"HERE, SIZE IS NO ACCIDENT": A NOVEL FOOD WEB ANALYSIS OF THE DRY MESA DINOSAUR QUARRY AND ECOLOGICAL IMPACT OF MORRISON FORMATION SAUROPOD FAUNA

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Abstract—The Morrison Formation is a well-preserved Upper Jurassic rock unit with a characteristic terrestrial fauna. Despite over a century of study, the complex ecological interactions remain poorly understood due to preservational bias. Understanding the complex food webs of the Morrison Formation, despite this bias, is important. The preserved biota remains one of the most unique and diverse from the terrestrial fossil record, and reconstructing ecological interactions across deep time remains understudied. Here we present the reconstructed trophic links and food web of Dry Mesa Dinosaur Quarry, a relatively well-preserved Morrison Formation ecosystem, using the R package *cheddar*. We recovered a complex food web with over 12,000 unique food chains. Sauropods had substantially more trophic interactions than their ornithischian counterparts, indicating a substantial and important role in the ecosystem. The ubiquity and diversity of sauropods throughout the ecosystem across deposition, combined with the large body size they attained, underscores their importance as ecosystem engineers. Reconstructing the food web of an extinct ecosystem is an important tool for understanding phylogeny and broader biological concepts, as it provides insight into how ancient organisms interacted, evolved, and influenced each other's adaptations. By understanding trophic links and interactions, the ecological roles and evolutionary pressures that shaped species traits and lineages over time could potentially be determined. This novel food web is the first study of its kind to use trophic analysis to examine Morrison Formation ecological interactions, paving the way for other deep-time food web analyses.

INTRODUCTION

The Morrison Formation is a fossiliferous rock unit deposited over approximately 7-9 Ma from the late Oxfordian to the Tithonian of the Late Jurassic and spreading over 1.2 million km^2 of the western United States (Kowallis et al., 1998; Foster, 2003; Trujillo and Kowallis, 2015; Whitlock et al., 2018; Woodruff, 2019; Foster, 2020; Richmond et al., 2020; Carpenter, 2022). The Morrison Formation fauna is among the best studied Mesozoic fossil fauna, being dominated by non-avian dinosaurs, including sauropods (Tschopp et al., 2015; van der Linden et al., 2025), non-coelurosaurian megatheropods (Farlow et al., 2023), and ornithischians (Foster, 2003, 2020; Barrett and Maidment, 2025), alongside freshwater turtles (Brinkman et al., 2000; Foster and McMullen, 2017), squamates (Evans and Chure, 1998), crocodilians (Foster and McMullen, 2017), fishes (Kirkland, 1998), small mammaliaformes (Foster, 2020), and pterosaurs (Padian, 1998). Of the Morrison Formation fauna, special interest has been given to individual megafaunal assemblages (animals >1,000 kg; Martin, 1973; Galetti et al., 2018) present at quarries representing a myriad of giant herbivores and carnivores. While mammalian megafaunal communities still exist today, such as in sub-Saharan Africa, and have significant effects on the local ecosystems (Sinclair, 2003), fundamental differences between Morrison Formation keystone species and extant keystone species prevent direct comparison, and warrants further investigation of paleoecological dynamics (Foster, 2013; Foth et al., 2015; Foster and McMullen, 2017; McHugh, 2018; Chiarenza, 2024). Additionally, the life cycles of giant dinosaurs, particularly sauropods, were in many ways radically different from those of large mammals (and likely shaped the dynamics of their ecosystems in unique ways), from ecomorphospace overlap (Wyenberg-Henzler, 2022) and morphological differences (Wiersma and Sander, 2017; Melstrom et al., 2021; Peterson et al., 2022) to ontogenetic niche differentiation (Woodruff et al., 2018) and tooth microwear (D'Emic et al., 2013; Price and Whitlock, 2022; D'Emic et al., 2024). Understanding individual Morrison Formation quarries is key to furthering our knowledge of the Morrison Formation as a functional bioregion.

We produced a case study for food web trophic analysis within the Dry Mesa Dinosaur Quarry (DMDQ) to better understand ecological interactions of the Morrison Formation. Modelling a food web is highly novel, and this is the first study of its kind to use trophic analysis to examine Morrison Formation ecological interactions. Food web analyses and comparisons are typically used in modern ecology to compare ecosystems, trophic links, ecosystem stability, and vulnerability through time. In paleo-ecosystems, this has only been applied in a limited capacity, such as in the Eocene Messel Lakes (Dunne et al., 2014). The ability to investigate ecosystem dynamics would enable us to improve our understanding of ecosystem

evolution and vulnerability throughout the Mesozoic, as well as shifts in ecological niches and trophic link interactions, with the potential of identifying keystone species. Modelling was done using the R package *cheddar*, which has been designed for trophic food web reconstructions and statistical food web generation. We applied a cenogram to the ecosystem, which is commonly used in mammalian paleoecology but is more novel for paleoecological analysis in Mesozoic ecosystems.

GEOLOGICAL SETTING

Dry Mesa Dinosaur Quarry

Dry Mesa Dinosaur Quarry (DMDQ) is located within the Colorado Plateau on the Uncompahgre Plateau (Fig. 1) and is a notable prolific Morrison Formation macrovertebrate locality (Chenoweth, 1987, Miller et al., 1991; Fig. 2). The DMDQ is thought to be roughly temporally coeval with Stovall Quarry 8, DMNH Quarry 1, Cactus Park Quarry, and the Dominguez Jones Quarry (Fig. 1), thereby placed in the lower to middle of the Brushy Basin Member of the Morrison Formation strata based on its lithostratigraphic position in the local section (Turner and Peterson, 1999, fig. 3; Boisvert et al., 2024; Boisvert et al., 2025). DMDQ is a conglomeratic sandstone, containing chert pebbles, trough cross bedding, mudstone rip-up clasts, and disarticulated fossils (Britt, 1991; Richmond and Morris, 1998). The fossil-bearing beds at DMDQ are <1.5 m thick and contain little mudstone, in contrast to the deposits alongside the quarry, which are rounded sands. These adjacent deposits are indicative of a broad drainage system that transported multiple rock types from different sources, which then collected in the quarry, with bones settling along the bottom of the depositional channel (Britt, 1991). The bottom of the quarry is located ~37 m above the contact between the Salt Wash and Brushy Basin Members of the Morrison Formation, and 25-32 m below the contact between Buckhorn Conglomerate Member of the Burro Canyon Formation and the Brushy Basin Member of the Morrison Formation (Britt, 1991; Richmond and Morris, 1998; Boisvert et al., 2024; Boisvert et al., 2025), placing it within the Lower-Middle Brushy Basin Member of the Morrison Formation, specifically Zone 4 of Foster's Stratigraphic Levels (Foster, 2003; Foster, 2020; J. Foster, personal commun. 2025).

DMDQ is known to have preserved both mature and immature individuals (Jensen and Padian, 1989; Miller et al., 1991; Curtice and Wilhite, 1996; Horner et al., 2009; Carpenter and Galton, 2018). However, the preservation mode at DMDQ has been the subject of debate. Richmond and Morris (1998) presented evidence for a single catastrophic flooding event after drought, whereas Britt (1991) hypothesized multiple depositional events on the basis of a theropod rib preserved in two modes, one half presumably buried in an initial depositional event, and the other half exposed until a secondary depositional event. Both hypotheses support a relatively short-term depositional regime at the DMDQ, consistent with other Morrison Formation channel deposits (Fig. 1; see Dodson et al., 1980; Morris et al., 1996; Richmond and Morris, 1998; Carpenter, 2013; Foster et al., 2018). Modern and fossil drought-induced assemblages are biased towards immature or small individuals (Conybeare and Haynes, 1984; Smith et al., 2022). Despite this bias, surveys of mass die-off sites in sub-Saharan Africa and North America have shown that extensive scavenging is likely to occur and create a bias against smaller bones remaining in the aggregation, either through on-site scavenging or transport for feeding elsewhere (Haynes, 1988). Dinosaurian ecosystems likely had an increased number of immature animals relative to mature animals compared to modern mammalian ecosystems, with there being a preservational bias against non-mature specimens (Hone and Rauhut, 2010). Modern taphonomic studies of drought assemblages in Africa do not show a total exclusion of smaller vertebrate material, only less than was present in the functional ecosystem (Haynes, 1988). However, Smith et al. (2022) showed that 'juvenile' *Lystrosaurus* spp. could be preserved in a drought assemblage induced by the conditions during the Permian-Triassic mass extinction. They proposed that the articulation of the 'juvenile' *Lystrosaurus* spp. is due to an overabundance of carcasses to scavenge from, and the drought conditions present at DMDQ could have led to similar preservation, only later disrupted by flash flooding (Britt, 1991; Richmond and Morris, 1998). The conditions leading to high preservation of small organisms at DMDQ make it a unique glimpse into the Morrison Formation.

Dry Mesa Dinosaur Quarry Faunal Assemblage

The paleoecology of the Dry Mesa Dinosaur Quarry fauna has been predominantly based on recovered morphospace (e.g., Button et al., 2014), isotopic (e.g., Tütken, 2011), dental microwear (e.g., D'Emic et al., 2013, 2024; Price and Whitlock, 2022), and general morphological evidence (e.g., Wedel and Taylor, 2013; Wiersma and Sander, 2017; Melstrom et al., 2021; Wyenberg-Henzler, 2022; Peterson et al., 2022) which demonstrates dietary differences between taxa such as *Apatosaurus* spp., *Camarasaurus* spp., and *Diplodocus* spp.. However, the absence of sauropod bromalites provides little to no direct data on the exact floral composition of their diets (Wings, 2014). Cranial biomechanical adaptations (Whitlock, 2011B) and tooth morphology changes (Woodruff et al., 2018) do provide clear evidence for ontogenetic niche shifts in sauropods. Their extreme growth trajectories (Chiappe et al., 1998) also support ontogenetic niche shifts, simply due to their inability to physically occupy the same niche when small and immature compared to when reaching skeletal maturity. Non-sauropod presence within the Morrison Formation is confirmed for megalosaurid theropods such as *Torvosaurus tanneri* and the ceratosaurian *Ceratosaurus* sp.*,* which are known to have had a preference for mesic habitats and consuming aquatic fauna (Bakker and Bir, 2004), resulting in potential habitat and dietary niche partitioning from *Allosaurus* spp. (Rauhut et al., 2016). Niche partitioning is further supported by the stomach contents from other megalosaurids such as *Dubreuillosaurus valesdunensis* (Allain, 2005) and slender crania and tooth morphology of *Eustreptospondylus oxoniensis,* indicating piscivory (Sadlier et al., 2006).

Body size is an important ecological functional trait (Calder, 1996; Guo et al., 2022; Parker et al., 2023) that influences the composition of faunal assemblages, such as organism distributions within ecosystems (Farlow et al., 2010), food acquisition/requirements (Kane et al., 2016), and ontogenetic dietary shifts (Schroeder et al., 2021). Of the minimum six sauropod taxa – *Apatosaurus* sp., *Brachiosaurus* sp., *Camarasaurus* sp., *Diplodocus* sp., *Haplocanthosaurus* sp., and *Supersaurus vivianae* – found in DMDQ (Jensen, 1985a, 1985b,1987; Boisvert et al., 2024), *Apatosaurus* sp., *Brachiosaurus* sp.*,* and *Supersaurus vivianae* are the three largest taxa found in DMDQ based on recent size estimates and growth rates of fossil remains found (Lovelace et al., 2007; Benson et al., 2014; Curtice, 2021; Curtice et al., 2023; D'Emic, 2023; Woodruff et al., 2024). It is additionally worth considering the paleobiogeography of DMDQ relative to other quarries, which supports spatial sympatric patterns and seasonal factors influencing growth, one being migration within taxa such as macronarians, including *Camarasaurus* sp. and *Brachiosaurus* sp. (Fricke et al., 2011; Whitlock et al., 2018; Drumheller et al., 2020; Malone et al., 2021). Although the flora of the Morrison Formation has been studied in detail (e.g., Brown, 1972, 1975; Miller, 1987; Tidwell, 1990; Ash and Tidwell, 1998; Tidwell et al., 1998; Parrish, et al. 2004; Tidwell et al., 2006; Gorman et al., 2008; Gee, 2011; Gee et al., 2014, 2019; Gill et al., 2018; Richmond et al., 2019; Xie et al., 2021; Foster et al., this

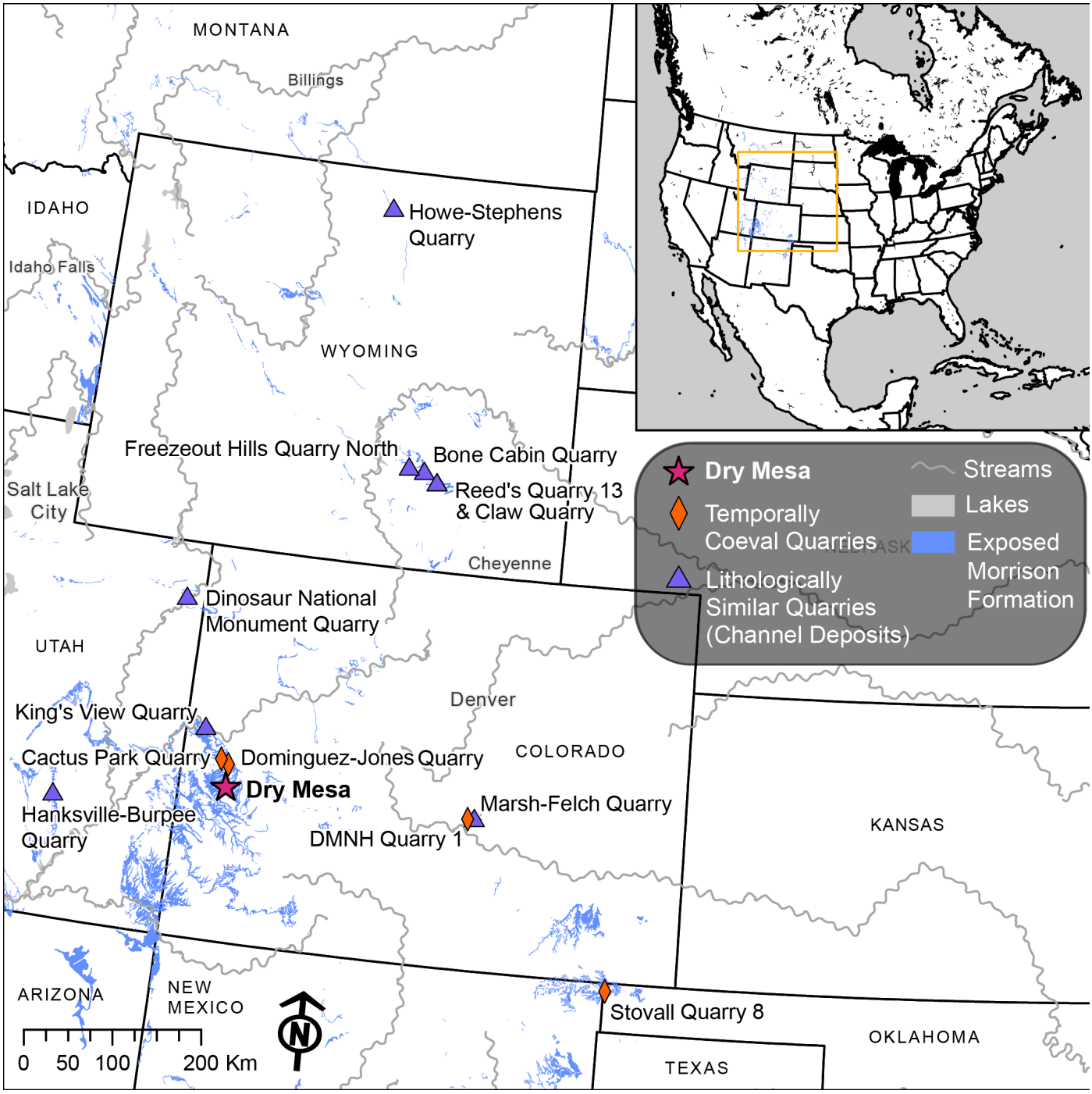

FIGURE 1. Dry Mesa study area overview with temporally coeval quarries indicated with orange rhombuses (modified from Turner and Peterson, 1999). Mapping resources from Natural Earth, U.S. Census Bureau, ESRI, TomTom, FAO, NOAA, USGS/USGS Mineral Database, Garmin, EPA, and USFWS.

volume), no flora from the DMDQ has been reported (Miller et al., 1991; Wings, 2014), but fossils have been recovered (B. Curtice, personal commun. 2025). While floral fossils have been discovered from the Uncompahgre Plateau at East McElmo Creek, another Morrison Formation locality (Tidwell and Ash, 1990; J. Foster, personal commun. 2025), it is unclear if these fossils are the same age as DMDQ and thus were not used.

The depositional setting and high diversity of taxa across multiple size classes and ontogenetic stages result in DMDQ representing one of the most complete dinosaurian assemblages from the Morrison Formation, despite preserving relatively few microvertebrate remains. Due to this brief deposition interval, the DMDQ can be interpreted as a single biota due to preservation over a geologically short period (<10,000 years in a singular timeframe; Britt, 1991; Richmond and Morris, 1998; Foster et al., 2018). During this time, the DMDQ appears to have been relatively stable, showing no signs of having undergone any rapid or major perturbations, suggesting that the preservation of specimens at Dry Mesa does not represent multiple or distinct ecosystems, biotas, or faunal assemblages (Britt, 1991; Richmond and Morris, 1998; Foster et al., 2018). Ergo, the DMDQ can serve as an ideal quarry, especially for dinosaurs, to

quantitatively study Morrison Formation ecosystem dynamics.

METHODS

Materials

We gathered taxonomic occurrences for the DMDQ from the PaleoBiology Database and Foster (2020). These data were used to create the nodes required for the food web (see Taxonomy). Nodes are the components that make up the food web. Fundamentally, nodes are the presence of different ecological units within a food web, i.e., a single taxon could have multiple nodes if there is a change in their ecological role in an ecosystem through ontogeny (Hudson et al., 2013; Dunne et al., 2014). The approach by Dunne et al. (2014) for Eocene food webs, where different ontogenetic stages had different diets and/or occupied different habitats and thus were included as separate nodes, was followed for this study. Furthermore, multiple taxa with an implied presence but little to no taxonomic details, such as flora and invertebrates that were assumed to have identical/similar ecological roles in our model, were assigned a singular node (see Assumptions and Limitations for more details).

Model Assumptions and Limitations

Eight biological principles were used to construct the food web ecological interactions: *Functional Life History Shifts in Dinosauria*, *Gregarious Behavior in Dinosauria*, *Ecological Niche Partitioning*, *Predator-Prey Interactions in Dinosauria*, *Generalism in Carnivorous Diets*, *Generalism in Herbivorous Diets*, *Ecological Nodes for Invertebrates and Floral Ecological Nodes*, *and Other Known Unknowns*, which are subsequently explained.

Functional Life History Shifts in Dinosauria

Dinosaurian faunas included taxa that inherently experienced greater size changes and ontogenetic shifts relative to their neonatal sizes than mammalian faunas (Codron et al., 2013). Mammalian newborns feed on the nutrient-rich milk produced by their mothers until they can eat the same food substrates as the 'adults', resulting in mammals experiencing little to no ontogenetic niche partitioning or shifts (Codron et al., 2013; Erickson, 2014; Nakazawa, 2015). Parental care is known within dinosaurs, though it is disparate and varied across taxa and likely absent in Sauropoda (e.g., nest production; see Chiappe et al., 1998; Horner, 2000; Jackson et al., 2008). For dinosaurs present in DMDQ, assessment of parental care is based on a combination of preserved nesting structures and phylogenetic bracketing. Sauropods typically laid large clutches of eggs into nests with minimal parental care (e.g., Chiappe et al., 2003), whereas known ornithischian (Horner, 1982; Bert et al., 2025) and theropod taxa (Young, 1991; Varrichio et al., 1999; Norell et al., 2018; Tanaka et al., 2019) appear to have employed parental guarding of eggs.

It is well-established that dietary ontogenetic niche shifts occurred within several dinosaurian taxa, and this is an important ecological factor to model (Frederickson et al., 2020; Schroeder et al., 2021; Therrien et al., 2023). Due to the extreme body size changes observed during ontogeny, we elected to categorize growth stages for many saurischian taxa (see Table 1). Using this approach, taxa are represented via multiple nodes of different size classes (size, here used as a proxy for ontogeny) rather than as a single node. This was applied to all sauropods and both *Allosaurus jimmadseni* and *Torvosaurus tenneri* due to their large size changes. *Ceratosaurus* sp. was not split into size classes due to its relatively smaller mature body size, compared to *Allosaurus jimmadseni* and *Torvosaurus tanneri*, and its rapid growth rate (Madsen and Welles 2000; Sombathy et al., 2025; Pereyra et al., 2025). Additionally, we modelled non-age-segregated gregarious behavior in Morrison Formation ornithischians (see Gregarious Behavior in Dinosauria), where

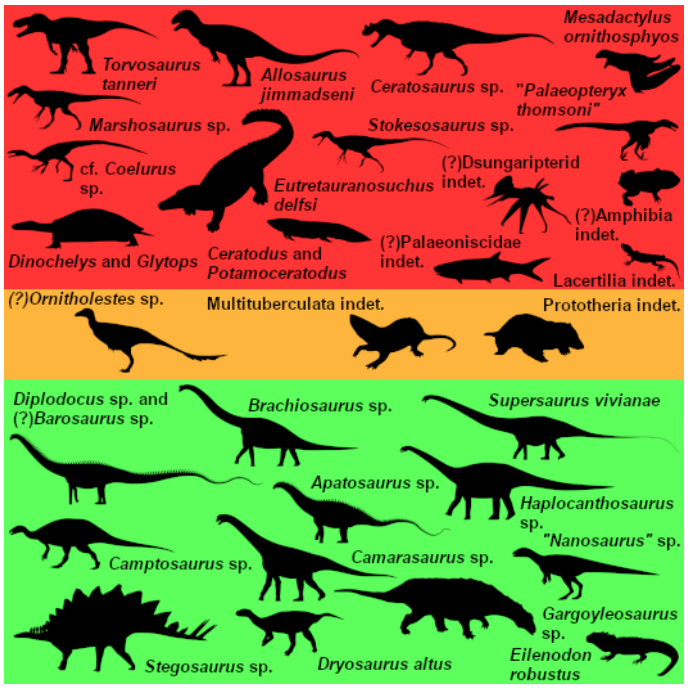

FIGURE 2. Silhouettes of DMDQ fauna arranged in generalized dietary categories. Silhouettes are not to scale. The different background colors relate to the diet of each animal, with green for herbivores, brown for omnivores, and red for carnivores. Phylopic credits (top to bottom via left to right): Jagged Fang Designs, Scott Hartman, Dean Schnabel, Mette Aumala, FunkMonk (Michael B. H.), Jacob Schick, Scott Hartman (modified by T. Michael Keesey), T. Michael Keesey (after Heinrich Harder), R. H. Traquair, Ghedo and T. Michael Keesey, Nobu Tamura, Matt Martyniuk, Nix Illustration, Mathew Wedel, Will Toosey, Andrew A. Farke, Benchill, Gareth Monger, and Robert Gay. Phylopic information for silhouettes, including licenses and license links, can be found in Appendix Table 1.

we elected not to split these taxa into nodes of different growth stages due to predators preferring to predate selectively upon immature, 'elder', or sick individuals and generally avoid healthy mature individuals, consistent with modern taxa that are also gregarious (Palmqvist et al., 1996; Genovart et al., 2010), see below for more details.

Gregarious Behavior in Dinosauria

Despite the evidence from the fossil record, gregarious behavior within Dinosauria remains poorly understood (Hone, 2024). Some modern extant large reptiles can form non-communicative mobs to increase prey capture success, such as in crocodilians (e.g., *Alligator mississippiensis*, *Caiman crocodilus*, *Crocodylus palustris*, *Cr. johnstoni*) (Dinets, 2010; 2015) or Komodo dragons (*Varanus komodoensis*; Shine and Somaweera, 2019). Coordinated hunting behavior has also been observed in extant avian dinosaurs, such as the Lanner falcon (*Falco biarmicus*; Leonardi, 1999) and Harris's hawk (*Parabuteo unicinctus*; Bednarz, 1988). Based on phylogenetic bracketing, it is possible that predatory dinosaurs may have had the capacity for mutualistic gregariousness, which we define as working toward a common goal such as food acquisition (Bednarz, 1988; Leonardi, 1999; Dinets, 2015) or cooperative nesting sites (Horner, 1982; Chiappe et al., 2003; Dinets, 2010).

Observed ontogenetic dietary and spatial niche shifting in Komodo dragons additionally includes cannibalism (Benton, 1991; Purwandana et al., 2016; Shine and Somaweera, 2019). Possible cannibalistic behavior has also been reported from

Allosaurus sp. at Mygatt-Moore Quarry (Drumheller et al., 2020). Conspecifics co-inhabiting a highly stressed environment have the potential to produce behaviors such as cannibalism due to heightened opportunism. While potential traces of craniofacial biting have been reported for *Allosaurus* spp., these could be due to intraspecific competition rather than social interactions between animals in a cooperative group (Hanna, 2002; Foth et al., 2015).

Indications of gregarious hunting in the Morrison Formation, and quarries such as DMDQ or Cleveland-Lloyd Dinosaur Quarry, with larger numbers of *Allosaurus* spp. preserved cannot be confidently treated as evidence of cooperative hunting (Gates, 2005). Furthermore, signs of healed pathologies, caused by traumatic injuries in some *Allosaurus* spp. specimens may indicate potential intraspecific gregarious behavior or scavenging among the taxa, allowing wounds to heal (Hanna, 2002; Foth et al., 2015). An individual of the saltwater crocodile (*Crocodylus porosus*) is known to have been missing approximately 20 cm of its dentary through injury and subsisted on scavenged material (Irwin, 1996), providing an alternative mechanism to gregarious behavior. The lack of strong evidence for social group hunting, cannibalism, and possible pathologies due to intraspecific fighting in Morrison Formation theropods indicates these animals were more likely been solitary hunters than co-operative group hunters.

Gregarious behavior in theropods could influence this study's results. Many authors have cited occurrences such as the discovery of multi-individual bonebeds (Currie and Eberth, 2010), trackways showing the parallel movement of conspecifics (Ostrom, 1972), and bite marks on skeletal elements (Foth et al., 2015) to represent gregarious social behaviors in theropods. Reports of social interactions in theropods are fairly balanced between coelurosaurs (Kobayashi and Lü, 2003 [Ornithomimosauria]; Currie, 2005; Currie and Eberth, 2010; McCrea et al., 2014 [Tyrannosauridae]; Ibiricu et al., 2013 [basal Coelurosauria]) and non-coelurosaurs (Raath, 1990 [Coelophysoidea]; Coria and Currie, 2006; Foth et al., 2015 [Allosauroidea]; Delcourt, 2018 [Ceratosauria]).

Of the large theropods included in this study, the social behavior hypothesis is best supported in *Allosaurus* spp. due to the discovery of associated skeletons and the observed survival of grievously wounded individuals, potentially supported by conspecifics (Foth et al., 2015). In contrast, no analyses have suggested such behavior in *Ceratosaurus* sp. or *Torvosaurus tanneri,* although this could be due to the unequal sample sizes of these taxa relative to *Allosaurus* spp. (Maidment, 2024). However, these hypotheses are contested, with alternative hypotheses, such as loose cooperative associations (Roach and Brinkman, 2007; Frederickson et al., 2020) and agonistic behaviors (Tanke and Currie, 1998) suggested for the purported evidence. Furthermore, a lack of social behavior may be supported by extant phylogenetic bracketing and character optimization (Roach and Brinkman, 2007). Social behavior does not equivalently result in gregarious hunting behavior, as hyenas live socially but generally hunt alone (Holekamp et al., 1997). As such, we chose to reconstruct the large theropods of the Morrison Formation as solitary hunters, pending stronger evidence supporting gregarious social interactions within these taxa. Gregarious behavior that would facilitate predation on sauropods of a greater mass than the maximum prey size (see Table 1) for a theropod at each ontogenetic stage is not factored into the model. As underscored above, the inconclusive nature of gregarious behavior in hunting made us elect this decision regarding the model.

Sauropod taxa found at DMDQ were split into different size classes based on evidence for age-segregated gregarious groups of sauropods (see Table 1). Skeletal associations of *Mussaurus* (Pol et al., 2021), debated aggregations of diplodocoids (Myers and Fiorillo, 2009; Waskow, 2019), and *Alamosaurus sanjuanensis* (Myers and Fiorillo, 2009) fossil remains, in addition to sauropod trackways (Lockley et al., 1986; Castanera et al., 2014), support Age-Segregated Gregarious (ASG) behavior in sauropod taxa. Potential exceptions include fossils of immature individuals and at least one 'adult' apatosaurine at the Cactus Park locality (Curry, 1999; B. Curtice, personal commun. 2025).

In contrast to sauropods, ornithischian taxa are treated as singular size classes rather than as ASG groupings. Support for gregariousness in ornithischian taxa includes a *Dryosaurus* sp. bonebed of individuals from embryonic to 'subadult' growth stages at the Uravan locality (Galton and Jensen, 1973; Scheetz, 1991) and trackways that support social behavior in ornithopods and thyreophorans (Foster and Lockley, 1995; Lockley et al., 1998; Lockley and Matsukawa, 1999; Foster, 2013; Piñuela et al., 2016; Castanera et al., 2024). Additional findings of Cretaceous Dinosaur Park Formation multi-taxic trackways moving in the same direction within a short timeframe also support multi-generic herding in ornithischians, including ceratopsians and ankylosaurs (Bell et al., 2025). It is unclear if Morrison Formation ankylosaurids lived in non-age-segregated gregarious groups, but potential associative skeletal evidence of Cretaceous ankylosaurs of different size classes has been reported and may suggest a widespread trend towards gregariousness within the clade (Britt et al., 2009; Currie et al., 2011; Burns et al., 2015; Kinneer et al., 2016).

Ecological Niche Partitioning

Dietary and spatial niche partitioning has been suggested in megatheropods in the Morrison Formation, as *Torvosaurus tanneri* (Bakker and Bir, 2004) and *Ceratosaurus* sp. (Bakker and Bir, 2004; Yun, 2019) have been inferred to have hunted in and around waterways, such as riverine forests, whereas *Allosaurus* spp. predated on floodplains (Bakker and Bir, 2004; Foster and Chure, 2006). Furthermore, megalosaurids have mostly been recorded from coastal and mesic environments where allosaurids have not been observed (Rauhut et al., 2016). This partitioning was accounted for in the model with trophic links between nodes with *Torvosaurus tanneri* and *Ceratosaurus* sp. interacting with taxa in both aquatic and terrestrial habitats, while these trophic links were not applied to *Allosaurus jimmadseni,* which are modelled to interact with terrestrial vertebrate nodes only; this reflects hypercarnivorous tendencies, whereas *Torvosaurus tanneri*, *Ceratosaurus* sp, and small-bodied theropods would be carnivorous (see Appendix Table 2).

Among herbivorous dinosaurs in the Morrison Formation, evidence suggests niche partitioning (McHugh, 2018; Norris et al., 2025). Diplodocids likely fed on lower, ground-level flora (foliage <1.5 meters) whilst macronarians browsed on higher vegetation (foliage >1.5 meters), impacting the spatial distribution of the sauropods within the ecosystem landscape (Button et al., 2014; McHugh, 2018). Norris et al. (2025) also indicated a difference in the feeding height of *Camptosaurus* sp. compared to *Diplodocus* sp. and *Camarasaurus* sp. at the Carnegie Quarry based on isotopic data. C*amptosaurus* sp. fed closer to the ground, with *Diplodocus* sp. being a mixed browser feeding at a low level, similar to *Camptosaurus* sp., despite the body size difference, and a higher level similar to *Camarasaurus* sp. (Norris et al., 2025).

Phylogenetic bracketing was used to interpret feeding for taxa for which the specific diet is unresolved. One example is the basal diplodocoid *Haplocanthosaurus* sp. (Whitlock, 2011A; Wedel and Taylor, 2013; Tschopp et al., 2015), for which there is no skull or teeth. Since no other well-studied genera are directly proximal to *Haplocanthosaurus* sp. phylogenetically in both time and space (except for possibly *Amphicoelias altus*, see Mannion et al., 2021; van der Linden et al., 2025), and due to

being consistently recovered as one of the basalmost diplocoids, this has made the paleoecology of *Haplocanthosaurus* sp. enigmatic (Dodson et al., 1980). However, the postcranium suggests a similar niche to either *Apatosaurus* spp. or other basal diplodocoids, due to tall cervical vertebrae, not as elongated as more derived diplodocoids (e.g., *Barosaurus* sp. or *Supersaurus vivianae*; see Tschopp et al., 2015; van der Linden et al., 2025). Ecologically, this makes more sense, as it falls in line with hypothesized feeding heights and microwear observed in other derived sauropods (Boisvert, 2024; Poropat et al., 2025; Winkler et al., 2025). Where direct evidence is unavailable, ecological and phylogenetic inferences were applied to other taxa within the model, such inferences thereby rendering *Haplocanthosaurus* sp. as a low-level browser akin to *Apatosaurus* sp..

Based on all ecological and phylogenetic inferences factored into the model assumptions, niche partitioning is accounted for by characterizing sauropods at DMDQ into three groups: low-level browsers (*Haplocanthosaurus* sp. and *Apatosaurus* sp.), mixed feeders (including *Diplodocus* sp., *Barosaurus* sp., and *Supersaurus vivianae*), and mid to high-level browsers (such as *Brachiosaurus* sp. and *Camarasaurus* sp.).

Pterosaur material is particularly sparse in the Morrison Formation, especially compared to the Lagerstätten Lower Cretaceous Yixian Formation (Unwin et al., 2000; King et al., 2006; Foster, 2020), and in DMDQ, they are represented by possible dsungaripterids (Unwin and Heinrich, 1999) and the potential anurognathid *Mesadactylus ornithophyros* (Jensen and Padian, 1989), although this taxonomic assignment has been disputed (Sprague et al., 2018). *Mesadactylus ornithophyros* is best understood to be an insectivore like other anurognathids (Clark and Hone, 2023), whilst derived dsungaripterids are known to be durophagous (Unwin and Heinrich, 1999; Chen et al., 2020). We used these dietary guilds in the model.

The lepidosaurs of DMDQ were modelled as insectivorous (Lacertilia indeterminate [Foster, 2020]), with *Eilenodon robustus* as herbivorous (Jones et al., 2018). All mammals present in DMDQ are assumed to be largely fossorial and insectivorous, due to dinosaurian dominance and relatively small mammalian body size during the Jurassic (Prothero and Jensen, 1983; Jensen, 1984; Agustí and Antón, 2002; Foster, 2009, 2020). All other vertebrates recovered from DMDQ are aquatic carnivores (i.e., dipnoine [Kirkland, 1998; Pardo et al., 2010; Foster, 2020] and paleoniscoid fish [Kirkland, 1998; Foster, 2020], amphibians [Jensen and Padian, 1989; Gardner and DeMar, 2013; Foster, 2020], testudines [Britt, 1991; Brinkman et al., 2000; Foster, 2020], and the goniopholidid crocodyliform *Eutretauranosuchus delfsi* [Smith et al., 2010; Foster, 2020]), which in the broader ecosystem constrains them to aquatic environments or habitats with a close proximity to water (see Appendix for full details).

Predator-Prey Interactions in Dinosauria

Therrien et al. (2023) applied a phylogenetically corrected regression model to infer the minimum and maximum prey size (body mass) of the Late Cretaceous tyrannosaurid *Gorgosaurus libratus*. We used the upper regression formula of the model in Therrien et al. (2023) to establish maximum prey sizes for *Allosaurus jimmadseni* and *Torvosaurus tanneri* at different growth stages for the model, expressed as body mass, thus calculating the body mass of sauropods when they become immune to predation from growth stages of *Allosaurus jimmadseni* and *Torvosaurus tanneri*. The upper regression formula of the model was used due to the strong prevalence of sauropods in our study biota, contrasting with the biota analyzed in Therrien et al. (2023) (see *Dry Mesa Dinosaur Quarry Compared to Late Cretaceous Tyrannosaurid-Dominated Ecosystems* below in Discussion). Because of this, using purely identical methods from Therrien et al. (2023) may induce errors due to untested differences in ecosystem structures between ecosystems containing a diverse array of large sauropod species. For instance, the Therrien et al. (2023) data suggested that the minimum potential prey size for *Gorgosaurus libratus* would be a mouse-sized mammal (<30 g) or insect. Therefore, a minimum prey size was generally not considered for the food web model due to the abundance of large-bodied sauropods, which would force almost all small-bodied theropods to feed upon other prey items (e.g., animals smaller than themselves; see Table 1; Schroeder et al., 2021; Holtz, 2021); this would be largely due to the immense size of the great majority of sauropods at DMDQ. Additionally, the upper limit of prey mass may not have been the standard typically acquired for predators in DMDQ, based on Therrien et al. (2023). Exploring the relationship between prey size hunted and the distribution of prey size preserved is beyond the scope of this study. In modern ecosystems, the same relationships in predator-prey body size have been observed (i.e., as predator body size increases, prey body size increases too; Li et al., 2023), which renders this generalized assumption reasonable for *Allosaurus jimmadseni* and *Torvosaurus tanneri* modelled herein.

Dinosaurian stomach contents can be rare, but for the small maniraptoran taxa, there appears to be a generalist rather than specialist nature (O'Connor et al., 2019; Hone et al., 2022; Cullen and Cousens, 2024). Combined with apparent paedomorphic conditions across Coelurosauria (Bhullar et al., 2012; Foth et al., 2016; Cau, 2024), this suggests that generalist diets could have been maintained throughout ontogeny, as found in this analysis. Generalism and opportunism have been observed on the African savanna, where lions (*Panthera leo*) will go after smaller and more agile gazelles, which are not their usual prey, or hunt the larger and more dangerous buffalo, giraffes, or elephants when the opportunity arises (Sinclair et al., 2003; Davidson et al., 2013). This analogy would support the reconstruction of predatory theropods consuming immature and weaker prey such as recently hatched sauropods, supporting the model assumption of not including a minimum prey body size (Hone and Rauhut, 2010). In Table 1, maximum prey body size for several ontogenetic stages of *Allosaurus jimmadseni* and *Torvosaurus tanneri* are shown, with maximum body masses inferred from literature and calculating body mass for *Allosaurus jimmadseni* via femoral circumference data (Madsen, 1976; Campione et al., 2014). Immunity from predation by *Allosaurus jimmadseni* and *Torvosaurus tanneri,* respectively, is set at the largest sauropod size classes (see Table 1).

Generalism in Carnivorous Diets

Theropods were assumed to exhibit dietary plasticity based on comparisons with extant carnivores and well-studied recent ecosystems. Habitat preferences have been found to exist in many extant carnivores; however, modern carnivores are unlikely to have specialized diets, instead selecting for a wide variety of prey. Within felids, *Puma concolor* has a varied seasonal diet consisting of deer, cattle, rabbits, and rodents, though *Puma concolor* will target 'adult' individuals of bighorn sheep where they co-occur, despite other prey being available (Cunningham et al., 1999; Rominger et al., 2004). *Panthera leo* feeds on prey ranging in size from small mice to 'adult' elephants (Hayward and Kerley, 2005; John Power and Shem Compion, 2009; Davidson et al., 2013). However, the broadest diet of any felid is found in *Panthera pardus*, and includes 92 species within sub-Saharan Africa alone, and includes other carnivorans such as the cheetah (*Acinonyx jubatus*) and multiple species of civets (Hayward et al., 2006). Extant crocodilians undergo ontogenetic niche shifts while maintaining diverse diets (Dinets, 2015; Hanson et al., 2015; Rosenblatt et al., 2015), as does *Varanus komodoensis* (Shine and Somaweera, 2019). Studies on Pleistocene fauna, including some extant taxa, also indicate variability in the diet of large carnivorans (Bocherens,

TABLE 1. Theropod maximum potential prey size (kg) based on sauropod size classes. Size classes contain gradients, yet the predator mass in our model is the maximum mass of the predator within a singular size class (*Allosaurus jimmadseni*/*Torvosaurus tanneri*). The sauropod size class corresponds to the maximum mass of prey compared to the same value of the predator size class. The mass values are rounded to the nearest kilogram.

***Torvosaurus* size class**	***Allosaurus* size class**	**Predator mass (kg)**	**Maximum potential mass in kg of prey**	**Sauropod size class**
Torvosaurus 1	*Allosaurus* 1	100	125	Sauropod 1
Torvosaurus 2	*Allosaurus* 2	400	629	Sauropod 2
Torvosaurus 3	*Allosaurus* 3	973	1772	Sauropod 3
Torvosaurus 4	*Allosaurus* 4	1238	2347	Sauropod 4
Torvosaurus 5	*Allosaurus* 5	1415	2742	Sauropod 5
Torvosaurus 6	*Allosaurus* 6	1979	4055	Sauropod 6
Torvosaurus 7	Immune from predation (from *Allosaurus*)	2433	5158	Sauropod 7
Immune from predation (from *Torvosaurus*)	Immune from predation (from *Allosaurus*)	N/A	>5158	Sauropod 8

2015; DeSantis et al., 2019). Even the previously hypothesized North American cheetah *Miracinonyx,* has more recently been found as having a highly variable diet in some populations (Higgins et al., 2023). This flexibility in diet is best exemplified by *Panthera pardus* having a much broader diet than the slightly larger *Panthera leo* (Hayward and Kerley, 2005; Hayward et al., 2006; John Power and Shem Compion, 2009; Davidson et al., 2013). The modern example between *Panthera leo* and *Panthera pardus* illustrates that new data on diet variability in Morrison Formation predatory theropods can alter the results of this study, yet the dietary plasticity of the model can account for future discoveries.

Variation in prey selection depends on multiple factors, such as prey availability and time of the year. Griffiths (1975) shows that a variety of extant aquatic predators, including copepods, certain plankton, and fish, vary their diet, including prey selection of zooplankton and shrimp, throughout ontogeny and season. Felids, notably *Puma concolor*, and *Panthera leo* also vary their diets considerably depending on the season (Cunningham et al., 1999; Hayward and Kerley, 2005; Davidson et al., 2013). Some aves have been shown to feed as energy maximizers, selecting for multiple sizes of prey depending on the variation in size and number of available prey, selecting for multiple sizes of prey depending on the variation in size and number of available prey (Griffiths, 1975). Similarly, feeding variation is expected in theropod dinosaurs, and varied diet, habitat, and functional morphology have been hypothesized in some Morrison Formation theropods. Farlow and Pianka (2002) examined how co-occurring theropods were likely partitioned along morphology, habitat, or size, while Bakker and Bir (2004) suggested evidence for spatial partitioning between *Allosaurus* spp., *Ceratosaurus* sp., and *Torvosaurus tanneri*, with the latter two being more likely to live in mesic habitats. Finite element analysis from Maggio et al. (2024) indicates differing feeding and predatory strategies in *Allosaurus* sp. and *Ceratosaurus* sp.. The collected data from extinct predatory theropods reveal flexibility that agrees with the flexibility observed in extant predators.

Theropod dinosaurs would have likely preferentially consumed small (e.g., ornithischians) and immature prey items (Hone and Rauhut, 2010; Lei et al., 2023). However, in modern ecosystems, abundance of large mature prey, or changes to a highly stressed environment can cause increased predation on 'adult' animals (Rominger 2004; Joubert, 2006; Davidson et al., 2013; Drumheller et al., 2020), meaning theropod predation upon the largest sauropods may have rarely occurred, such as under heightened opportunism or desperation. The theropod clade Megalosauroidea exhibits dietary variations within the broader clade and individual taxa. Firstly, *Baryonyx walkeri* is understood to have consumed fish and dinosaurian prey (Charig and Milner, 1997). Secondly, *Poekilopleuron bucklandii* and *Dubreuillosaurus valesdunensis* are known to have consumed fish (Eudes-Deslongchamps, 1838; Allain, 2005). Lastly, the derived megalosauroid clade Spinosauridae consumed pterosaurs, which were either hunted or scavenged (Buffetaut et al., 2004), in addition to fish and aquatic prey (Amiot et al., 2010; Hassler et al., 2018; Beevor et al., 2021). This generalism has been integrated into the model by incorporating different ecological trophic links between prey and predators when evidence is available (see Appendix Table 2).

Generalism in Herbivorous Diets

Similar to theropods, sauropods have been proposed to have exhibited spatial niche partitioning; however, dietary generalism should also be expected due to both being not mutually exclusive. Generalism in modern herbivore diets has been observed, notably in mammals of the African savanna, where browsers consume a range of foliage types and dietary shifts occur in response to seasonal changes in vegetation (e.g., Shannon et al., 2013; Owen-Smith, 2021). Few extant herbivorous mammals rely on an extremely specialized diet, such as the *Eucalyptus* spp. diet of koalas (*Phascolarctos cinereus*; Moore et al., 2005) and the predominantly bamboo diet of giant pandas (*Ailuropoda melanoleuca*; Wei et al., 2015). This is despite generalist herbivorous mammal taxa from the Miocene to the present day, conversely suggested to be mostly composed of specialists, where this is a potential mechanism reducing intraspecific competition (DeSantis et al., 2022). However, fossil evidence largely points to dietary generalism in different megafaunal mammals (seen in Late Pleistocene North American bison assemblages, Rivals and Semprebon, 2011; large herbivores from Pleistocene Britain, Rivals and Lister, 2016; Late Pleistocene ungulates from Spain, Rivals and Álvarez-Lao, 2018; North American herbivorous mammals across the last seven million years, Pardi and DeSantis, 2021) and herbivorous dinosaurs (inferred from phytoliths in Late Cretaceous coprolites from India [Prasad et al., 2005]; forage quality and biomass availability for large herbivores [Clauss et al., 2013]; contents of coprolites from Late Cretaceous megaherbivorous dinosaurs [Chin et al., 2017]; Jurassic flora digestibility [Howell et al., 2023]). As dietary generalism largely occurs within extant and extinct herbivores, we decided to include dietary generalism in the herbivores present at DMDQ in the model. This was accounted for in the model by using broad plant categories; see "Floral Ecological Nodes and Other Known Unknowns" for more details.

For Morrison Formation herbivores, ornithischian dinosaurs likely functioned as relatively low-level browsers. *Stegosaurus* sp. may have browsed approximately 1 m above ground level (Weishampel, 1984; Coe et al., 1987; Galton and Upchurch, 2004), feeding on low-level foliage such as ferns, horsetails (Barrett, 2014), a range of gymnosperm soft parts such as leaves and shoots (Weishampel, 1984), and possibly the fleshy sarcotesta of cycad seeds (Mustoe, 2007). The ornithopods *Camptosaurus* sp. and *Dryosaurus altus,* and the neornithischian *Nanosaurus* sp., also likely fed on low-level vegetation like ferns (Foster, 2020), with *Camptosaurus* possibly also feeding up to 2 m above ground (Dodson et al., 1980) and on tougher vegetation such as horsetail shoots (Foster, 2020). While there is no direct evidence for the diets of the ankylosaurids *Gargoyleosaurus parkpinorum* and *Mymoorapelta maysi*, they can be inferred as selective browsers of low-level plants based on plant remains from preserved gut contents of an Australian ankylosaurid (Molnar and Clifford, 2000; Foster, 2020). Considering all these factors, our model assumption of grouping foliage by height is reasonable for ornithischians, as these herbivores likely

consumed a range of foliage types from plants they could reach.

Ecological Nodes for Invertebrates

Whilst no arthropods have been found in the DMDQ, they are assumed to have been present due to their ubiquity within terrestrial ecosystems. Evidence of terrestrial fossil arthropods, namely boring traces and other trace fossils of purported hymenoptera such as ants, beetles, and bees (Hasiotis, 2004; Britt et al., 2008; McHugh et al., 2020), has been observed in various Morrison Formation quarries. It should be noted that insect body fossils from the clades Orthoptera, Hemiptera, and Coleoptera have been found in the Morrison Formation (Smith et al., 2011; Lara et al., 2020, 2023). Additional evidence for aquatic invertebrates, including arthropods such as horseshoe crabs and crayfish (body fossils; Hasiotis and Kirkland, 1996; Lara et al., 2023; ichnofossils; Hasiotis, 2004), mollusks, such as unionid mussels (Stokes, 1985; Lockley et al., 1986; Evanoff et al., 1998; Good, 2004), and gastropods (Stokes, 1985; Lockley et al., 1986), has equally been observed. Potential predators of invertebrates and possible insectivores in DMDQ (e.g., pterosaurs, mammals, and small non-avian dinosaurs) have not been preserved well enough to have isotopic and/or microwear analysis carried out to differentiate invertebrate prey. This prevents trophic links from being modelled at a finer resolution than the large ecological functional groups of terrestrial or aquatic invertebrates. DMDQ lacks the exceptional preservation conditions observed in other depositional settings (e.g., the lacustrine Eocene Messel Lakes, see Dunne et al., 2014), used to reconstruct invertebrate and floral interaction in the fossil record and to reconstruct the faunal-floral interactions at a high resolution. Based on the limitations and past procedures in prior literature, we used a similar approach as Carrano and Velez-Juarbe (2006), by dividing invertebrates into two separate nodes: terrestrial invertebrates and aquatic invertebrates.

Floral Ecological Nodes and Other Known Unknowns

Regarding Morrison Formation flora, even if we used a well-preserved floral composition from a comparable site, no unambiguous trophic links can be made between herbivore taxa and specific floral taxa. For example, it is difficult to know which ferns or cycads an individual diplodocoid taxon might have fed upon, or which conifers may have fed a specific macronarian. Possible plant groups which may have had present taxa at DMDQ or within the surrounding region in which the Morrison Formation outcrops include: Conifers (Araucariaceae, Podocarpaceae, Cupressaceae, and Pinaceae), *Gingko* sp., horsetails (*Equisetum* sp.), ferns (Polypodiopsida), cycads (Cycadophyta), Bennettitales, and seed ferns (Pteridospermatophyta) (Tidwell et al., 1998; Gee, 2011; Gill et al., 2018; Foster et al., 2023; Gee, 2023A, 2023B).

Isotopic data may help to constrain further trophic levels, but specific food sources cannot be determined as discrepancies between apatite and collagen $\delta^{13}C$ values vary with trophic level due to differences in the macronutrient sources utilized by vertebrates (Kreuger and Sullivan, 1984). Carnivores derive their energy primarily from prey lipids and proteins, which are isotopically lighter than the plant-derived carbohydrates consumed by herbivores (Lee-Thorp et al., 1989). This reliance on energy sources that are depleted in $\delta^{13}C$ is reflected in the bone tissues of carnivores, where the collagen-apatite $\delta^{13}C$ spacing narrows with increasing trophic level (Lee-Thorp et al., 1989; Bocherens and Drucker, 2003). The $\delta^{13}C$ offset between predator and prey in bone collagen and enamel typically ranges from 0 to 2‰ (Bocherens and Drucker, 2003).

Whereas variation in $\delta^{13}C$ values may indicate a broader diversity of consumed plant types, increased variability in this signal can also suggest that the local vegetation was subjected to greater environmental stress—such as nutrient limitations, waterlogging, or drought—which would have influenced stomatal regulation and CO_2 uptake (Fricke and Pearson, 2008). Isotopic analysis on the late Campanian ornithischians of Laramidia revealed that dietary niche partitioning occurred between hadrosaurids, ceratopsids, and ankylosaurids, but there was also overlap in at least some of their diets, with the isotopes unable to resolve specific diets to the flora level (Cullen et al., 2020; Cullen et al., 2022).

The laying of eggs and their appearance within the ecosystem are considered an annual event with fluctuations via upticks in resources and seasonal gathering, where pathologies can be inflicted by a lack of resources, and an uptick in resources can induce population increase (Varricchio, 2011; Dhiman et al., 2022; Chapelle et al., 2025). We did not include eggs as a food source in the model, as there is no evidence for them being a food source for any Morrison Formation taxon specifically. Furthermore, there is no evidence for particular breeding periods for any dinosaurs, though it has been suggested that the Morrison Formation likely had wet and dry seasons (Turner and Peterson, 2004; Parrish et al., 2004), and, therefore, eggs as a food source were not continuously available. This is despite the preservational bias against eggs in the Morrison Formation, although rare specimens have been recovered, such as eggshell fragments of a small carnivorous coelurosaur in Delta County, Colorado (Young, 1991), a nearly complete dinosaur egg from Cleveland-Lloyd Dinosaur Quarry that exhibits a pathological eggshell layer (Hirsch et al., 1989), and an embryonic ornithopod in Garden Park, Colorado (Brill and Carpenter, 2001). The Kirkland Egg site, however, has preserved both eggshell and hatchling bone, unheard of elsewhere in the Morrison Formation (Foster et al., 2016).

Despite their importance in extant ecosystem biodiversity (e.g., Howison et al., 2016), no detritivores were modelled into the food web as per other paleo food web reconstructions (Carrano and Velez-Juarbe, 2006; Matsukawa et al., 2014), especially as there is no evidence for any taxonomic or functional difference between the detritus-feeding invertebrates at DMDQ.

Taxonomy

Assessing the diversity within the DMDQ stems from a strong taxonomic foundation – albeit contentious for select specimens – which in turn impacts food web structure, even if certain taxa fill in similar roles. Small-bodied vertebrates are generally more taxonomically diverse compared to larger-bodied vertebrates within the same ecosystems (Dunne et al., 2014; Matsukawa et al., 2014). However, taphonomic biases against small-bodied vertebrates (Conybeare and Haynes, 1984; Haynes, 1988; Brown et al., 2022) make it unlikely that all small-bodied vertebrates in the DMDQ are preserved. Three different pterosaur genera are known from the Morrison Formation (Foster, 2020). However, pterosaur diversity is likely to be higher in the Morrison Formation (Unwin and Heinrich, 1999), as the Yixian Formation shows exceptional preservation of small-bodied vertebrates (i.e., pterosaurs), yielding a substantially higher number of genera than previously thought (Unwin et al., 2000). Hence, we acknowledge that the small vertebrate taxa are not fully represented, but this is a limitation of the fossil record. We attempted to incorporate the known functional diversity at DMDQ by representing different ecological functional nodes of smaller taxa.

To account for the possible presence of *Barosaurus* sp. (Britt, 1991), which has been questioned in recent literature (e.g., Curtice, 1996; Curtice and Wilhite, 1996; Tschopp et al., 2022–2025; B. Curtice, personal commun. 2025), the analysis was run with and without *Barosaurus* sp. as ecological nodes representing ontogenetic stages like the other sauropod genera. Historically indeterminate ankylosaurian remains have been reported from the DMDQ (Kirkland et al., 1998; Foster, 2020),

but these have been assigned to *Gargoyleosaurus* sp. (J. I. Kirkland, personal commun. 2025) in our analysis. A review of all Morrison Formation small-bodied ornithischian material, including *Nanosaurus agilis, Laosaurus celer,* and *Drinker nisti,* rendered these taxa as dubious (Barrett and Maidment, 2025), yet the recorded abundance of small-bodied ornithischian material in the DMDQ should not be discounted due to abundant remains and other well-studied taxa outside of the DMDQ (e.g., *Dryosaurus* spp., *Fruitadens haagarorum*, and *Camptosaurus spp.* [Scheetz, 1991; Horner et al., 2009; Carpenter and Galton, 2018]). Since the food web is fundamentally based on ecological units derived from taxonomy, we retain *Nanosaurus* sp. as an ecological functional faunal unit of a small-bodied ornithischian (referring to it as "*Nanosaurus*" sp., see Fig. 2).

Several small-bodied theropods of the Morrison Formation are fragmentary and currently not well understood despite occurrences at DMDQ (Britt, 1991; Miller et al., 1991), such as "*Palaeopteryx thomsoni"* (Jensen, 1981; Jensen and Padian, 1989), cf. "*Archaeopteryx* sp." (Jensen, 1981), *Ornitholestes* sp. (Chapelle et al., 2021), and *Coelurus* sp. (A. Ruebenstahl, personal commun. 2025). Given the unparsimonious likelihood that "*Archaeopteryx* sp." is present in the Morrison Formation, and considering the remains of *Ornitholestes* sp. and *Coelurus* sp. in DMDQ are highly fragmentary and uncertain taxonomically (A. Ruebenstahl, personal commun. 2025), we excluded them from the food web. These reports may represent "*Palaeopteryx thomsoni"* or possibly another paravian yet to be named via sophisticated diagnostic criteria. Yet it can be concluded that at least one small maniraptoran theropod was present at DMDQ. We retain "*Palaeopteryx thomsoni"* as an ecological unit that represents at least one paravian present in the DMDQ.

We have elected to exclude indeterminate remains of: (?) Dromaeosauridae, Maniraptora, Mammalia, (?)Pterodactyloidea, and 'Crocodylidae' (=Crocodylomorpha; Brochu, 2003) within the food web, since the higher clade taxonomic occurrences are reported at DMDQ and these indeterminate remains cannot be ruled out as belonging to the higher taxonomic occurrence reported (Prothero and Jensen, 1983; Jensen, 1984; Jensen, 1985b; Jensen and Padian, 1989; Britt, 1991).

Reconstructing Trophic Connections and Model Generation

We used the R package *cheddar* to analyze the nodes and trophic links (Hudson et al., 2013) to generate the food web along with accompanying metrics (see Results and Discussion). A trophic link is defined as a link between two food web nodes (Cohen and Briand, 1984) and is reconstructed herein based on literature, adopting similar approaches and principles as Dunne et al. (2014). Due to limited data, however, we did not weigh the links of the food web as in Dunne et al. (2014), where we could not define portions of the diet per taxon (e.g., *Torvosaurus tanneri* was eating 30% fish and 70% terrestrial vertebrates). Instead, we used the following proxies to determine ecological dietary interactions: dental microwear data, isotopic analyses, phylogenetic bracketing, morphometrics, biomechanics, spatial partitioning, occurrence data, predator-prey interactions, and size (see Model Assumptions and Limitations, and for details on the proxies, see Appendices). We calculated maximum prey size using a regression formula in Therrien et al. (2023, fig. 5) for predators of different size classes (Table 1) to determine potential maximum prey size (see Predator-Prey Interactions). Predatory cannibalistic links for theropods of the smaller size classes were included if they were within the prey size limit of the larger size class.

DMDQ is interpreted to represent a drought assemblage with one or multiple potential flooding events (Britt, 1991; Richmond and Morris,1998). Rather than focus on infrequent seasonal events, such as droughts, that may occur once a decade (or century) and can lead to extreme conditions and cannibalistic behavior, or far more dangerous acquisition of prey compared to normal ecological regimes (Gates, 2005; Peterson et al., 2017; Drumheller et al., 2020), we assigned trophic links based on a static ecological regime and climatic conditions based off the assumptions in 'Model Assumptions and Limitations' (see above). Furthermore, while some of the genera, especially the larger sauropods, may have traveled to DMDQ from elsewhere as a potential water source, we interpret the fauna preserved here as representative of a regional biota (every faunal organism within a single depositional basin as defined in Patzkowsky, 2017).

Based on this assumption, while DMDQ may represent a more extreme faunal sample in terms of taxa present than other quarries such as Carnegie Quarry, Mygatt-Moore Quarry, or the Marsh-Felch Quarry, it is still representative of the regional fauna present in the area at this time in the Late Jurassic. While it is unlikely that every taxon used the environment in identical ways, interactions between taxa and populations along environmental gradients are expected based on recent work on the origins and evolution of regional biotas (Patzkowsky, 2017). If it is assumed that taxa congregated at DMDQ from multiple parts of the environment, then it stands to reason that the evidence of some sauropods migrating long distances means that those sauropods would have been traveling along environmental gradients, rather than remaining in a single homogenous habitat (Fricke et al., 2011; Winkler et al., 2025). Otherwise, all taxa preserved must have lived in the same habitat. Varied environmental conditions in the Morrison Formation suggest the former as the more likely occurrence at the DMDQ (Whitlock et al., 2018). DMDQ therefore provides a unique opportunity, as organisms living along portions of the environmental gradients not normally preserved are represented at DMDQ, allowing for a more in-depth analysis of complex interactions than would be possible at other localities.

In addition to this, the R package *cheddar* does not have a specific feature to model carcass utilization/scavengers, which, depending on the body mass, would greatly increase the amount of accessible food as an abrupt, short-term influx for secondary consumers (i.e., theropods, Hone & Rauhut, 2010). It is also important to note that no other terrestrial vertebrates have reached the body masses of sauropods (Benson et al., 2014; D'Emic, 2023), and integrating this with *cheddar* (i.e., an R package built for assessing extant ecosystems) would be rigorous and outside of the scope of this paper. Because this feature isn't available in *cheddar* at this time, carcasses were not modelled into the generated food webs from the analysis. We recognize that these trophic links assigned to the model affect the results (e.g., *Allosaurus jimmadseni* is set to only eat a discrete number of preferred prey items and be eaten by a discrete number of specific predators), yet this holds true in extant food webs, despite substantially more data available in modern food webs contrast to extinct food webs. *Cheddar* can use the ecological nodes to generate statistical values for trophic chain links and food web connectivity (see Results). The reconstructed food web can provide a basis for comparison to other megafaunal paleoecosystems. Utilizing *cheddar* enables the comparisons of paleoecosystems, and here we establish a framework for generating the Mesozoic terrestrial food webs with DMDQ as a case study.

As addressed above, scavenging is not included in this analysis. The impact of scavenging is not important despite the biases it would have produced, based on the ability or inability of scavengers to move or wholly consume large bones (Henderson and Nicholls, 2015; Lei et al., 2023), as seen with a displaced and damaged apatosaurine pelvis and mid-axial skeleton with bite marks from Mill Canyon Quarry (Boisvert et al., 2022; Boisvert, 2024). Lei et al. (2023) surveyed Morrison Formation bite marks on sauropods, revealing relatively few bite marks on

immature individuals, but also relatively few bones of immature sauropods, supporting the idea that large theropods would be able to consume the majority of the carcasses of small animals in the environment (Hone and Rauhut, 2010). However, a plethora of carcasses can lead to preservation of small skeletons in severe drought assemblages, as not all can be consumed by carnivores (Smith et al., 2022). A drought-induced assemblage is supported by geological and taphonomic evidence (Britt, 1991; Richmond and Morris, 1998), meaning the low number of small individuals preserved is likely a taphonomic artifact brought about by scavenging, but as this analysis does not need precise numbers of individuals, the impact of scavenging on the model is minimal.

Key Aspects of *cheddar* for Food Webs Comparison

Hudson et al. (2013) introduced the R package *cheddar*, which was used in this study due to its ability to produce standardized analyses of trophic web interactions. It allows for analyses at the community level and broader, meaning the limiting factor is taxa preservation, which is why DMDQ was selected (see Dry Mesa Quarry Faunal Assemblage, above). The standardization of the package enables future comparisons to other assemblages, in addition to comparing trophic interactions within a single assemblage. Additionally, our food web analyses were derived from translating taxonomic diversity into ecological nodes at various positions (e.g., basal nodes, mid-level nodes, and top-level nodes) to generate statistical data that can demonstrate if our novel food webs (e.g., food chain lengths) can be compared to other food webs.

Cenograms for Dinosaurian Communities

Cenograms (Valverde, 1964, 1967; Legendre, 1989) are graphic representations of body sizes among members of a single biota, typically applied only to mammals, and here applied exclusively to dinosaurs (Rodriguez, 1999). Cenograms are log-transformed plots of rank-ordered body mass in which species are plotted in rank order (largest to smallest body mass) along the x-axis and their corresponding body masses are plotted along the y-axis (Valverde, 1964; Rodriguez, 1999). Cenograms are commonly used in mammalian palaeoecological studies to obtain information about the environment (Gingerich, 1989; Rodriguez, 1999). Data from modern mammalian communities show that there is a gap in the medium-sized species (500-8000 grams in mammals) in open environments visible on the cenogram. Cenograms have been widely applied throughout the Cenozoic mammalian fossil record to interpret paleohabitats throughout the Cenozoic (Legendre, 1986, 1989; Gingerich, 1989; de Bonis et al., 1992; Ducroq et al., 1994; Gunnell, 1994, 1997; Montuire and Desclaux, 1997; Wilf et al., 1998; Croft, 2001; Flynn et al., 2003). Cenograms have not been widely applied to Mesozoic faunas, however, as they are dominated by non-analog reptilian megafauna rather than mammals. Still, given similar metabolic rates and ecological roles between Mesozoic dinosaurs and Cenozoic mammals, cenograms may have some utility in inferring the habitat type present at Dry Mesa (Farlow et al., 2010; Foster, 2020). A cenogram was created using *ggplot2* (Wickham, 2016) of the Morrison Formation fauna, using log-transformed plots of adult body mass in rank order from largest to smallest (i.e., *Brachiosaurus sp.* is in the largest size class based on its estimated mass, so its Rank 1, followed by *Supersaurus vivianae* at Rank 2, and so forth).

RESULTS

Some of the results have been reported for future food web comparisons with similarly constructed paleo food webs. Two models were recovered using the R *cheddar* package, with Model 1 including *Barosaurus* sp. and Model 2 excluding *Barosaurus* sp., with associated metrics and statistical values. Model 1 contains 97 nodes and 706 trophic links, whereas Model 2 contains 89 nodes with 642 trophic links. Our analysis of DMDQ taxa indicated 12961 unique food chains in Model 1 (represented in Fig. 3), with Model 2 indicating 12605 unique food chains (represented in Fig. 4). The longest food chain is 13 links in Model 2. In total, within Model 1, nine of these nodes were modelled to have no predators (i.e., top-level nodes, typically species at the highest trophic level). In Model 1, seven of these were the largest size class of each of the sauropod species: *Apatosaurus* sp.*, Barosaurus* sp.*, Diplodocus* sp.*, Haplocanthosaurus* sp.*, Supersaurus vivianae, Camarasaurus* sp.*,* and *Brachiosaurus* sp.. The remaining two nodes were the largest size classes for the two largest theropods found at Dry Mesa: *Torvosaurus tanneri* and *Allosaurus jimmadseni*. In Model 2, eight nodes had no predators, and these were the same as Model 1, excluding *Barosaurus* sp.. The key interactions are summarized in Figure 5.

Models 1 and 2 both have low basal nodes (i.e., primary producers) comprising 4.1% and 4.4% of the modelled food web respectively, which is most likely a consequence of grouping them into the wide ecological functional units of: aquatic, ground height plants (<1.5 meters from the ground), mid-height plants (1.5 - 3.5 meters), and high-height plants/trees (>3.5 meters). The intermediate nodes (both consumers and resources for other nodes) are 86.5% in both models. Top nodes are 9.2% and 8.9% respectively, in Models 1 and 2. The percentage of top nodes demonstrates that numerous mature animals within the Dry Mesa ecosystem were immune to predation, which aligns with preservational biases (Conybeare and Haynes 1984; Haynes, 1988).

Trophic Level statistics produced by the r *cheddar* package (see Table 2) showed no differences between the models (when rounded to one decimal place), suggesting that the inclusion of *Barosaurus* sp. had minimal impact due to it fulfilling the same ecological role as the other diplodocoids, thus not altering the food web structure whether it was present or not. These minimal differences between the respective modelled food webs are reflected in similar values of trophic level statistics generated for both food web models (see Table 2). Furthermore, the median was 2.0 for the shortest, short weighted, longest, long weighted, chain average, and prey averaged Trophic Level, whereas there was greater variation in the mean of these values from 2.2 to 3.3, with the latter being for the longest Trophic Level. This suggests that the majority of the food web was based on a primary producer - primary consumer- secondary consumer relationship (i.e., ground plant - a herbivore [such as a diplodocoid] - to carnivorous theropod; Fig. 6). This is most energetically favorable, with the plants and primary consumers effectively fueling the food web for the predatory guilds as these were the majority of the trophic chain lengths. 75% of the Trophic Levels generated had fewer than three trophic chain links. Ultimately, these recovered values support a primary consumer and secondary consumer-dominated ecosystem (see Table 2).

While longer Trophic Levels can be envisioned (e.g., plant, aquatic invertebrate, fish, *Marshosaurus* sp., *Ceratosaurus* sp.*, Torvosaurus tanneri* Size Class 7), such an occurrence would be rarer, and they are not as energetically favorable due to the loss of energy from the increase in trophic levels (Ripple et al., 2016). Many predators tend to consume the most nutrient dense parts of the carcass first, or target those individuals that are most energetically favorable to acquire (e.g., brown bears [*Ursus arctos*] and black bears [*Ursus americanus*] consume Pacific salmon [*Oncorhynchus* spp., Gende et al., 2004]; carnivorous theropods preferentially hunt and feed on immature dinosaurs [Hone and Rauhut, 2010]; cheetah [*Acinonyx jubatus*], African lion [*Panthera leo*], and spotted hyaena [*Crocuta crocuta*] exhibit differential bone consumption rates [Schubert et al.,

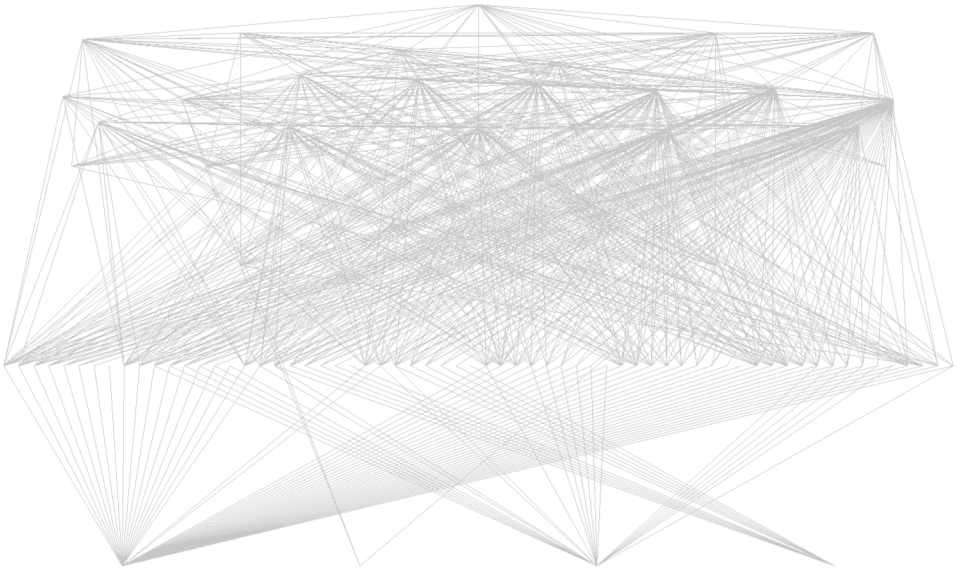

FIGURE 3. The food web generated for DMDQ with *Barosaurus* sp. included (Model 1).

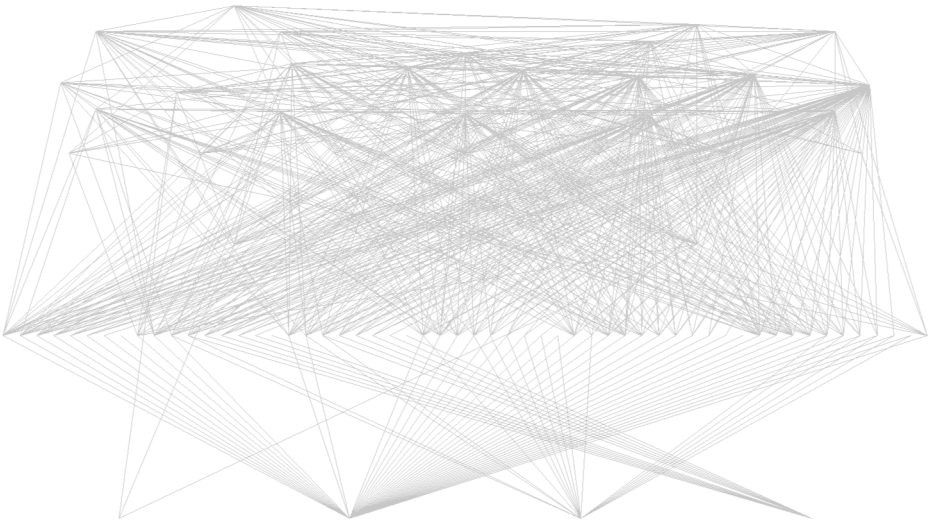

FIGURE 4. The food web generated for DMDQ without *Barosaurus* sp. included (Model 2).

2010]; *Thylacosmilus atrox* craniodental features indicate a soft tissue, meat-specialized diet [Janis et al., 2020]). This provides evidence to support dinosaurian predators being no different from modern-day predators and hunting the most energetically optimal prey under normal conditions, while opportunism enabled exploitation of less favorable prey, as seen on the African savanna today (Owen-Smith, 2021).

Generality and Vulnerability Within the DMDQ Food Web

In-degree and out-degree metrics represent different food options for consumption. In-degree indicates the number of resources an organism consumes, and out-degree represents the number of predators an organism has, based on the nodes produced by the models. For species with large body sizes and varying mass throughout ontogeny, such as the sauropods or large theropods, several unique changes were observed. Animals with a low in-degree tend to be specialists and more vulnerable to extinction and ecosystem collapse, whereas generalists tend to be less susceptible due to a wider range of food sources (Reed and Tosh, 2019; Machado et al., 2023).

The caveat of all small-bodied prey being preserved or not is a reality of paleontology. While in-degrees of predatory taxa may be higher due to increased taxonomic diversity of small-bodied taxa that existed, there is no fossil record for certain vertebrates (e.g., lepidosaurs, small ornithopods, and maniraptorans), even if the preservational rates for these taxa are similar across Mesozoic formations (Brown et al., 2022). Despite this, meaningful comparisons can be made between

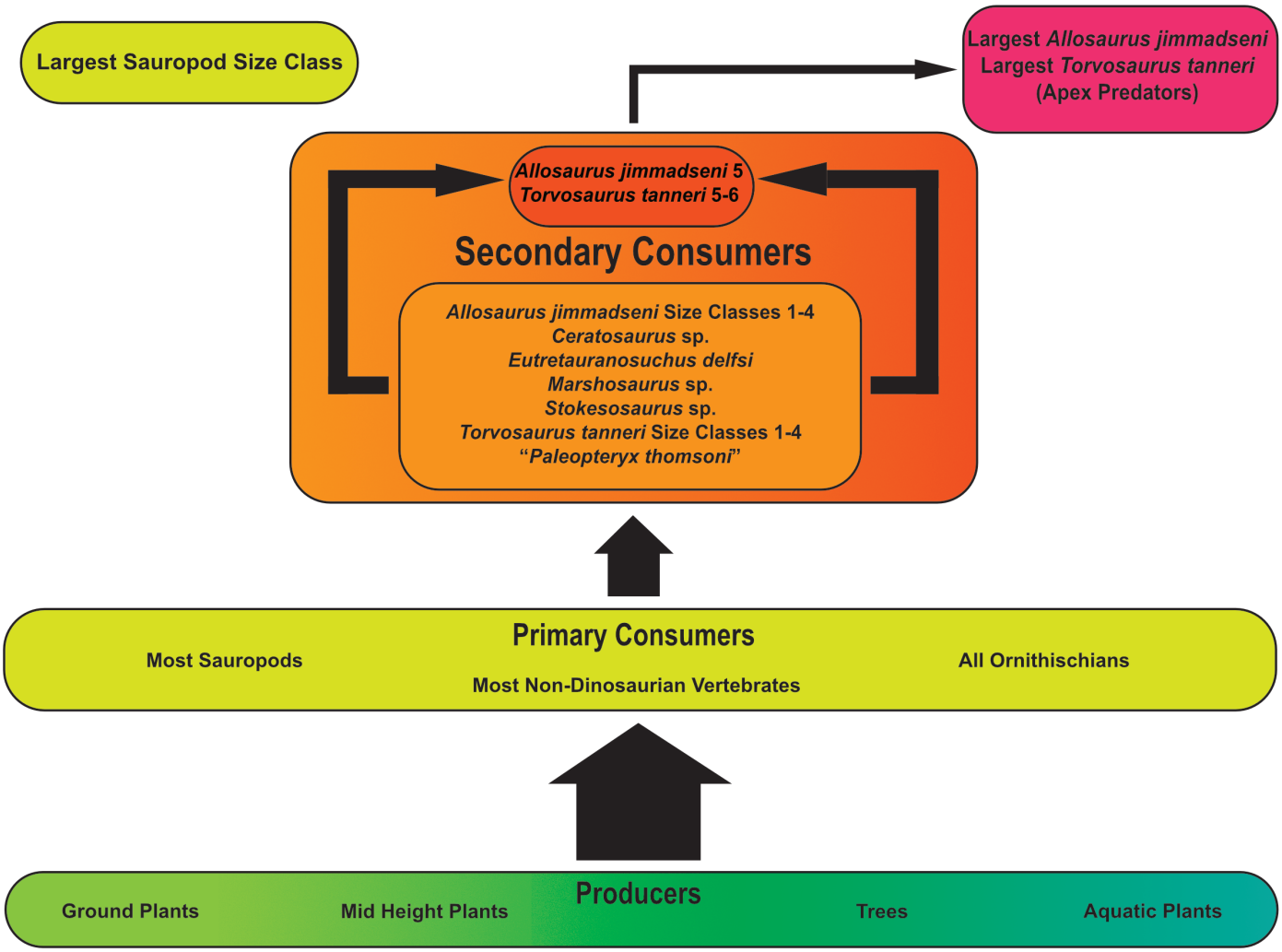

FIGURE 5. A graphical summary of both recovered food web models of (DMDQ).

them, even if the full diversity is not truly preserved.

At their smallest size classes, predatory theropods such as *Allosaurus jimmadseni* and *Torvosaurus tenneri* had their lowest in-degree and their highest out-degrees. This relationship is reversed in their largest size classes (6 and 7). In these largest size classes, predatory theropods had the highest in-degrees, with *Allosaurus jimmadseni* having 47 in-degrees, whereas *Torvosaurus tanneri* possessed 72. The model suggests that *Torvosaurus tanneri* had a wider range of food sources than *Allosaurus jimmadseni*. From our results, large 'adult' theropods preyed upon a broad array of fauna within their ecosystems, whereas small theropods, especially coelurosaurs, were the opposite. Small theropods such as *Stokesosaurus clevelandi* and "*Palaeopteryx thomsoni"* had lower in-degrees (7 and 6, respectively) and higher out-degrees (14 and 17, respectively). This suggests that they occupied a lower trophic level compared to larger theropods such as *Allosaurus jimmadseni*. This distinction appears to be more specific to coelurosaurs, with slightly larger-sized theropods such as *Marshosaurus* sp. possessing relatively higher in-degrees and somewhat lower out-degrees (20 and 7, respectively).

Similar to the large bodied theropods, as sauropods increased in size, their out-degrees were noticeably reduced as sauropod size class 1 has 15, class 2 has 11, class 3 has 9, class 4 has 7, class 5 has 5, class 6 has 3, class size 7 has 1, and size class 8 (the largest) has 0, indicating reduced predation as the sauropods matured. Low-level browsers only consumed ground plants, whereas mixed feeders had both ground plants and, then from size class 3, mid-height plants additionally. Browsers went from ground plants in size class 1, to ground plants and mid-height plants in class 2, and mid-height plants and high-height plants/high-height plants/trees in class 3. From class 4 onwards, they only had high-height plants/trees as their in-degrees.

Ornithischian dinosaurs similarly had limited in-degrees due to the grouping of the flora functionally, although smaller taxa had higher out-degrees than larger ones. *Nanosaurus agilis* was found to have 17 out-degrees, and *Stegosaurus* sp., 12 out-degrees. The ornithischians *Stegosaurus* sp., *Gargoyleosaurus* sp., and *Camptosaurus* sp. all had an out-degree of 12, suggesting similar ecological functioning roles to each other in the food web compared to the sauropod dinosaurs due to similar levels of lower vulnerability to predators.

Most primary consumers had low in-degree metrics due to the grouping of flora into ecological functional groups (aquatic, ground, mid-height plants, and trees). Small secondary consumers, such as mammals and insectivores, have lower in-degree values, but this is due to the simplification of the model, for example, an insectivorous mammal may have consumed different species of insect, arthropods, and/or mollusks, thus having a larger in-degree value, but such differentiation was not possible in the model.

The cenogram in Figure 7 is similar to that seen in open habitats today (e.g., African savannas), where there is a break in slope between the largest size classes and smaller

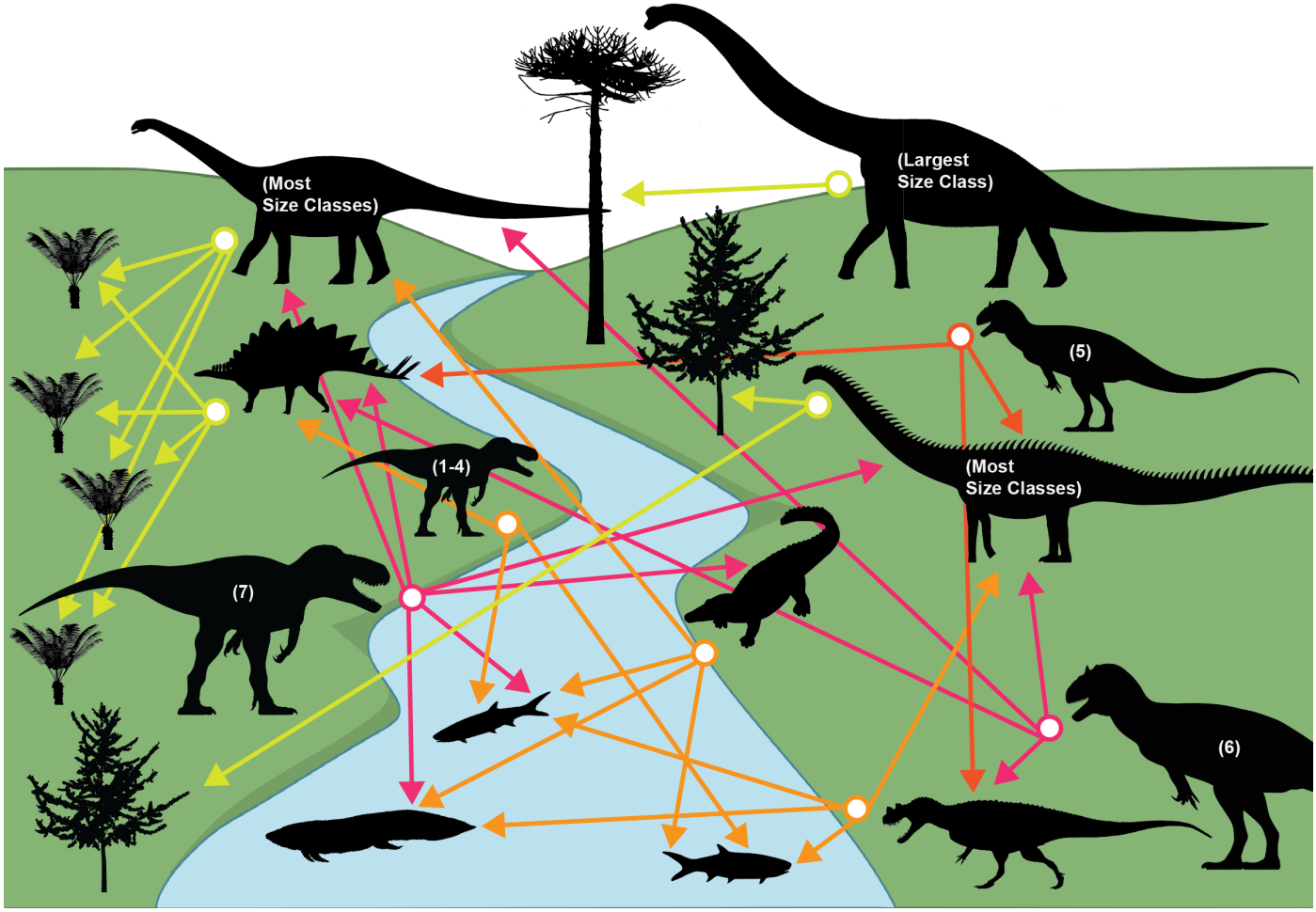

FIGURE 6. Graphical representation of an ecosystem microcosm from both generated food web models of DMDQ. Not all connections are represented, yet the majority are visualized here to demonstrate the general trends derived from all results recovered. Colors are derived from Figure 5. Circles represent InDegree, and arrow represents InDegree. Background provided by BioRender. Silhouette credits from PhyloPic, following silhouettes left to right: Mathew Wedel, Edwin Price, Mason McNair, Andrew Farke, Guillaume Dera, Jacob Schick, R. H. Traquair, T. Michael Keesey (after Heinrich Harder), and Scott Hartman. Phylopic information for silhouettes, including licenses and license links, can be found in Appendix Table 1.

taxa, representing a gap in body size. In this cenogram, there are two gaps: one between the megaherbivores (sauropods and *Stegosaurus* sp.) and the two largest predators at DMQ (*Allosaurus jimmadseni* and *Torvosaurus tanneri*), and another gap between the largest two theropods and the medium-small taxa (Fig. 7). The cenogram's similarity to Cenozoic mammalian open-habitat communities persists despite presumed functional differences in community structure between dinosaurian and mammalian communities due to ontogenetic niche shifts (Codron et al., 2013).

DISCUSSION

Importance of Sauropods within their Ecosystems

Our results illustrate the importance of sauropods as ecological units in their environments, affecting their ecosystems far more when compared to non-age-segregated ornithischians in Morrison Formation ecosystems. This important ecological role is reinforced by the high diversity of sympatric sauropods in the Morrison Formation, particularly in comparison to the megatheropod fauna in the Morrison Formation, which is taxonomically restricted in comparison. Sauropod diversity is uniquely shown at the DMDQ, with six distinct genera preserved minimum, and potentially seven depending on the taxonomic identity of "*Barosaurus* sp." from the quarry (Tschopp and Mateus, 2017; Foster, 2020; Boisvert et al., 2024; van der Linden et al., 2024; van der Linden et al., 2025). Sauropods were likely similar in importance to African elephants (*Loxodonta africana* and *Loxodonta cyclotis*) today in sub-Saharan Africa, being foundational keystone taxa via acting as ecosystem engineers both through destructive and constructive means (Bond, 1994; Haynes, 2012; Coverdale et al., 2016; Guldemond et al., 2017; Poulsen et al., 2017; Cardoso et al., 2019). For example, *L. cyclotis* engineers the boundary between grassland and forest through walking paths forming fire breaks, preventing grassland fires from spreading to the forest, and forest seeds from spreading into the grassland (Coverdale et al., 2016; Guldemond et al., 2017; Poulsen et al., 2017; Cardoso et al., 2019). This shows that direct evidence of tree felling isn't needed for sauropods to act as engineers, as should be expected due to the large size of some Morrison Formation trees (Gee et al., 2014; Gee, 2023A; Gee et al., 2023).

The growth trajectories of sauropods impact ecosystems in several ways, as their fast growth rates (Griebeler et al.,

TABLE 2. Summary Table of the Trophic Level statistics generated by the *cheddar* R package. The definitions for each of the Trophic Level statistics are as follows: Shortest Trophic Level: returns 1 plus the shortest chain length from a node to a basal species; Short weighted Trophic Level: returns the average of Shortest Trophic Level and Prey Averaged Trophic Level; Longest Trophic Level: is the longest chain length from each node to a basal species; Longest weighted Trophic Level: is the average of Longest Trophic Level and Prey Averaged Trophic Level; Chain averaged Trophic Level: is 1 plus the average chain length of all paths from each node to a basal species; Prey averaged Trophic Level: returns 1 plus the mean trophic level of the node's resources, using the matrix inversion method of Levine (1980) that is very fast and accounts for flow through loops.

Model	Statistics	Shortest Trophic Level	Short weighted Trophic	Longest Trophic Level	Longest weighted Trophic Level	Chain averaged Trophic	Prey averaged Trophic
Model 1	Minimum	1.00	1.00	1.00	1.00	1.00	1.00
Model 2	Minimum	1.00	1.00	1.00	1.00	1.00	1.00
Model 1	1st Quartile	2.00	2.00	2.00	2.00	2.00	2.00
Model 2	1st Quartile	2.00	2.00	2.00	2.00	2.00	2.00
Model 1	Median	2.00	2.00	2.00	2.00	2.00	2.00
Model 2	Median	2.00	2.00	2.00	2.00	2.00	2.00
Model 1	Mean	2.23	2.28	3.28	2.81	2.70	2.34
Model 2	Mean	2.25	2.31	3.39	2.88	2.77	2.37
Model 1	3rd Quartile	3.00	3.00	3.00	3.00	3.00	3.00
Model 2	3rd Quartile	3.00	3.00	3.00	3.00	3.00	3.00
Model 1	Maximum	3.00	3.41	13.00	8.17	7.62	3.81
Model 2	Maximum	3.00	3.41	13.00	8.19	7.63	3.81

2013; Benson et al., 2014; Cerda et al., 2017) and endothermic metabolism (e.g., Wiemann et al., 2022) warranted substantial food intake (e.g., Gill et al., 2018) to achieve sizes above 15 tons. Two dental morphotypes are observed in immature diplodocids that are interpreted as feeding adaptations towards a more general diet or a shift in habitat/spatial occupation (Woodruff et al., 2018). Both the dental and cranial characteristics of these immature specimens suggest niche partitioning between different growth stages. The observed dental transformation during maturation could reflect both a dietary and habitat shift to a more specialized diet in more open areas, as these animals had a reduction in predation as they grew. This is further supported by the significant mass discrepancies between immature and mature forms (Griebeler et al., 2013; Benson et al., 2014; D'Emic, 2023).

We find tentative additional evidence to support the niche partitioning model between immature sauropods, especially between the browsing diplodocids (McHugh, 2018), as a mechanism for the high sauropod diversity observed within DMDQ and the Morrison Formation. However, our study and others investigating niche partitioning among sauropods in the Morrison Formation are hindered by the lack of data on precise floral compositions of sauropod diets. The apparent competitive environment (McHugh, 2018) and similar feeding heights (Whitlock, 2011B) indicate that dietary niche partitioning is the most likely mechanism for the co-occurrence of these multi-ton herbivores in a resource-limited environment.

Sauropod importance is also illustrated through the differences in results of the two models with the inclusion/exclusion of *Barosaurus* sp. as a potential seventh sauropod genus at DMDQ (Fig. 3, Fig. 4). In our control model, where *Barosaurus* sp. is not included, we found 89 nodes with 642 trophic links and 12605 unique food chains (Fig. 4). For comparison, Model 1 with *Barosaurus* sp. included as a distinct genus contains 97 nodes, 706 trophic links, and 12961 unique food chains (Fig. 3). This indicates a difference of 8 nodes, 64 trophic links, and 356 unique chains added with just the inclusion of *Barosaurus* sp. into the model. The differences surrouding *Barosaurus* sp. illustrates how the model is still robust with the removal/addition of one sauropod taxon, but the food web does lose some nodes, trophic links, and unique food chains if altered (Fig. 3, Fig. 4). Therefore, different quarries may have slightly different structures based on their taxonomic compositions, but similar results in terms of the importance of sauropods might be expected within the Morrison Formation ecosystems, including those quarries with lesser taxonomic sauropod diversity.

Prey and Predator Diversity at Dry Mesa Dinosaur Quarry

Prey diversity appears to be a strong component in driving mega predator sympatry within the DMDQ. While later tyrannosaurid-dominated faunas may have had clear ontogenetic dietary niche partitioning between mature and immature individuals, the reduction in competition between Morrison Formation theropods could be attributed to the sheer abundance of r-selected immature sauropods (Chiappe et al., 2003; Sander, 2008; Farlow et al., 2010; Therrien et al., 2023).

The prey items at DMDQ have differing defense mechanisms to avoid predation between the immature sauropods (smaller size classes) compared to the ornithischians present. The "thagomizer" of *Stegosaurus* sp. displays clear risk for theropods with evidence supporting an *Allosaurus* sp. pubis suffering a potential thagomizer injury (Carpenter et al., 2005; Mallison, 2011A; Bakker et al., 2014). *Gargoyleosaurus* sp. displays osteoderm armor with shoulder spines projected posterolaterally from the body (Kilbourne and Carpenter, 2005). *Camptosaurus* sp. has been attributed as a fast–moving prey item with estimates of 16 km/h (Thulborn, 1982), although higher estimates are quite plausible (Organ, 2006). All of these adaptations add extra cost to prey acquisition and thus are a high-energy investment for theropods in the DMDQ. Additionally, mixed herding of co-occurring prey species (potentially *Stegosaurus* sp. And *Camptosaurus* sp. (Foster, 2013) is a potential contributing factor to disparities in prey opportunity, as seen in modern mixed-species herds containing Plains Zebra (*Equus quagga*) and either the kudu (*Tragelaphus strepsiceros*), wildebeest (*Connochaetes taurinus*), or the waterbuck (*Kobus ellipsiprymnus*) (Stears et al., 2020).

Megatheropods in the Morrison Formation greatly benefited from and influenced the ecosystem via a broad selection of preferred prey items and habitat space, coupled with large body size. This extended to scavenging, where this and fluvial transport scouring result in the reduced preservational potential of small taxa, making DMDQ a unique snapshot into the broader Morrison Formation fauna, due to rare occurrences of small taxa in the quarry. The rare preservation of small taxa is indicative of a drought-induced assemblage, similar to those in Tanzania's Chewore Safari area and Hwange National Park (Haynes, 1988). Secondary transport of disarticulated material in multiple large flooding events (Britt, 1991; Richmond and Morris, 1998) would have likely scoured material from the smallest terrestrial representatives of the environment (e.g., Mammaliaformes; see Richmond and Morris, 1998). While the fossil record is intrinsically incomplete, DMDQ provides a unique opportunity to study a relatively well-constrained and well-represented regional biota within the Morrison Formation, again, following the definition of Patzkowsky (2017), which describes regional biota as existing and interacting along gradients, meaning the concentration of individuals at DMDQ is a more representative sampling of the regional fauna, when accounting for gradational interactions between taxa.

Implications from Dry Mesa Dinosaur Quarry regarding *Allosaurus* spp. Paleoecology

Allosaurus spp. is the most abundant and widespread

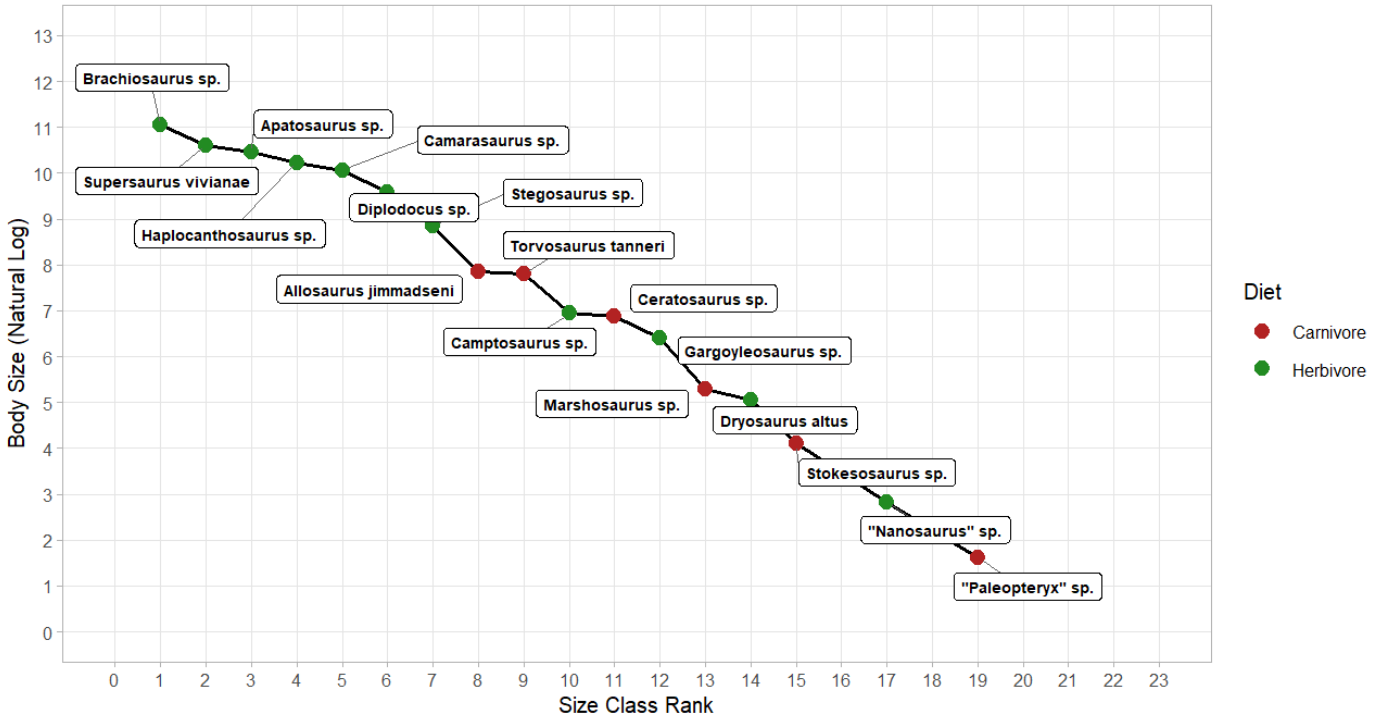

FIGURE 7. Cenogram of the Dry Mesa dinosaurs by log-transformed body mass. Taxa were categorized as herbivores (green) or carnivores (red). Body size in kilograms was log-transformed, with the smallest taxa in the highest values and the largest taxa in the lowest values.

theropod genus within the DMDQ and the Morrison Formation (Foster and Chure, 2006; Foster, 2020; Maidment, 2024), having been the subject of studies including pathologies, growth, and biomechanics (Bybee et al., 2006; Snively et al., 2013; Foth et al., 2015; Prondvai, 2017). *Allosaurus* spp. specimens record a wide variety of severe pathologies, including stress fractures, bone infections, and healed bone fractures, heavily implying an active lifestyle with a high risk of injury (Rothschild et al., 2001; Foth et al., 2015). Paleopathological evidence for an *Allosaurus* individual potentially indicates a failed hunt and/or receiving a fatal injury from a *Stegosaurus* sp., as the animal did not survive long after the injury based on evidence of limited bone remodelling (Carpenter et al., 2005). Additional pathologies show severity, which would have significantly impacted an animal's ability to acquire prey and hunt (Hanna, 2002; Bakker et al., 2014; Foth et al., 2015). While injury was likely fatal, others have survived with severe injuries (Rothschild et al., 2001; Foth et al., 2015), suggesting the availability of readily available and easier-to-acquire prey such as sauropod size classes 1 to 3 (as seen in our model), due to their smaller size and limited defenses. This study finds support for the difficulty and danger of *Allosaurus* sp. actively hunting *Stegosaurus* sp. and larger sauropods (size classes 4 and above), compared to the abundance of other prey items (high in-degrees metric) within the food web.

Although long-term scavenging has been proven to be impossible for large–bodied endotherms (Carbone et al., 2011), carrion could have supplemented prey acquisition, but the distribution of this may have been limited. Immature sauropods (size classes 1 to 3) were most likely the preferred prey over ornithischians (Hone and Chure, 2018), as they were abundant, and immature sauropods had few defensive options (Sellers et al., 2013) compared to the former and likely partook in age-segregated gregariousness. As such, sauropod reproductive dynamics in the Morrison Formation likely played a key role in the ecology of the various predatory species, especially *Allosaurus* sp., and could have facilitated the ability of injured predators to recover from otherwise debilitating injuries.

Dry Mesa Dinosaur Quarry Compared to Late Cretaceous Tyrannosaurid-Dominated Ecosystems

Approximately 70 million years separate the Dry Mesa Dinosaur Quarry from Late Cretaceous tyrannosaurid-dominated ecosystems, but both include megatheropods (taxa greater than 1,000 kg; Schroeder et al., 2021) and diverse herbivorous dinosaurian faunas (Loewen et al., 2013; Farlow et al., 2023). Yet, Late Cretaceous ecosystems are notable latter for the majority being dominated by a more limited quantity of tyrannosaurid taxa in the megatheropod guild and lack of other medium-sized predators, compared to the diverse megatheropods and mesopredators present at DMDQ (Foster et al., 2001; Foster, 2003; Foster, 2020; Schroeder et al., 2021; Holtz, 2021; Cau, 2024). Morrison Formation quarry ecosystems often contained several sympatric sauropod taxa (Button et al., 2014; McHugh, 2018; Wyenberg-Henzler, 2022; Boisvert et al., 2024), whereas most tyrannosaurid-dominated ecosystems lacked sauropods, with exceptions in southern Laramidia and Asia (Sampson and Loewen, 2005; D'Emic and Forman, 2012; Averianov and Lopatin, 2019; Holtz, 2021; Wyenberg-Henzler, 2022). Rather than a diverse sauropod fauna, Late Cretaceous tyrannosaurid-dominated communities include diverse ornithischians such as cursorial, multi-ton hadrosaurs (Sellers et al., 2009; Persons et al., 2014), ceratopsids (Benson et al., 2018), pachycephalosaurids, and ankylosaurids alongside small maniraptoran theropods (White et al., 1998; Gates et al., 2010).

While some ornithischians often exceed several tons in mass (Wosik and Evans, 2022), there are exceptions of very large ornithischians greater than 15 tons in mass (e.g., *Shantungosaurus giganteus* and *Edmontosaurus regalis* [Benson et al., 2018]). Consequently, ornithischians typically would have been unable to feed from the canopy of living trees, as some sauropods may have instead, due to ornithischians' lower feeding height. Even low-browsing sauropods may have been

able to exploit trees by knocking them down, something that ornithischians were likely unable to accomplish. This is based on the large body size and rearing ability of sauropods (Jensen, 1988; Mallison, 2011B), although differences in the behavior and sizes of forest and bush elephants in regards to tree destruction does not mean that all sauropods, or any sauropods must have done so (Coverdale et al., 2016; Guldemond et al., 2017; Poulsen et al., 2017; Cardoso et al., 2019). The presence of parental care in at least some taxa within Hadrosauridae and Ceratopsidae, a behavior most likely absent in sauropods (Thulborn, 1992; Horner, 1999; Sander, 2008). Studies have recovered bonebeds from Late Cretaceous tyrannosaurid-dominated ecosystems as being composed of non-age segregated groups of ornithischians (Mathews et al., 2009; Snyder et al., 2020), suggesting that these animals were less r-selected than sauropods. Additionally, many immature ornithischians were likely more mobile and better able to potentially evade predators than immature sauropods of similar age and/or size (Sellers et al., 2009). This suggests that there were fewer immature and defenseless animals in Late Cretaceous tyrannosaurid-dominated ecosystems to serve as an easy food source for the various predatory theropods, compared to Morrison Formation ecosystems such as DMDQ. Our model supports the abundance of immature sauropods having a greater impact on the ecosystem compared to ornithischians. Thus, the staple food source of immature sauropods in Morrison Formation ecosystems was not available in later tyrannosaurid-dominated ecosystems, potentially impacting the availability of easy-to-acquire prey for the theropod megapredatory guilds, especially at different stages through ontogeny.

This study recovers *Allosaurus jimmadseni* and *Torvosaurus tanneri* as consuming a wide variety of prey species through ontogeny based on In-degree metrics. Assimilation of niches from different ontogenetic stages of *Allosaurus jimmadseni* and *Torvosaurus tanneri* did not appear to have demarcated dietary niches in the same manner as tyrannosaurids, which were able to specialize more effectively within their respective niches throughout their ontogeny (Hutchinson et al., 2011; Schroeder et al., 2021; Holtz, 2021; Therrien et al., 2021; Therrien et al., 2023). This may be due to the consumption of the same/similar prey items for *Allosaurus jimmadseni* and *Torvosaurus tanneri*.

It is debated if this tyrannosaurid dominance in the Late Cretaceous was due to the drop in megatheropod diversity around the Cenomanian-Turonian that preceded the rise of tyrannosaurid-dominated ecosystems (Schroeder et al., 2021; Holtz, 2021; Morrison et al., 2025), or morphological traits that allowed tyrannosaurids to outcompete other theropod clades (Snively and Russell, 2002; Witmer and Ridgely, 2009; Hurlburt et al., 2013; Persons and Currie, 2016; Nesbitt et al., 2019; Snively et al., 2019; Sakamoto, 2022). In Late Cretaceous ecosystems, niche assimilation occurred across different ontogenetic stages of tyrannosaurids (Schroeder et al., 2021). In comparison, the Morrison Formation likely did not experience the same degree of ontogenetic dietary niche partitioning within singular megatheropod genera. In effect, a smaller number of predatory tyrannosaurid taxa played a more significant role in their ecosystems across multiple different trophic levels when compared to the more limited roles played by individual predatory taxa in the Morrison Formation.

The two largest predators of the Morrison Formation, *Allosaurus jimmadseni* and *Torvosaurus tanneri,* were comparable to many Late Cretaceous tyrannosaurids in size but were smaller than the largest tyrannosaurines, with animals like *Tyrannosaurus rex* massing in over 8000 kg compared to the 3000 to 4000 kg seen in *Allosaurus jimmadseni and Torvosaurus tanneri* (Campione et al., 2014; Persons et al., 2020; Dempsey et al., 2025). Morrison Formation megatheropods did not possess adaptations that were likely useful to tyrannosaurids for hunting their preferred prey, such as a more cursorial build for increased agility (Persons and Currie, 2016), the arctometatarsus (Snively and Russell, 2002), expanded ilium and caudal chevrons for greater hindlimb musculature (Snively et al., 2019), heightened senses and expanded cerebrums (Witmer and Ridgely, 2009), and more powerful jaws (Sakamoto, 2022). Tyrannosaurids and the Morrison Formation megatheropods *Allosaurus* spp. and *Torvosaurus tanneri* were unlikely to prey upon the largest individual prey items in their environments individually; however, the lesser size disparity between tyrannosaurids and their largest sympatric herbivores presents a dichotomy wherein tyrannosaurids were likely targeting prey species that may have achieved sizes closer to their own size when compared to Jurassic megatheropods (Therrien et al., 2023). While there is debate about the presence or absence of gregarious group hunting in these predatory taxa (Dinets, 2010; Dinets, 2015; Shine and Somaweera, 2019), these events may have been infrequent if they occurred at all, resulting in the largest herbivores within the Morrison Formation (mature sauropods) being immune from predation under normal circumstances as per the model and Table 1. This suggests that the key drivers of the Morrison Formation ecology were the sauropods via bottom-up control, with the rest of the ecosystem being shaped around them, whereas tyrannosaur-dominated ecosystems likely had more top-down control exerted by the predators.

Ecological Comparison to Cenozoic Faunas

The Morrison Formation's strong sampling makes it an ideal case study of a dinosaurian-dominated biota to compare to Cenozoic mammal-dominated ones (Bakker, 1975, 1986; Farlow et al., 2023). While dinosaurian and mammalian comparative ecological studies have been commonplace, differences in dinosaurian and mammalian life histories, body size, and co-occurring floral assemblages complicate comparisons between the two (Rees et al., 2000; Van Valkenburgh and Molnar, 2002; Farlow and Pianka, 2002; Parrish et al., 2004; Sander et al., 2011; D'Emic, 2013; Codron et al., 2013; Woodruff, 2019; Frederickson et al., 2020; Chapelle et al., 2025). Bakker (1975, 1986) made comparisons of community structure between Morrison Formation dinosaurs and Cenozoic mammals, noting that the Morrison Formation predator/prey ratio was similar to that of the modern African savanna. These conclusions have since been questioned due to collection and taphonomic biases (Gates, 2005; Foster et al., 2018; Schroeder et al., 2021), implying that future work should emphasize that dinosaurian ecosystems had fundamentally different biota structure and function compared to later mammalian communities (Farlow, 1993).

Farlow et al. (2010, 2023) reexamined the abundance of Morrison Formation megaherbivores and megatheropods, respectively. Population densities of mature *Allosaurus* spp. in the Morrison Formation were much higher than expected, based on extrapolations from extant predatory mammals, with the predator/prey biomass ratio in the Morrison Formation varying greatly across differing quarries but averaging between 1–2%, comparable to the predator/prey ratio in extant mammalian communities (Farlow et al., 2023). These ratios are based on 'adult' animals, when in reality, immature individuals may have made up more than half of dinosaurian populations (Erickson et al., 2009; Farlow et al., 2010; Erickson et al., 2014; Wyenberg-Henzler et al., 2022). Based on the high predicted population densities of *Allosaurus* spp., Farlow et al. (2023) suggested that, unlike extant large terrestrial carnivores, dinosaurian predators must have frequently preyed on animals smaller than themselves in addition to megaherbivores, which our model supports. Body size in the Morrison Formation differs greatly in comparison to Cenozoic communities greatly in scale and distribution, where a duo of apex predator taxa (i.e., *Torvosaurus tanneri* and *Allosaurus jimmadseni*) and the largest sauropods (e.g., *Supersaurus vivianae*) dwarf contemporaneous fauna as well as

later Cenozoic fauna via mass disparity alone. However, despite noteworthy distinctions between the body size of Morrison Formation fauna and Cenozoic mammalian communities, there are also noteworthy similarities.

The cenogram of body size distribution of the Morrison Formation taxa (Fig. 6) resembles the patterns of niche partitioning seen in predation-controlled mammalian ecosystems, suggesting predation is also the controlling factor for the Morrison Formation body size distribution despite the ubiquity and diversity of sauropods (Rodríguez, 1999; Croft, 2001). The effectiveness of large predators in open habitats has been invoked to explain this pattern, and as such, it is an important alternative hypothesis to explain gaps in body size among the Morrison Formation taxa (Noto and Grossman, 2010; Whitlock et al., 2018; Foster, 2020). The Morrison Formation has an overall body size distribution pattern similar to the modern tropical savanna and wooded savanna habitats, where there is a pronounced gap between smaller and larger body sizes (Noto and Grossman, 2010; Foster, 2020), despite the presence of gigantic sauropods. Ontogenetic dietary and niche shifts need not be invoked to explain gaps in body size, as habitat type and the effectiveness of predators could be alternative explanations for why there is a big gap in herbivore body size between *Camptosaurus* spp./*Gargoyleosaurus parkpinorum* and *Stegosaurus* spp. + sauropods (Codron et al., 2013).

In extant mammalian ecosystems, immature individuals are fed by 'adults' via milk until they are mature enough to feed upon the same resources as 'adults' (Pond, 1977). In extant reptiles, however, 'juveniles' forage independently from birth and, as such, may feed on different resources than mature individuals of the same species (Codron et al., 2013; Purwandana et al., 2016; Shine and Somaweera, 2019). While extended parental care cannot be excluded, particularly in smaller-sized taxa (Horner, 1982; Forster, 1990; Scheetz, 1991), the size disparity between mature and immature large-bodied taxa implies the existence of niche shifting throughout ontogeny, despite the inability of 'adults' to care for immature individuals many orders of magnitude smaller in size whilst supporting massive nesting areas, where typically no 'adult' remains are recovered alongside the nest (Sander, 2008; Shine and Somaweera, 2019; Codron et al., 2013). Therefore, immature sauropods, ankylosaurians, or stegosaurids may have filled niches that would otherwise have been occupied by intermediate-sized herbivores, though this is outside of this study's scope.

Portions of the Morrison Formation are hypothesized to represent a seasonal environment, consisting of a wet season and semi-arid season during drier cycles across open environments, like eastern Africa today (Dodson et al., 1980; Myers et al., 2014). However, evidence of extensive forests across the formation challenges this hypothesis of large-scale open environments (Gee et al., 2014, 2019; Xie et al., 2021; Foster et al., this volume). Unlike present-day communities, the Morrison Formation was dominated by conifers, ferns, and horsetails, with the absence of angiosperms, and it has been hypothesized that herbaceous shrubs were concentrated in the drier areas and arboreal vegetation was limited to riparian habitats (Parrish et al., 2004). Unfortunately, direct testing of this hypothesis has not resolved the structure of floral community composition in the Morrison Formation; however, variation in habitats found by Whitlock et al. (2018) indicates that further study of Morrison Formation floral communities is warranted, though outside the scope of this work. Caloric evaluation tests have demonstrated that horsetails, conifers, and ferns are comparable in energy content to extant angiosperms (Hummel et al., 2008; Gill et al., 2018). Farlow et al. (2010) also found that while dinosaur population density may have been smaller than in mammalian communities, dinosaur biomass would have been greater. Based on the evidence of age-segregated herding in sauropods, the feeding of such groups may have produced mobile hotspots of intense impact on the local flora (Farlow et al., 2010). Extant African savanna elephants (*Loxodonta africana*) have a pronounced effect on vegetative communities due to their role as ecosystem engineers, wherein uprooting and consuming entire trees causes local habitat heterogeneity to increase, which can increase the biomass and species richness of understory plants (Coverdale et al., 2016). Based then on the currently understood Morrison Formation flora, differential biomass and energy requirements between mammals and dinosaurs, age-segretated herding and other general similarities to *L. africana*, mobile groups of large sauropods in the Morrison Formation may have had an even greater impact on floral communities, concerning potential long-distance or limited seasonal migrations in addition to their colossal size (Fricke et al., 2011; Malone et al., 2021; D'Emic, 2023; Agusti et al., 2024; Winkler et al., 2025), which may have prevented plant communities from reaching their most diverse taxonomic communities. Seasonal floral abundance may have also been affected by eusocial insects (potentially early termites) similar to those in eastern African savannas (Smith et al., 2020), yet more study on Morrison Formation invertebrate paleoecology is needed to confirm this.

The presence of low to non-existent in-degrees and high out-degrees in the basal part of the trophic web may indicate model similarities to modern-day ecosystems (e.g., bottom-up control, see Power, 1992; Rosemond et al., 2001; Kagata and Ohguchi, 2006). Dinosaurian group hunting has been hypothesized, but data for such behavior remains limited; however, it has been observed in large predatory extant reptiles such as crocodilians and varanids (Dinets, 2010; Dinets, 2015; Shine and Somaweera, 2019). Lions have also been known to hunt elephants in packs, along with coordinated hunting in crocodilians (John Power and Shem Compion, 2009; Davidson et al., 2013; Dinets, 2015). Theropods may have participated in social hunting behavior, though distinctions between group mobbing and coordinated hunting are elusive.

Future Research

As we are not able to differentiate all the plant taxa species each herbivore would have consumed, we focused on grouping plant types for the food web analysis. To better differentiate the flora that Morrison Formation herbivorous dinosaurs would eat, separate isotopic analyses similar to Norris et al. (2025) would need to be conducted in addition to microwear analysis, which still may not fully differentiate the exact plants each herbivore fed upon due to limitations of the data gained using these methods (Cullen et al., 2022; Kubo et al., 2023). This is especially true if there was genuine plasticity and overlap in herbivore diets. Stomach contents would be ideal; however, more complete plant remains are rare, and articulated skeletons are limited in the Morrison Formation (Foster, 2020). Further, if the Morrison Formation was seasonal (Turner and Peterson, 2004; Parrish et al., 2004), such remains could represent seasonal variation or abundance as seen in modern mammals (Stevens et al., 2006; Codron et al., 2007), giving a false dietary signal to be incorporated into an annual food web. Future work may help elucidate further assumptions, limitations, and factors for constructing food webs across Mesozoic localities.

CONCLUSIONS

This study provides a unique analysis of food web interactions for the DMDQ, the broader Morrison Formation, and Mesozoic ecosystems. This case study highlights the importance of the largest *Torvosaurus tanneri* individuals interacting heavily with taxa across the environment, and how high sauropod diversity and size classes influence food web interactions. Furthermore, this methodology can be applied to other large quarries in the Morrison Formation for comparison

with DMDQ. It can also be used for other formations with well-represented sympatric faunal assemblages across the Mesozoic Era for studying changes in fauna and their respective food web links.

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APPENDICES

TABLE 1. Phylopic taxa used, authors, licenses, and license links.

Genus/species	Phylopic author	License	License link
Allosaurus europaeus (*Allosaurus jimmadseni*)	Jagged Fang Designs	CC0 1.0 Universal Public Domain Dedication	https://www.phylopic.org/images/9ed97c13-95f2-4133-8ee2-083fc3a2b1b7/allosaurus-europaeus
Anurognathus ammoni (*Mesadactylus ornithosphyos*)	Dean Schnabel	CC0 1.0 Universal Public Domain Dedication	https://www.phylopic.org/images/56b1aae4-f330-47cf-a36a-8123149044e0/anurognathus-ammoni
Apatosaurus louisae	Jagged Fang Designs	CC0 1.0 Universal Public Domain Dedication	https://www.phylopic.org/images/0a53dee8-ea6a-44f9-95b1-d142846110cd/apatosaurus-louisae
Araucaria araucana	Edwin Price	Attribution 4.0 International	https://www.phylopic.org/images/05e70626-c9b8-4024-8fcc-685f7e9431d3/araucaria-araucana
Ardeosaurus brevipes (=Lacertilia indet.)	Ghedo and T. Michael Keesey	Attribution-ShareAlike 3.0 Unported	https://www.phylopic.org/images/83053aee-0f56-4cf3-bbfa-9207e6f13f46/ardeosaurus-brevipes
Atrociraptor marshalli ("*Paleopteryx thomsoni*")	Mette Aumala	Attribution 3.0 Unported	https://www.phylopic.org/images/277ceeda-a1ca-4d81-a97e-07a66907d4cc/atrociraptor-marshalli
Brachiosaurus altithorax	Mathew Wedel	Attribution 3.0 Unported	https://www.phylopic.org/images/18f947ce-1c93-4652-8497-

			bf72f58a3dae/brachiosaurus-altithorax
Camarasaurus lentus	Scott Hartman	Attribution-NonCommercial-ShareAlike 3.0 Unported	https://www.phylopic.org/images/bae62f3c-acac-410d-b5c6-b6d1d3e2ef59/camarasaurus-lentus
Camptosaurus dispar	Scott Hartman	Public Domain Mark 1.0	https://www.phylopic.org/images/a97ee226-fed8-4431-a008-15a6cccf98bd/camptosaurus-dispar
Ceratodus (=Ceratodus and Potamoceratodus)	T. Michael Keesey (after Heinrich Harder)	CC0 1.0 Universal Public Domain Dedication	https://www.phylopic.org/images/de33e9bd-643d-4a68-a3c4-c3206f9b508e/ceratodus
Ceratosaurus nasicornis	Scott Hartman	Attribution-NonCommercial-ShareAlike 3.0 Unported	https://www.phylopic.org/images/139a258e-6e93-44d7-b679-91e7fb16a5e7/ceratosaurus-nasicornis
Coelurus agilis	FunkMonk	Attribution-NonCommercial-ShareAlike 3.0 Unported	https://www.phylopic.org/images/d3ae8c0d-107d-45de-992e-177c551e079d/coelurus-agilis
Cycas circinalis	Mason McNair	CC0 1.0 Universal Public Domain Dedication	https://www.phylopic.org/images/38433185-7804-4c7e-8c0d-fa885001794e/cycas-circinalis
Diplodocus carnegii	Jagged Fang Designs	CC0 1.0 Universal Public Domain Dedication	https://www.phylopic.org/images/e3c44862-20f0-407c-9776-bcbbadf87229/diplodocus-carnegii
Dryosaurus altus	Gareth Monger	Attribution 3.0 Unported	https://www.phylopic.org/images/14184e4e-0777-4d0b-8cb4-

			00dedd216af4/dryosaurus-altus
Eutretauranosuchus delfsi	Jacob Schick	Attribution 4.0 International	https://www.phylopic.org/images/b2dbf278-6894-41ba-8ad6-c2dbe3d46956/eutretauranosuchus-delfsi
Gideonmantellia amosanjuanae (="Nanosaurus" sp.)	Will Toosey	Attribution 4.0 International	https://www.phylopic.org/images/7e9733bc-fa6c-49c0-a6e0-80f5a5377fcd/gideonmantellia-amosanjuanae
Ginkgo biloba	Guillaume Dera	CC0 1.0 Universal Public Domain Dedication	https://www.phylopic.org/images/798f147f-fe2a-4227-8805-228f5aea9bb6/ginkgo-biloba
Glyptops utahensis (=Glyptops and Dinochelys)	Scott Hartman	Attribution-NonCommercial-ShareAlike 3.0 Unported	https://www.phylopic.org/images/3827b9bf-ca2f-4613-aa9c-28c4101e04d8/glyptops-utahensis
Haplocanthosaurus priscus	Mathew Wedel	Attribution 3.0 Unported	https://www.phylopic.org/images/326d30ac-0568-4fb4-a41e-692bf7e4dfd0/haplocanthosaurus-priscus
Kollikodon ritchiei (=Prototheria indet.)	Nix Illustration	Attribution-NonCommercial 3.0 Unported	https://www.phylopic.org/images/fc667c87-1e27-4ca9-9bf0-133d3e4a466b/kollikodon-ritchiei
Marshosaurus bicentesimus	Scott Hartman	Attribution-NonCommercial-ShareAlike 3.0 Unported	https://www.phylopic.org/images/872eccf3-1624-4286-a101-0675954094f8/marshosaurus-bicentesimus
Mymoorapelta maysi (=Gargoyleosaurus sp.)	Robert Gay	Attribution-ShareAlike 3.0 Unported	https://www.phylopic.org/images/16119d33-89ee-4c7a-ab16-

			9841ff1bda67/mymoorapelta-maysi
Noripterus complicidens ([?]Dsungaripterid indet.)	Nix Illustration	Attribution-NonCommercial-ShareAlike 3.0 Unported	https://www.phylopic.org/images/5edb87b6-2bb6-4087-a945-599e1f131804/noripterus-complicidens
Ornitholestes hermanni	Matt Martyniuk	Attribution-NonCommercial-ShareAlike 3.0 Unported	https://www.phylopic.org/images/1bda7374-b721-4a8f-bef0-84ae09d6bf54/ornitholestes-hermanni
Palaeoniscum freieslebeni (=Palaeoniscidae indet.)	R. H. Traquair	Public Domain Mark 1.0	https://www.phylopic.org/images/7360374f-8860-44c5-b74b-af53ca1a8af4/palaeoniscum-freieslebeni
Sphenodon punctatus (=Eilenodon robustus)	Benchill	Attribution 3.0 Unported	https://www.phylopic.org/images/bb16d7af-7d0b-43db-b44e-22a1a564bf49/sphenodon-punctatus
Stegosaurus	Andrew Farke	Attribution 3.0 Unported	https://www.phylopic.org/images/173f44e3-2db7-4c98-b41f-6ab58093a145/stegosaurus
Stokesosaurus clevelandi	Scott Hartman (modified by T. Michael Keesey)	Attribution-NonCommercial-ShareAlike 3.0 Unported	https://www.phylopic.org/images/fdb5dd1f-acad-46c0-b1cc-194939ce86a0/stokesosaurus-clevelandi
Sunnyodon notleyi (=Multituberculata indet.)	FunkMonk (Michael B. H.)	Attribution-ShareAlike 3.0 Unported	https://www.phylopic.org/images/63b5a09a-e39c-43d2-9d92-0e3c800ea5b6/sunnyodon-notleyi

Supersaurus vivianae	Scott Hartman	Attribution-NonCommercial-ShareAlike 3.0 Unported	https://www.phylopic.org/images/b1e5b1c3-9154-4458-b6fd-e24db6ef8425/supersaurus-vivianae
Triadobatrachus massinoti ([?]Amphibia indet.)	Nobu Tamura	Attribution 3.0 Unported	https://www.phylopic.org/images/a3b917bc-142d-4314-aa82-2215f5487daf/triadobatrachus-massinoti
Torvosaurus tanneri	Jagged Fang Designs	CC0 1.0 Universal Public Domain Dedication	https://www.phylopic.org/images/13d6de32-507a-4d96-ba11-897f71cecad1/torvosaurus-tanneri

TABLE 2. Fauna of the Dry Mesa Dinosaur Quarry

Clade	Taxonomic Assignment	Hypothesized Diet	Sources
(?)Palaeonscidae	Indeterminate	(?)Carnivore	Kirkland, 1998; Foster, 2020
Dipnoi	*Ceratodus* sp.	Carnivore	Kirkland, 1998; Foster, 2020
Dipnoi	*Potamoceratodus* sp.	Carnivore	Pardo et al., 2010; Foster, 2020
(?)Amphibia	Indeterminate	(?)Carnivore	Jensen and Padian, 1989; Gardner and DeMar, 2013; Foster, 2020
Lacertilia	Indeterminate	(?)Carnivore	Foster, 2020
Rhynchocephalia	*Eilenodon robustus*	Herbivore	Rasmussen and Callison, 1981; Jones et al., 2018; Foster, 2020
Testudinata	*Dinochelys* sp.	Carnivore/Piscivore	Britt, 1991; Brinkman et al., 2000; Foster, 2020
Testudinata	*Glyptops* sp.	Carnivore/Piscivore	Britt, 1991; Foster, 2020
Crocodyliformes (Goniopholididae)	*Eutretauranosuchus delfsi*	Carnivore	Smith et al., 2010; Foster, 2020
Mammalia (Multituberculata)	Indeterminate	Omnivore	Jensen, 1984
Mammalia (Prototheria)	Indeterminate	Omnivore	Britt, 1991
Pterosauria ([?]Dsungaripteroids)	Indeterminate	Carnivore/Durophagous	Unwin and Heinrich, 1999; Chen et al., 2020
Pterosauria (Anurognathidae)	*Mesadactylus ornithophyos*	Carnivore/Insectivorous	Jensen and Padian, 1989; Clark and Hone, 2022
Dinosauria (Ornithschia)	*Camptosaurus* sp.	Herbivorous low grazer/mixed feeder	Dodson et al., 1980; Britt, 1991; Foster, 2020
Dinosauria (Ornithschia)	*Dryosaurus altus*	Herbivorous low grazer	Horner et al., 2009; Foster, 2020
Dinosauria (Ornithschia)	*Nanosaurus* sp.	Herbivorous low grazer	Britt, 1991; Carpenter and Galton, 2018; Foster, 2020
Dinosauria (Thyreophora)	*Stegosaurus* sp.	Herbivorous low grazer	Weishampel, 1984; Coe et al., 1987; Britt, 1991
Dinosauria (Thyreophora)	*Gargoyleosaurus* sp.	Herbivorous low browser	Kirkland et al., 1998; Molnar and Clifford, 2000; Foster, 2020; Kirkland pers. comm., 2025
Dinosauria (Sauropoda)	*Apatosaurus* sp.	Herbivorous low grazer	Britt, 1991

Dinosauria (Sauropoda)	*Brachiosaurus* sp.	Herbivorous high browser	D'Emic and Carrano, 2020; Curtice et al., 2023
Dinosauria (Sauropoda)	*Camarasaurus* sp.	Herbivorous high browser	Britt, 1991; Tütken, 2011; D'Emic et al., 2013
Dinosauria (Sauropoda)	*Diplodocus* sp. and *Barosaurus* sp.	Herbivorous low grazer/mixed feeder	Britt, 1991; Curtice and Wilhite, 1996; Tütken, 2011; Whitlock, 2011; McHugh, 2018; Peterson et al., 2022; Tschopp et al., 2019; Curtice pers. comm.
Dinosauria (Sauropoda)	*Haplocanthosaurus* sp.	Herbivorous low grazer	Tschopp et al., 2015; Curtice et al., 2023; Boisvert et al., 2024; Boisvert et al., 2025
Dinosauria (Sauropoda)	*Supersaurus vivanae*	Herbivorous low grazer/mixed feeder	Jensen, 1985; Tschopp et al., 2015
Dinosauria (Theropoda)	*Allosaurus jimmadsenii*	Hypercarnivorous generalist	Foster, 2020; Chure and Loewen, 2020
Dinosauria (Theropoda)	*Ceratosaurus* sp.	Carnivore/(?)Piscivore	Britt, 1991; Bakker and Bir, 2004; Foster and Chure, 2006; Yun, 2019
Dinosauria (Theropoda)	"cf. *Coelurus* sp."	(?)Carnivore	Miller et al., 1991; Rubensthal et al. pers. comm., 2025
Dinosauria (Theropoda)	*Marshosaurus* sp.	Carnivore/(?)Piscivore	Eudes-Deslongchamps, 1883; Miller et al., 1991; Charig et al., 1997; Bakker and Bir, 2004; Buffetaut et al., 2004; Allain, 2005; Sadleir et al., 2006; Amiot et al., 2010; Rauhut et al., 2016; Hassler et al., 2018
Dinosauria (Theropoda)	"(?)*Ornitholestes* sp."	(?)Omnivore	Zanno and Makovicky, 2011; Turner et al., 2012; Chapelle et al., 2021; Rubensthal et al. pers. comm., 2025
Dinosauria (Theropoda)	*Stokesosaurus* sp.	Carnivore	Miller et al., 1991
Dinosauria (Theropoda)	*Torvosaurus tanneri*	Carnivore/ Piscivore	Eudes-Deslongchamps, 1883; Galton and Jensen, 1979; Bakker and Bir, 2004; Charig et al., 1997; Buffetaut et al., 2004; Allain, 2005;

Dinosauria (Theropoda)	"*Paleopteryx thomsoni*"	(?)Carnivore	Jensen and Padian, 1989; Britt, 1991; Padian, 1998

TABLE 3. Ec**ological nodes for Dry Mesa Dinosaur Quarry**

Ecological Node	Model 1: In Degree	Model 2: In Degree	Model 1: Out Degree	Model 2: Out Degree	Model 1: Total Degree	Model 2: Total Degree
Allosaurus 1	10	9	5	5	15	14
Allosaurus 2	22	20	4	4	26	24
Allosaurus 3	29	27	3	3	32	30
Allosaurus 4	37	34	2	2	39	36
Allosaurus 5	45	41	1	1	46	42
Allosaurus 6	46	42	0	0	46	42
Amphibia	2	2	5	5	7	7
Apatosaurus 1	1	1	15	15	16	16
Apatosaurus 2	1	1	11	11	12	12
Apatosaurus 3	1	1	9	9	10	10
Apatosaurus 4	1	1	7	7	8	8
Apatosaurus 5	1	1	5	5	6	6
Apatosaurus 6	1	1	3	3	4	4
Apatosaurus 7	1	1	1	1	2	2
Apatosaurus 8	1	1	0	0	1	1
aquatic invertebrates	1	1	8	8	9	9
aquatic plants	0	0	3	3	3	3
Barosaurus 1	1	n/a	14	n/a	15	n/a
Barosaurus 2	1	n/a	11	n/a	12	n/a
Barosaurus 3	2	n/a	9	n/a	11	n/a
Barosaurus 4	2	n/a	7	n/a	9	n/a
Barosaurus 5	2	n/a	5	n/a	7	n/a
Barosaurus 6	2	n/a	3	n/a	5	n/a
Barosaurus 7	2	n/a	1	n/a	3	n/a
Barosaurus 8	2	n/a	0	n/a	2	n/a
Brachiosaurus 1	1	1	14	14	15	15
Brachiosaurus 2	2	2	11	11	13	13
Brachiosaurus 3	2	2	9	9	11	11
Brachiosaurus 4	1	1	7	7	8	8
Brachiosaurus 5	1	1	5	5	6	6

Brachiosaurus 6	1	1	3	3	4	4
Brachiosaurus 7	1	1	1	1	2	2
Brachiosaurus 8	1	1	0	0	1	1
Camarasaurus 1	1	1	14	14	15	15
Camarasaurus 2	2	2	11	11	13	13
Camarasaurus 3	2	2	9	9	11	11
Camarasaurus 4	1	1	7	7	8	8
Camarasaurus 5	1	1	5	5	6	6
Camarasaurus 6	1	1	3	3	4	4
Camarasaurus 7	1	1	1	1	2	2
Camarasaurus 8	1	1	0	0	1	1
Camptosaurus	2	2	11	12	13	14
Ceratodus	2	2	12	12	14	14
Ceratosaurus	22	23	4	4	26	27
Dinochelys whitei	6	6	10	10	16	16
Diplodocus 1	1	1	14	14	15	15
Diplodocus 2	1	1	11	11	12	12
Diplodocus 3	2	2	9	9	11	11
Diplodocus 4	2	2	7	7	9	9
Diplodocus 5	2	2	5	5	7	7
Diplodocus 6	2	2	3	3	5	5
Diplodocus 7	2	2	1	1	3	3
Diplodocus 8	2	2	0	0	2	2
Dryosaurus	1	1	13	13	14	14
Dsungaripteroidea	7	7	10	10	17	17
Eliendon robutus	2	2	4	4	6	6
Eutretauranosuchus delfsi	21	20	7	7	28	27
Gargoyleosaurus	1	1	11	12	12	13
Glyptops	1	1	9	9	10	10
Haplocanthosaurus 1	1	1	14	14	15	15
Haplocanthosaurus 2	1	1	11	11	12	12
Haplocanthosaurus 3	1	1	9	9	10	10
Haplocanthosaurus 4	1	1	7	7	8	8
Haplocanthosaurus 5	1	1	5	5	6	6
Haplocanthosaurus 6	1	1	3	3	4	4
Haplocanthosaurus 7	1	1	1	1	2	2
Haplocanthosaurus 8	1	1	0	0	1	1
Lacertila indet	1	1	4	4	5	5

Marshosaurus	20	19	7	7	27	26
Mesadactylus	2	2	11	11	13	13
Multituberculata	1	1	4	4	5	5
Nanosaurus	1	1	8	17	9	18
Palaeoniscidae	1	1	12	12	13	13
Palaeopteryx	6	6	17	17	23	23
plants ground	0	0	52	44	52	44
plants mid	0	0	24	18	24	18
plants trees	0	0	12	12	12	12
Potamoceratodus	2	2	12	12	14	14
Prototheria	1	1	4	4	5	5
Stegosaurus	1	1	11	12	12	13
Stokesosaurus	7	7	14	14	21	21
Supersaurus 1	1	1	14	14	15	15
Supersaurus 2	1	1	11	11	12	12
Supersaurus 3	2	2	9	9	11	11
Supersaurus 4	2	2	7	7	9	9
Supersaurus 5	2	2	5	5	7	7
Supersaurus 6	2	2	3	3	5	5
Supersaurus 7	2	2	1	1	3	3
Supersaurus 8	2	2	0	0	2	2
terrestrial invertebrates	1	1	7	7	8	8
Torvosaurus 1	18	17	7	7	25	24
Torvosaurus 2	29	28	5	5	34	33
Torvosaurus 3	38	36	4	4	42	40
Torvosaurus 4	47	44	3	3	50	47
Torvosaurus 5	55	51	2	2	57	53
Torvosaurus 6	57	53	1	1	58	54
Torvosaurus 7	71	65	0	0	71	65

TABLE 4. Statistical Summary of the Dry Mesa Dinosaur Quarry In-Degrees, Out-Degrees, and Total-Degrees for the whole model

Model	Statistics	In Degree	Out Degree	Total Degree
Model 1	Minimum	0	0	1
Model 2	Minimum	0	0	1
Model 1	1st Quartile	1	3	5
Model 2	1st Quartile	1	3	6
Model 1	Median	1	7	10
Model 2	Median	1	7	10

TABLE 5: Rec**onstructed Node Fractions Across Recovered Models**

Model	Fraction Basal Nodes	Fraction Intermediate Nodes	Fraction Top Level Nodes	Fraction Isolated Nodes
Model 1	0.04123711	0.8659794	0.09278351	0.8659794
Model 2	0.04494382	0.8651685	0.08988764	0