeted by the Terminal Pleistocene extinction were clustered in functional space, both members of functional nearest neighbour pairs often went extinct, leaving many extant pairs intact. For the few surviving megafauna, however, functional uniqueness skyrocketed: *Bison bison*, *Canis lupus* and *Ursus americanus* rose from the bottom 50% in the Terminal Pleistocene to the first, second and fourth most unique species, respectively, in the Early Holocene (Supporting Information Table S10). Thus, the immediate effect of the extinction

on functional redundancy was not widely distributed throughout the surviving community, but rather concentrated on surviving large mammals.

The stark lack of redundancy behind certain ecosystem functions provided uniquely by megafauna, such as maintenance of open habitats and top-down trophic control, may have influenced our understanding of their modern ecological role. Both bison and grey wolf are considered keystone species in modern and historical ecosystems (Knapp et al., 1999; Smith, Peterson, et al., 2003); however, our analysis suggests this might be largely attributable to their artificially high unique functional contribution following the extinction filter rather than innate functional rarity. It is unsurprising, then, that the extirpation of several remaining megafauna from the Hall's Cave community preceding the Historical and Modern time bins once again brought about dramatic declines in functional diversity. In the case of FRic, the decline between the Early Holocene and Historic was much greater than that following the initial megafaunal extinction (Figure 2b). This pattern underscores the importance of understanding recent biodiversity loss within the context of prolonged biodiversity erosion and community disassembly of the Late Quaternary.

Indeed, continued extirpation of species from the Hall's Cave community up to the present (owing to either climatic shifts or human impacts) ultimately led to pronounced changes in functional uniqueness among the remaining species. We found that the median NTD in the Modern community was significantly farther than in the Terminal Pleistocene (Wilcoxon–Mann–Whitney test, $p = .045$; Figure 5b). Moreover, there is a distinct shift in the shape of the distribution of NTDs in the modern community, with a substantial decrease in the number of relatively short distances, a large peak in medium distances and a second, smaller peak emerging among relatively far distances (Figure 5b). Thus, the modern community supports fewer species pairs of high functional similarity, despite the reduction in functional breadth of the community as a whole. Simply put, species in the modern community represent a smaller range of ecological function but are farther apart within that functional space. Each species, therefore, contributes on average more unique ecological function than in the past, heightening the potential consequences of future biodiversity loss.

3.4 | Impact of introduced species

Human influences on natural ecosystems extend beyond the removal of species; the introduction of species can also have substantial ecological consequences. Since the early 1900s, the state of Texas has been home to many naturalized exotic large-bodied mammals, which range on public lands in addition to private ranches (Schmidly & Bradley, 2016; Traweek & Welch, 1992). Although influenced by human intervention, these mammals undoubtedly interact with native mammals and their surrounding environment, and therefore warrant consideration in the analysis of community function. We included in our analyses the five most common exotics found near

Hall's Cave (blackbuck antelope, axis deer, sika deer, fallow deer and scimitar-horned oryx) along with seven typical domestic or commensal mammals (domestic cow, horse, sheep, goat, pig, dog and cat).

We found that introduced mammals restored a large degree of functional diversity. Specifically, the inclusion of these species expanded the functional space of the modern community into areas once occupied by the original Terminal Pleistocene assemblage (Figure 1; Supporting Information Appendix Figures S5–S7). Introduced species increased the overall functional richness (FVol) of the modern community from 59.0% to 70.3% of the Terminal Pleistocene value and the maximum trait range (FRic) from 34.4 to 58.5% (Supporting Information Table S11). Moreover, functional dispersion increased to levels comparable to the Holocene community ($FD_{is} = .192$), indicating that introduced species filled in more peripheral areas of modern functional space and increased the average distance to the centroid (Figure 1). In particular, two species (domestic cow and horse, *Bos taurus* and *Equus caballus*) have exceptionally high functional distinctiveness, signalling that they contribute relatively rare trait contributions. Indeed, the average functional distinctiveness of introduced species is significantly higher than that of extant species at an alpha level of .1 ($p = .07$).

Although introduced species restored some of the lost functional diversity, they also introduced novel traits that resulted in a non-analogue community trait distribution. We measured dissimilarity between functional hypervolumes described by two components: Net difference in volume (β_{diff}) and shift in position (β_{repl}). Total functional dissimilarity between the Terminal Pleistocene and Modern + introduced community was substantially lower compared with the native-only Modern community ($\beta_{total} = .45$ and $.37$, respectively; Supporting Information Appendix Figure S8; Table S11). Nonetheless, the Modern + introduced community had the highest proportion of functional replacement of any temporal community ($\beta_{repl} = .10$, 26.3% of β_{total} ; Supporting Information Appendix Figure S8; Table S11), implying that introduced species contributed novel function in addition to restoring some of the lost functional richness. This is supported by the functional composition of the Modern + introduced community (Figure 3), which shifted toward the Terminal Pleistocene community in terms of mean body size, group size and prevalence of grazing, but was distinct from all other temporal communities, with especially high mean cursoriality and low vertebrate consumption (Figure 3). Given that many of the introduced species are large herbivores, it is unsurprising that the functional composition of the community reflected a shift toward this niche and away from traits associated with large carnivores.

Quixotically, we find that a community containing both native and exotic species might function in a more similar manner to the pre-human baseline than the surrounding environment, despite a more direct human influence on the faunal assemblage. Introduced species are typically considered to be detrimental ecologically; however, our results support a growing recognition that certain intentionally selected non-native species may help to restore ecosystem processes as functional replacements for extinct or extirpated taxa (Griffiths et al., 2010; Lundgren et al., 2020), consistent with the idea

of “rewilding” (Donlan et al., 2006; Svenning et al., 2016). Proposed several decades ago, the approach of restoring lost ecological function with selective introductions has become popular in Europe (Helmer et al., 2015; Navarro & Pereira, 2012; Pettorelli et al., 2018), although slow to materialize in North America. Importantly, a much more detailed assessment of the ecological impact of exotic species would be required to determine their full functional role and potential effect on native species. Furthermore, as demonstrated by the non-analogue functional composition of the Modern + introduced community, restoration of certain key ecological functions (e.g., grazing by large herbivores) without others (e.g., prey regulation by apex carnivores) could lead to novel trait distributions with unintended ecological consequences.

3.5 | Conclusion

Our fine-scale analysis of the mammalian community over the past 21 ka at Hall's Cave revealed a striking loss of functional diversity and significant alterations to the underlying trait distribution. Declines in functional richness and dispersion exceeded null expectation given the declines in species richness, resulting in a functionally depauperate modern community. This is consistent with the growing recognition that large animals have an oversized impact on their local environment and provide ecological functions not readily replicated by smaller-bodied fauna (Doughty et al., 2016; Malhi et al., 2016; Smith, Doughty, et al., 2016). The size selectivity of the terminal Pleistocene extinction was not unique to Hall's Cave; hence, we expect similar patterns in functional diversity loss in communities throughout North America. However, we do not yet know whether different environments experienced disparate changes in functional diversity; for example, did areas with lower species diversity overall experience greater functional diversity loss? Further characterization of these nuances is necessary to enhance our understanding of how prolonged biodiversity erosion affects local environments.

Perhaps one of the most important insights from our analysis is that communities in the past supported much higher levels of functional redundancy among species. Mammals within modern communities tend to be more functionally unique, meaning that future extinctions could lead to greater functional diversity loss than they did in the past, underscoring the precarious position of our modern ecosystems. This legacy of degraded ecological resilience has far-reaching conservation implications and might accelerate the negative effects of continued biodiversity erosion on ecosystem processes. In contrast, the acute declines in functional diversity sustained historically by the extirpation of key native mammals, such as bison and grey wolf, imply that the successful reintroduction of these species would lead to considerable functional restoration. The wide-ranging ecological effects of targeted introductions have been demonstrated in areas such as Yellowstone National Park (Smith, Peterson, et al., 2003) and Konza Prairie (Knapp et al., 1999), encouraging support for other reintroduction efforts throughout the continent. Beyond further stressing the need to protect remaining native

biodiversity, our study suggests that some crucial ecological functions might also be restored or reinforced by careful introductions of non-native species functionally similar to bygone fauna. Thus, consideration of the broader temporal context of modern mammalian functional diversity is vital for understanding the current state of biodiversity and developing effective conservation strategies.

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CONFLICT OF INTEREST

The authors state no competing interests.

AUTHOR CONTRIBUTIONS

C.P.H. designed the project, gathered and analysed data and wrote the manuscript. F.A.S. and S.K.L. contributed data, assisted with project design and edited the manuscript.

DATA AVAILABILITY STATEMENT

All occurrence and trait data and the R code used for this analysis are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.w6m905qp>). Additional results and derived data are included in the Supporting Information.

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BIOSKETCH

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SUPPORTING INFORMATION

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