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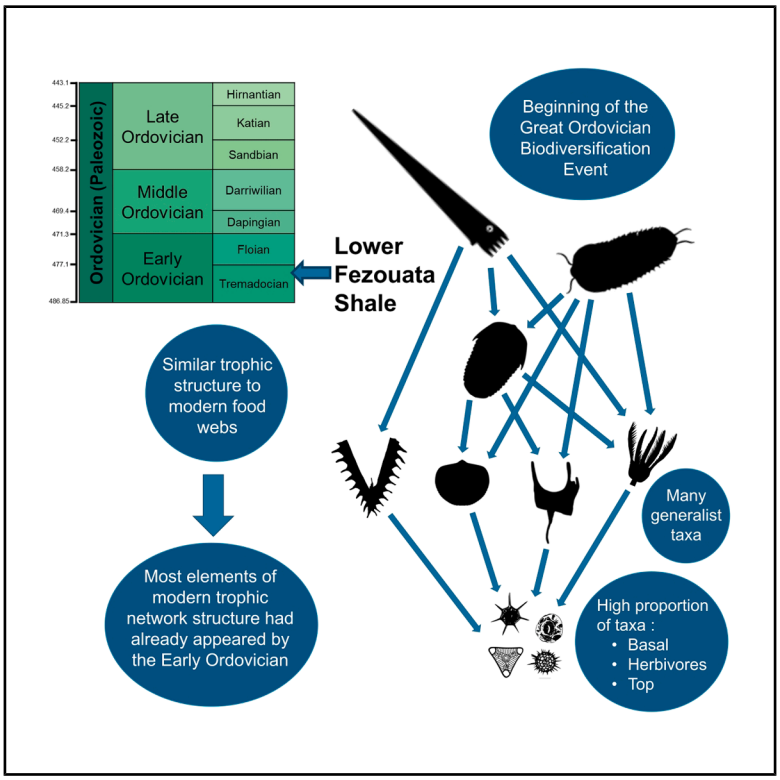
Graphical abstract



Highlights

- We assembled a comprehensive taxa list for the Lower and Upper Fezouata Shales
- We built a trophic network model of the Early Ordovician Lower Fezouata Shale fauna
- It showed high numbers of basal taxa, herbivores, top predators, and generalists
- Most elements of modern trophic network structure had already appeared by then

Authors

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In brief

Evolutionary biology; Paleobiology; Computer science

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A paleoecological trophic network model of the Early Ordovician Lower Fezouata Shale (Morocco) fossil fauna

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SUMMARY

The fauna of the Fezouata Shale, an Early Ordovician fossil Lagerstätte from Morocco, is transitional between the Cambrian and the Great Ordovician Biodiversification Event (GOBE). We compiled a comprehensive taxa list for the Lower Fezouata Shale and developed its empirical trophic network. We compared it to four modern marine networks and a modeling by the niche model, known for accurately representing modern trophic networks. The Fezouata network, compared with modern ones, had higher proportions of top, herbivore, and basal taxa, indicating a community defined by the coexistance of top predators typical of both the Cambrian and the Ordovician and the dominance of low-trophic-level taxa such as filter-feeders, whose expansion characterized the GOBE. These diversifying taxa were also mostly generalists. The Lower Fezouata trophic network did not significantly differ from its niche model prediction, suggesting that most elements of modern trophic network structure had already appeared by the Early Ordovician.

INTRODUCTION

Through time, animals have evolved various body plans and other morphological characteristics, some of which still exist today, while others, many of which possess no modern equivalent, have gone extinct. This is why a great part of research on paleontological sites focuses on cataloging the discovered taxa and describing their biological traits. However, a simple enumeration of species provides only a partial view of the ecosystem. These ancient creatures were also defined by their ecology, in terms of interactions with sympatric species that defined their community. After all, a community, because of all the ways its constituent species interact, is more than the sum of its parts.[1,2] Its ecological structure, such as the trophic interactions between species, must be characterized to fully appreciate the evolution of ecosystems over time as they relate to changes in community structure, the earth, the ocean, and the atmosphere. Quantitative trophic network models highlight community properties' structure and changes,[3] including stability and resilience,[4,5] two characteristics relevant in the context of massive extinctions or the origination of new species and ecologies. These can be linked to a network's omnivory[6] or connectance (the number of realized trophic interactions compared to the maximum amount of interactions),[7] among others, and can inform on a network's response to events such as extinctions and diversifications.[8,9]

Reconstruction of trophic interactions of living communities is difficult because we cannot know all species and species interactions.[10] This difficulty is greater in the context of fossil faunas, as species interactions rarely fossilize. Instead, paleotrophic interactions are inferred by using information gathered from the fossils, sympatric occurrences, gut contents, mouth parts, or by inference from comparable extant species, but uncertainties remain.[8,11–14] Further complicating this exercise is the absence of comparable extant species for some fossil groups and the preservation bias of animals with skeletons over soft bodied animals. The ideal fossil faunas for ecological trophic analyses are Konservat-Lagerstätten, communities that preserve lightly sclerotized organisms, soft-bodied organisms, and animal traces. These offer more complete records of ancient biodiversity and behavior and capture a wide variety of trophic interactions. They, however, are not the only suitable faunas, as others might have more complete species composition, but poor preservation. Despite these inherent biases to constructing food web models with fossils, simulations have suggested that trophic network reconstruction allows the recreation of food webs that are representative of the ancient communities from which they are derived,[15] especially if taphonomic bias is considered.[3] To add to this new and rapidly developing literature, which permits the opportunity to study a community's trophic structure quantitatively,[16,17] here we construct a new trophic network on the

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basis of trophic interactions of the Early Ordovician Moroccan Lagerstätte of the Lower Fezouata Shale Formation.

The Fezouata Shale fossil location was discovered in the early 2000s in the Anti-Atlas Mountain range of Morocco near Zagora.[18] It is the best known exceptionally preserved fossil site of an open marine environment from the Early Ordovician. Its fossils are restricted to two rock intervals, one dating back to the end of the Tremadocian (*Sagenograptus murrayi* graptolite Zone), in the Lower Fezouata Formation, and the other to the mid Floian (*Baltograptus jacksoni* Zone),[19–21] in the Upper Fezouata Formation. The exceptionally preserved Lower Fezouata fauna is used here to build a trophic network. Most fossils are flat carbonaceous compressions in a "Burgess Shale" type preservation, but with more three-dimensionality[22,23] and, consequently, many soft-bodied organisms and structures are preserved, allowing for a more complete reconstitution of the fauna.[22,24,25] Exceptional preservation is rare in the Ordovician, even more so in the Early Ordovician.[26–29] The few exceptionally preserved sites are from the Late Ordovician and generally represent more unusual or restricted paleoenvironments.[21,29] This contrasts with the Fezouata Shale that preserves animals from an open marine environment,[18] where organisms from the entire water column are preserved.[24,30]

During the Early Ordovician, the Fezouata ecosystem, both Lower and Upper, was located very close to the South Pole, with a latitude of 65°S, on the southern margin of Gondwana[21,31,32] making it a cold-water habitat.[33] It was a shallow open marine environment situated between the offshore and lower shoreface at a depth just below the storm-wave base (≈ 50 – 150 m depth).[21,34] Its shelly fauna was typical for a high-latitude ecosystem of that time,[35] but species distribution varied between the Lower and Upper Fezouata formations.[20,36] The Lower Fezouata ecosystem was quite heterogeneous spatially and saw lots of disturbances due to storms and bouts of anoxia or dysoxia.[37–39] Its fossilized specimens were primarily buried *in situ* rather than being transported.[21,37] As a result, the species distribution is patchy and fossils are often found in lenses of low species diversity, while a high specific diversity is observed in the formation as a whole.[29,36,39,40] The Upper Fezouata Formation, on the other hand, has fossils that are generally diverse and similar from one location to the next.[36] Exceptionally preserved fossils are common to the Lower Fezouata Formation while comparatively rarer in the Upper Fezouata Formation. This, and the higher taxonomic diversity of the lower formation compared with the upper one, is why we focused our trophic network modeling efforts on the Lower Fezouata ecosystem.

The species composition of the Fezouata Shale as a whole is remarkable as it is an amalgam of typical Cambrian species, some of which were previously thought to have gone extinct, and other typical Ordovician species.[18,29] Typical Cambrian taxa include demosponges,[39,41] eocrinoids,[40,42] lobopodians, radiodonts,[43–45] marrellomophs,[21,46,47] and siphogonuchitids.[48] The typical Ordovician taxa comprise asterozoans,[40,49] bivalves,[50] articulate brachiopods,[18,51,52] cephalopods,[53] crinoids,[40,54] planktonic graptolites,[19,55] and various other taxa.[18,19,32,56–61] For some taxa, such as horseshoe crabs, eurypterids, or barnacles, it represents their earliest appearance in the fossil record.[21,22,29,32,62] The Fezouata fauna fills temporal and ecological gaps in our understanding of animal evolution. It marks the beginning of the Great Ordovician Biodiversification Event (GOBE). The GOBE represents the second great radiation in animals (though its separation and independence from the Cambrian Explosion has recently been questioned[63–65]). These animals diversified within the established phyla from the Cambrian and at lower taxonomic levels such as families and genera.[66,67] The origination of new species was accompanied by a complexification of food webs and tiering within the now-dominant filter feeders.[66]

Previous work on Cambrian faunas has shown that most elements of modern trophic networks had already appeared by then.[12] If such crucial ecological structures were already in place so early into animal communities' evolution, it begs the question as to which are the characteristics within these conserved structures that changed through time and evolution. Sepkoski,[68] through the creation of his taxa biodiversity curves, identified three great Phanerozoic metazoan faunas: the Cambrian Evolutionary Fauna, the Paleozoic Evolutionary Fauna, and the Modern Evolutionary Fauna, each becoming dominant in turn. These faunas are distinguished by different dominant taxonomic compositions, levels of taxonomic diversity, and different dominant ecologies of their taxa.[68,69] The Paleozoic Evolutionary Fauna, which started in the Ordovician and would have been in its beginnings in the Fezouata Shale, was characterized by a dominance of brachiopods, as well as suspension feeders, among others, while the Modern Evolutionary Fauna is dominated by molluscs.[68,69] Quantitative ecological differences, such as trophic structure, between these faunas are less examined. Our study explores this by providing an ecological facet to the Fezouata fauna to find whether it indeed possesses the same base structure of food webs as modern communities, what differences do then exist in trophic structure between Paleozoic and modern faunas, and where is most variation in trophic structure observed through the long-term evolution of ecosystems.

Here, we provide a comprehensive and current account of the Lower Fezouata species and their trophic interactions. From this, we construct a trophic network model and provide an ecological analysis that includes the proportions of basal, herbivore, intermediate, and top taxa. Since working with paleontological data is accompanied by uncertainty, we performed an uncertainty analysis to evaluate the presence of potential bias in our data. We then compare our network with comparable networks of four modern marine faunas. Additional comparisons between its size and that of three modern freshwater trophic networks, and between its connectance and that of fossil networks of the Cambrian Chengjiang Shale fauna, the Cambrian Burgess Shale fauna, and the Cretaceous Paja Formation are also carried out.

RESULTS

The full taxa list of the Fezouata Shale included a total of 457 species (+5 functional groups, see STAR Methods), 289 of which were known to be found in the Lower Fezouata Formation, while the Upper Fezouata Formation possessed 170 taxa. Of those, 62 taxa could be found in both formations. For the Lower Fezouata Formation, only 202 taxa (including the 5 functional groups) were

Table 1. Properties of the Fezouata trophic network

Trophic network	S	L	L/S	C	TL	MaxTL
Lower Fezouata Shale species network	202	3930	18.986	0.092	2.430	3.611
Lower Fezouata Shale trophic species network	106	1405	13.255	0.125	2.431	3.528

Included are the number of nodes (species or trophic species), S; number of links, L; link density, L/S; connectance, C; mean trophic level, TL; and the maximum trophic level, MaxTL.

further used to construct our trophic network, as the others' feeding modes were unknown or too uncertain.

The Lower Fezouata Shale trophic network

The empirical trophic network created for the Lower Fezouata Shale comprised 202 taxa and 3,930 interactions. It had a mean trophic level (TL) of 2.430 and a connectance equal to 0.090. On the other hand, the empirical network of trophic species from the Lower Fezouata Shale contained 106 trophic taxa and 1405 interactions. Its TL was 2.431 and its connectance 0.125 (Table 1). The number of trophic species represents 52.47% of the original number of taxa in the trophic network.

The mean values and model errors (ME) of the 15 properties (Box 1) calculated for the empirical Lower Fezouata Shale species and trophic species networks and the niche model simulations are presented in Table 2, while their mode and median are in Table 3. When looking at the values of those properties for the trophic species network, we see a proportion of top species (Top) of 14.2%, of basal species (Bas) of 9.4%, and of herbivore species (Herb) of 35.8%, all three of which are higher (especially Top and Herb) than those for four extant marine webs[70–73] (see Table 4). The proportion of intermediate species (Int) of 76.4% in the Lower Fezouata Formation is, on the contrary, lower than what was found in those extant networks.[70–73] Omnivores (Omn) represent 51.9% of the food web, which is much lower than those of the four modern marine trophic networks. The mean maximum trophic similarity (MaxSim) of the Lower Fezouata network was relatively high, being 0.795.

Box 1. Abbreviations of calculated network metrics

Abbreviation	Definition
Bas	proportion of basal species (i.e., without resources)
C	connectance ($C = L/S^2$)
ChLen	mean length of food chains
ChNum	log number of food chains
ChSD	standard deviation of food chain length
Clust	mean clustering coefficient
GenSD	standard deviation of species generality
Herb	proportion of herbivores (i.e., feeding only on basal species)
Int	proportion of intermediate species (i.e., not top or basal)
L	total number of links
LinkSD	standard deviation of species links
MaxSim	mean maximum trophic similarity
Omn	proportion of omnivores (i.e., feeding from multiple trophic levels)
Path	mean shortest path
S	number of species
TL	mean trophic level
Top	proportion of species at highest trophic level (i.e., without consumers)
VulSD	standard deviation of species vulnerability

We notice that all ME values of both the species and trophic species networks are between -1 and 1 and are, therefore, not meaningfully different from what would be expected in an average modern trophic network that would have the same number of species (*S*) and connectance (*C*). A few properties in the species trophic network have MEs that are close to being meaningfully different (ME between 0.9 and 1 or -0.9 and -1; Top and Herb), while only one property in the network of trophic species remains with an ME between 0.9 and 1 or -0.9 and -1, namely Top. The niche model almost meaningfully underestimated (ME between 0.9 and 1 or -0.9 and -1) the proportion of Top in the Lower Fezouata Shale, with a mean ME of -0.926, meaning that this property is slightly higher in that fauna than what is expected for an average modern fauna, as the niche model is known to reliably predict modern faunas.[12,70,74] For the remaining 14 properties, the niche model did not meaningfully over- or underestimate their values. The ME values of most properties are quite similar between the species and trophic species network, apart from Bas and Clust where those values are quite different (0.697 vs. 0.071 and 0.035 vs. 0.674, respectively).

In twelve of the properties, the median and mode of the ME values are similar to the mean (Table 3). Among them, Top has an ME median and mode of -1, further emphasizing the higher proportion of Top taxa compared with what is expected in average modern faunas. The three properties whose median and mode diverged more importantly from the mean are the ones whose distribution is bimodal, which include the mean length of food chains (ChLen), the standard deviation of food chain length (ChSD), and the log number of food chains (ChNum) (Figures 1F–1H). Both their ME median and mode are -1, indicating that this value is the most typical of these bimodal distributions and is often produced. Despite the mean ME of these three properties being relatively close to 0, this shows a tendency of underestimation by the niche model of chain properties.

On a more methodological aspect, MEs of the Lower Fezouata trophic network's properties (Bas and Clust [mean clustering coefficient]) varied importantly between the species and trophic species (Table 1). This may indicate that for some properties, the creation of a trophic species web might alter the tendencies found in data. However, for Bas, this discrepancy in the niche model's prediction accuracy may be due to the relatively poorer

Table 2. Empirical values, mean niche model values, and mean model errors of all 15 network properties for the Lower Fezouata network

	Empirical value		Mean niche model value		Mean ME	
Network property	Species network	Trophic species network	Species network	Trophic species network	Species network	Trophic species network
Top	0.126	0.142	0.007	0.010	*–0.946*	*–0.926*
Bas	0.048	0.094	0.082	0.101	0.697	0.071
Int	0.826	0.764	0.911	0.889	0.103	0.163
Herb	0.401	0.358	0.031	0.039	*–0.923*	–0.891
Omn	0.531	0.519	0.840	0.806	0.581	0.552
ChLen	1.586	1.645	2.049	1.963	–0.595	–0.574
ChSD	0.494	0.481	0.520	0.539	–0.677	0.613
ChNum	2.124	1.968	1.614	1.312	–0.761	–0.762
TL	2.430	2.431	4.202	3.920	0.730	0.612
MaxSim	0.920	0.795	0.730	0.722	–0.206	–0.092
VulSD	0.453	0.437	0.274	0.271	–0.396	–0.379
GenSD	0.786	0.674	0.561	0.533	–0.286	–0.208
LinkSD	0.745	0.609	0.519	0.498	–0.304	–0.183
Path	1.431	1.297	1.854	1.772	0.295	0.366
Clust	0.315	0.254	0.326	0.424	0.035	0.674

There are no MEs that indicate meaningful differences (|ME|≥ 1). MEs that are almost meaningfully different (|ME|≥ 0.9) are indicated in italics. See also Figures S1 and S2 for the distributions of model predictions.

resolution of basal taxa compared with the taxa higher up in the network. It would indicate that in faunas with poorly resolved or aggregated basal taxa, which is not an uncommon occurrence,[70] trophic species might present a more accurate rendition of their proportion. As for Clust, the niche model's tendency to overestimate the clustering in the trophic species web but not in the species web could be due to several of the most clustered species being redundant in their interactions and, therefore, aggregated in trophic species. A certain heterogeneity in the clustering's distribution within the entire trophic network may not have been reproduced in the niche model simulations. The other properties did not show discrepancies between the MEs of the trophic species and the species network.

Table 3. Mode and median of model errors of all 15 network properties for the Lower Fezouata network

	Mode		Median	
Network property	Species network	Trophic species network	Species network	Trophic species network
Top	**–1.000**	**–1.000**	**–1.000**	**–1.000**
Bas	0.700	0.000	0.700	0.100
Int	0.111	0.185	0.105	0.173
Herb	*–0.952*	*–0.921*	*–0.928*	–0.895
Omn	0.573	0.545	0.582	0.555
ChLen	**–1.000**	**–1.000**	**–1.000**	**–1.000**
ChSD	**–1.000**	**–1.000**	**–1.000**	**–1.000**
ChNum	**–1.000**	**–1.000**	**–1.000**	**–1.000**
TL	–0.732	0.554	0.716	0.593
MaxSim	–0.212	–0.710	–0.206	–0.090
VulSD	–0.407	–0.336	–0.400	–0.384
GenSD	–0.281	–0.225	–0.289	0.211
LinkSD	–0.302	–0.190	–0.306	–0.184
Path	0.306	0.353	0.287	0.352
Clust	–0.025	0.715	0.032	0.676

MEs that are significantly different (|ME|≥ 1) are in bold. MEs that are almost meaningfully different (|ME|≥ 0.9) are indicated in italics.

Uncertainty analysis

Results of the uncertainty analysis yielded some differences between networks in which random links were removed and networks in which low-certainty links were removed (Figure 2). Larger differences between networks with random and low-certainty link removals could be found for the proportions of basal species, herbivores, intermediate species, and omnivores, as well as the length of food chains, the log number of food chains, the mean TL, and standard deviation of generality (GenSD), vulnerability (VulSD), and links (LinkSD). Most of these metrics were, however, more sensitive to link removals when random links were removed as opposed to low-certainty links (Bas, Herb, Int, Omn, ChNum, and TL; Figures S7–S12), suggesting some redundancy in low-certainty links. These results suggest minimal systematic bias in the distributions of low-certainty links and indicate that low-certainty links in the empirical trophic network generally do not introduce significant bias.

Four properties, however, had more sensitivity to link removals when low-certainty links were removed: ChLen, VulSD, GensSD, and LinkSD (Figures S13–S16). In the case of all except VulSD, the numerical differences observed were very small. Removing

Table 4. Empirical values of various properties of the trophic species networks of the Lower Fezouata Formation and four extant marine ecosystems

Network property	Lower Fezouata Formation	Benguela (Yodzis[71])	Carribbean reef, small (Opitz[72])	NE US shelf (Link[73])	Carribbean reef, large (Opitz[72])
Taxa	202	29	50	81	249
S	106	29	50	79	245
C	0.125	0.24	0.22	0.22	0.05
L	1405	203	555	1406	3381
Top (%)	14.2	0	0	4	0
Bas (%)	9.4	7	6	3	2
Int (%)	76.4	93	94	94	98
Herb (%)	35.8	7	6	19	4
Omn (%)	51.9	76	86	78	87
TL	2.431	3.2	2.9	3.1	3.1
MaxSim	0.795	0.66	0.58	0.70	0.61
Path	1.297	1.6	1.6	1.6	1.9
Clust	0.254	0.30	0.36	0.31	0.16

Taxa is the number of taxa in the species network, and *S* is the number of trophic species in the trophic species network.

50% of uncertain links changed ChLen, GenSD, and LinkSD by less than 7.5%, indicating that while some bias might have been introduced here, it was most likely negligible. In the case of VulSD, the variations observed were greater, meaning that uncertain links would introduce bias in the value of those properties, which needs to be taken into consideration when analyzing results involving them. Interestingly, VulSD tended to stabilize when uncertain links from only one trophic guild was removed.

Because the proportion of top species was not sensitive to link removals, we only performed the trophic-level uncertainty analysis for species assigned to basal, herbivore, and omnivore roles. The uncertainty analysis in which links were removed by trophic guild generally yielded qualitatively similar results to the aforementioned analysis (Figures S4–S6). However, removing links for any one trophic guild reduced differences between networks with random and low-certainty removals in estimates of the proportion of omnivore species (Figure S6).

DISCUSSION

The Lower Fezouata Shale was a shallow open ocean community. Its trophic network was of similar size to some extant marine and other aquatic networks (see Table 4), which are heterogeneous in terms of taxon resolution, missing taxa, and omitted taxa. Its species network size was especially comparable to the species networks of Little Rock Lake (lake ecosystem, 182 species)[75] and a large Caribbean Reef (marine ecosystem, 249 species).[72] On the other hand, its trophic species network has a size similar to the trophic species networks of Little Rock Lake (92 trophic species), the northeast (NE) US Shelf (marine ecosystem, 79 trophic species),[70] as well as those of Canton Creek and Stony Stream (stream ecosystems; 102 and 109 trophic species, respectively).[76] The size of our Fezouata model is important as it influences many network properties affected by scale,[74,77,78] such as degree distribution[78] and proportions of top, intermediate, and basal species.[77,79] The Fezouata fauna represents preserved animals of all ecological types equally, but it lacks preserved taxa that were composed entirely of soft tissues,[24] such as early chordates.

The Lower Fezouata Shale trophic network possessed a combination of properties that were similar to and others that diverged from those of four modern marine food webs. From here on out, only the trophic network of trophic species will be discussed, hereby referred to as the "trophic network". The Lower Fezouata Shale trophic network's connectance (0.125), a measure of its complexity, falls within the interval usually observed in extant webs (0.071–0.315[12]). It is also close to the connectance found in other marine fossil food webs, such as the Cambrian Chengjiang Shale (0.091), the Burgess Shale (0.108),[12] and the Cretaceous Paja Formation (0.(177).[11] Other properties of the Early Ordovician trophic network do differ from modern trophic networks.[70–73] Filter-feeders, such as graptolites, mostly accounted for a higher proportion of Fezouata herbivores compared with the four extant marine trophic networks.[70–73] The high proportion of filter-feeders is even more increased by the fact that not all filter-feeders would be considered as herbivores, since some feed on zooplankton who, in turn, feed on phytoplankton, effectively including these filter-feeders in the group of first-level carnivores. Filter-feeding became dominant during the GOBE,[66,80] following the Ordovician Plankton Revolution.[80] This event started in the late Cambrian, then continued throughout the Ordovician, and saw the diversification and expansion of plankton species and communities,[80–82] on which filter-feeders foraged. The high proportion of herbivores in the Lower Fezouata ecosystem is furthermore supported by its relatively high ME of -0.891, which comes close to -1, even if it does not exceed it, meaning that the niche model tended to underestimate the number of herbivores in this fauna. In addition, the Lower Fezouata Shale network was

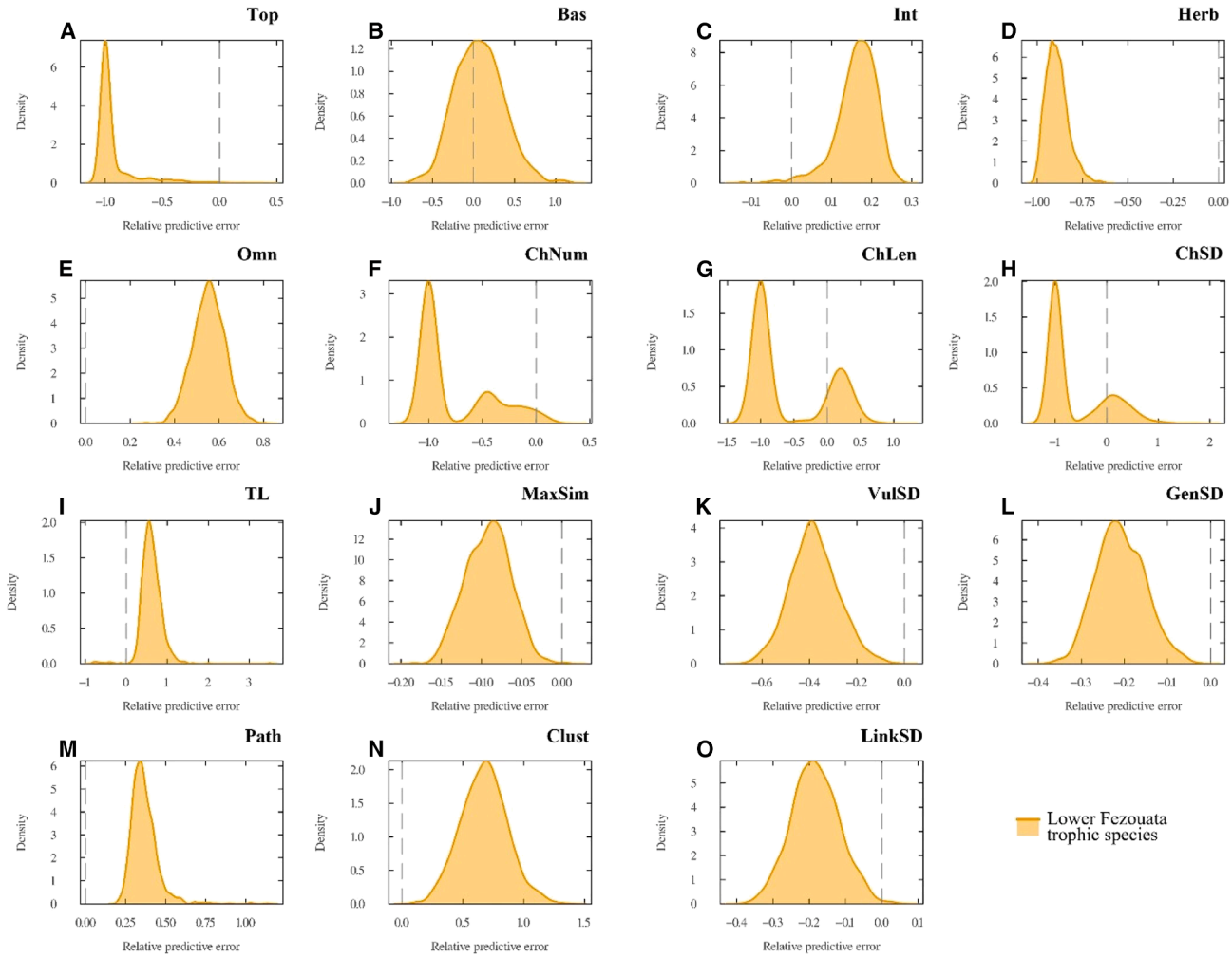

Figure 1. Distribution of MEs for all 15 network properties of the Early Ordovician Lower Fezouata Formation trophic network of trophic species

MEs are considered to indicate a significant difference when higher than 1 or lower than -1. See Figure S3 for the distribution of MEs for the trophic network of species.

characterized by a mean TL of 2.431, meaning that the average animal in that ecosystem was between an herbivore and a predator of herbivores. In a marine environment, the former would have been a deposit feeder or a filter-feeder eating phytoplankton, bacterioplankton, and/or suspended organic matter, while the latter included various hunting predators (e.g., cephalopods, eurypterids, and carnivorous trilobites) or filter-feeders that ate zooplankton. The Lower Fezouata's mean TL was slightly lower than that of several modern marine trophic networks[70] because of the higher levels of filter-feeders.

Other properties of the Lower Fezouata Formation with different values than that of modern networks include proportions of top and basal species, which are both higher. This difference especially stands out for top species, and this might be due to the retention of some great Cambrian predators, such as predatory trilobites[29] and the origination of new Ordovician predators like the nautiloid cephalopod *Polymeres* sp.[53] The latter benefitted from the new prey opportunities in the nekton.[80,83] Filter-feeders that lacked predators due to large size, such as *Aegirocassis benmoulai* and other radiodonts,[43,45] added to the number of top species. In addition, while the Lower Fezouata trophic network's ME for Top did not reach -1, it came quite close with a value of -0.926, indicating that the niche model tended to underestimate the number of top predators, which aligns with a fauna comprised of a greater number of top predators than most modern webs. This is further supported by the -1 value of the median and mode of Top's ME (Table 3). As for basal species, while their proportion does not significantly differ from the predictions of the niche model, their amount is higher than what is observed in the four modern marine food webs, which reflects the Ordovician Plankton Revolution being observable in the Lower Fezouata ecosystem. Intermediate species, on the other hand, represent a smaller proportion of the taxa in Fezouata than in the modern webs. As herbivores are included in intermediate

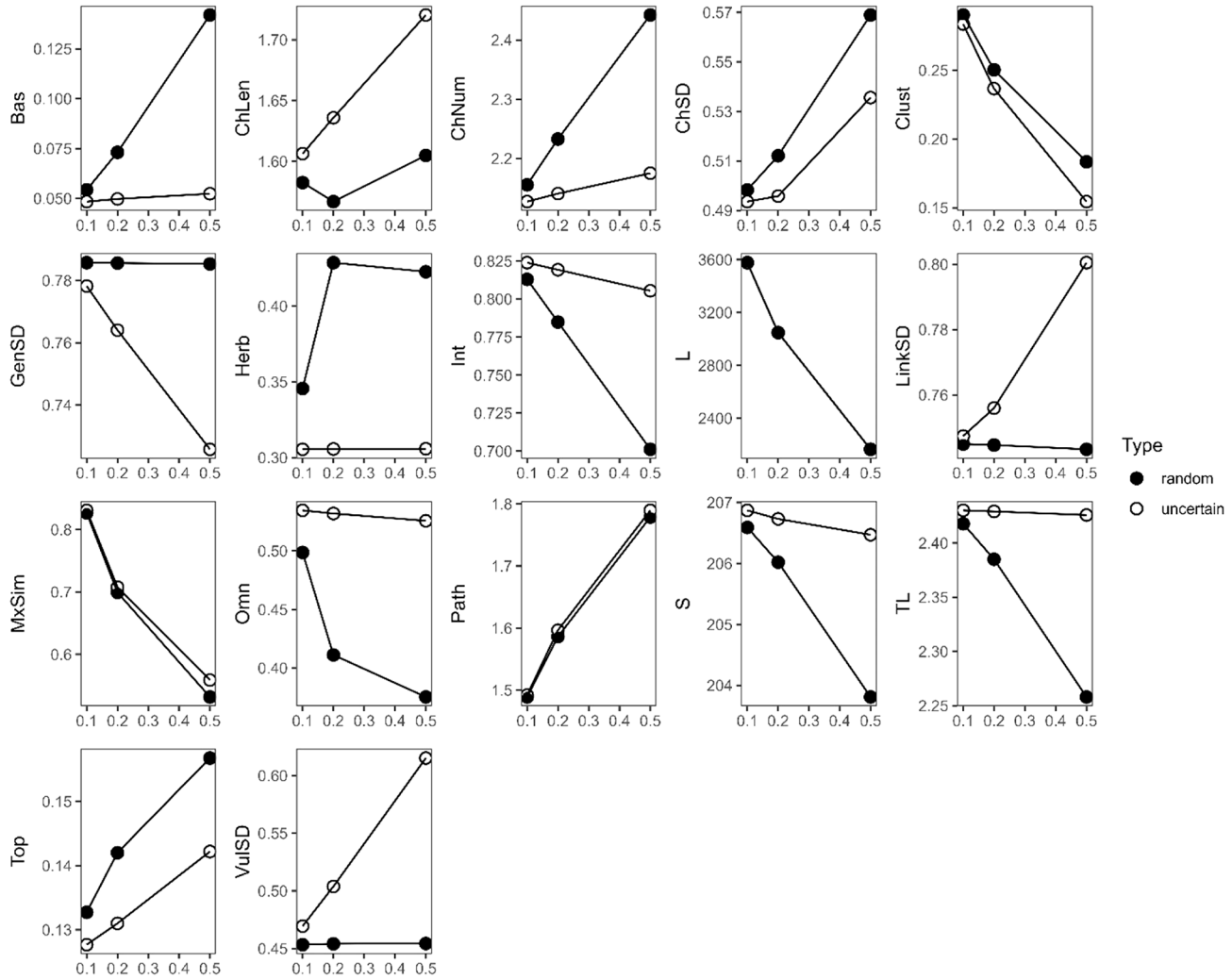

Figure 2. Mean estimates of network metrics for networks in which random links (black) and low-certainty links (white) were removed

Values on the *x* axis denote the proportion of random or low-certainty links that were removed. See Figures S4–S16 for figures of further analyses.

species, non-herbivore intermediate taxa become an even smaller proportion of the Lower Fezouata fauna. In the case of ChLen, ChSD, and ChNum, one peak of the bimodal ME distribution being around -1, the most representative peak according to the median and mode, indicates a fauna that generally would have had longer chain lengths, higher variation in those lengths, and a higher number of chains than what is expected in average modern food webs. The high variation of chain lengths might reflect a trophic network where many species of low TL (such as filter-feeders, with short chains to basal species) are eaten by some generalist predators (with longer chains to the basal species through the various filter-feeders). In addition, the higher number of chains (ChNum) indicates a slightly more widely connected network, which could hint at a lack of specialization of predators in terms of choice of prey in the Early Ordovician of Fezouata.

When considering all those properties together, the Lower Fezouata trophic network is characterized by a high level of taxa in both ends of the food chains. It comprises a great diversity of species in its low and highest trophic levels, the former having the greatest weight and lowering the average TL of the whole web. The number of intermediate species, especially non-herbivores, is lower than in modern trophic networks. This could indicate two things: a redundancy of trophic roles within high and especially low trophic levels or a high degree of specialization allowing such diversity. We reject the second hypothesis due to a high degree of maximum trophic similarity (MaxSim) in the network. The Fezouata fauna, therefore, comprised a high diversity of species having similar generalist diets, which is further supported by our results for the three chain properties. This might be due to diversifying prey taxa having yet to develop new predator defenses. It, therefore, seems that in the Tremadocian, the beginnings of the GOBE could be observed: a diversification of taxa, especially those in lower trophic levels, and mostly generalist species having yet to specialize. The high diversity of high and low TL taxa would be connected directly but also through a smaller amount

of non-herbivore intermediate species, creating more variation in chain lengths. This effect is most likely also favored by the heterogeneity and instability of the Lower Fezouata environment,[36–39] as heterogeneous environments favor the development and maintenance of generalist taxa and higher diversity.[84] Indeed, the Fezouata ecosystem experienced changes in oxygenation (anoxia and dysoxia)[36,38,39] and storm disturbances.[37] The early diversification of low TL taxa not yet followed by that of non-herbivore intermediate taxa decreased top species' direct dependence on intermediate taxa compared with what was observed in modern networks, where the majority of diversity was found in non-herbivore intermediate species.[70]

None of the Lower Fezouata trophic network's mean MEs indicate a property that was significantly over or underestimated by the niche model. The niche model predicts broad trophic structures at the scale of entire communities on the basis of potential distribution of links between tropho-species[85]; therefore, these results should be meant to indicate that even if specific interactions have changed throughout evolutionary times, the overall trophic structure may have remained stable. We found that several characteristics for neontological trophic interactions and food webs were in place about 477 million years ago. This parallels Dunne et al.,[12] who concluded that most elements of modern trophic networks had appeared by the Cambrian.

We have confirmed, thanks to the niche model's accurate predictions of network properties, that the topology and elements that characterize modern trophic structures had already been established by the Early Ordovician.[12] The element that differed when comparing with modern networks was the distribution of taxa between top, herbivore, and basal species, which seems to best characterize the ecological differences between these ecosystems of the Paleozoic Evolutionary Fauna and of the Modern Evolutionary Fauna. Seeing such variation in ecological groups, it would be interesting to verify whether the same differences are observed when studying the energy distribution between those groups. Previous work on Cambrian and Ordovician trilobites and brachiopods has shown that a decrease in a group's diversity does not necessarily rhyme with a decrease in energy if it is accompanied by an increase in biomass.[86] Furthermore, network analysis of paleofaunas is an emerging approach in paleontology. Studies like this one highlight the need for similar network analyses with other faunas that are temporally and spatially distinct, as these faunas were heterogeneous in geography and taxonomy.[87] These include comparing the Lower Fezouata Shale to the Upper Fezouata Shale fauna.[18,21] Then, comparing these faunas to the Ordovician-Silurian transition faunas of Anticosti Island, Quebec.[88–90] These comparisons will inform on whether the diversification of trophic groups during the GOBE is similarly heterogeneous to what is more precisely observed between different taxonomic clades and different regions. The creation of more Ordovician and other later Paleozoic trophic networks will also show whether other Paleozoic faunas from different locations and times reflect the same differences when compared with modern faunas, therefore precising and detailing the most defining differences between the Paleozoic and Modern Evolutionary Faunas. The Lower Fezouata fauna being only one example of a Paleozoic ecosystem, it would indeed need to be combined with others to form a complete portrait of these differences between the two evolutionary faunas.

Limitations of the study

Working with paleontological data comes with a certain level of uncertainty. We compiled a taxa list of the Lower Fezouata Shale intended to be as complete as possible, but having complete information on the fauna of that ecosystem would be impossible, as not all organisms fossilize. The absence of some taxa is, however, counterbalanced by our use of trophic species, as trophic network properties such as connectance need much smaller sampling effort to stabilize in trophic species networks than in species networks.[91] In addition, the trophic structure of a network built with trophic species instead of species fluctuates less with varying sampling efforts.[91] While useful, the trophic species do diminish the precision of the data. Feeding interactions in the Lower Fezouata Shale were based on fossils and thus, inferred. We tried to mitigate the bias created by this uncertainty through our uncertainty analysis. As the field of paleontological trophic networks develops, new techniques will be available to further diminish the impacts of these limits.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Corinne P. Soucy (corinne.soucy@umontreal.ca).

Materials availability

No new materials were generated in this study.

Data and code availability

- All data is available in Tables S1, S2, S3, S4, S5, and S6 and at Mendeley Data: https://doi.org/10.17632/txkb6gd9zb.
- All original code has been deposited on Zenodo and is publicly available at Zenodo: https://doi.org/10.5281/zenodo.20437943.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

C.P.S., conceptualization, data curation, formal analysis, funding acquisition, investigation, visualization, and writing – original draft; F.B., formal analysis, methodology, software, and writing – review and editing; E.B., formal analysis, methodology, software, visualization, and writing – review and editing; B.L., validation and writing – review and editing; J.C.G.-M., validation and writing – review and editing; T.P., software and writing – review and editing; C.B.C., conceptualization, funding acquisition, methodology, supervision, and writing – review and editing

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Trophic interaction data	This paper	Mendeley Data: https://doi.org/10.17632/txkb6gd9zb.2
Software and algorithms		
Julia v.1.189.2 (to build networks and calculate properties)	Julia Programming Language[92]	https://julialang.org/
Julia v1.12.2 (for the uncertainty analysis)	Julia Programming Language[92]	https://julialang.org/
EcologicalNetworks.jl package v.0.5.2	Poisot et al.[93]	https://doi.org/10.1111/ecog.04310
R 4.5.3	R software[94]	https://www.r-project.org/
Code for trophic network and uncertainty analyses	This paper	Zenodo: https://doi.org/10.5281/zenodo.20437943

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Omitted as our study does not involve biological models.

METHOD DETAILS

Species list and trophic roles

A list of all fossil species found in the Fezouata fauna was compiled and comprises a total of 462 taxa (Tables S1, S2, S3, S4, and S5). As is often done when building trophic networks,[12,73,95] this list was assembled by recording all species mentioned in the literature concerning the Fezouata Shale and was revised by co-authors Bertrand Lefebvre and Juan Carlos Gutiérrez-Marco who have considerable hands-on experience with these fossils. The same species referred to by different names in different articles were combined as one entry (e.g., *Auraeopirana auraeum* and *Pirania auraeum*), as were species for which the identification had changed (e.g., *Villebrunaster fezouataensis* and *Cantabrigiaster fezouataensis*).

To build the trophic network, only taxa found in the Lower Fezouata Formation were included, while some taxa had to be excluded due to lack of necessary information (e.g.,: Polychaete 1, Stalked flower-like organism, *Thelxiope* sp., or *Mollisonia* sp. 1). Following previous work,[71] only adults were considered in this trophic network because juveniles and their feeding biology are poorly known.[96] Larvae were omitted because they are absent from the Fezouata Shale and they occupy the same trophic role as zooplankton.[80,97] Acritarchs are numerous,[98–100] but were excluded from the analysis, as their nature is uncertain. These organic-walled microfossils are most likely the resting cysts of extinct phytoplankton.[98,101] Had they been included, they would have been aggregated in a trophic species (explained later) with the phytoplankton. Following Dunne et al.,[12] five functional groups were added to the list: phytoplankton,[80] bacterioplankton,[66] suspended organic matter (SOM), benthic detritus, and zooplankton[80] (other than planktic graptolites). While phytoplankton, bacterioplankton and non-graptolite zooplankton were not evident fossils in the Fezouata fauna, their presence was deduced by the existence of various filter-feeders in the community.

Identifying a species' trophic role (Tables S1, S2, S3, S4, and S5, columns ''Ecology'') was done based on its literature or on a similar species in the literature. The diet of some species was determined according to that of modern equivalent species. Species' feeding habits were also deduced according to their morphological characteristics. For instance, conodonts may possess jaws adapted to herbivory or to carnivory of soft-bodied prey,[102] and some lobopodians have limbs adorned with spines, which could filter organic particles in the water,[103] while others do not.[29] No Fezouata Shale fossils preserve gut contents that could be used to ascertain trophic interactions. The final species list upon which the trophic network was built comprised 202 taxa from the Lower Fezouata fauna.

Trophic links and trophic species

Trophic links between species (Table S2) were established according to these species' previously determined ecology. A species eating another is considered a consumer, while its prey is a resource.[12] This included their feeding technique (e.g., predator, filter-feeder, grazer, detritivore) and their habitat. As a consequence, none of the interactions included a benthic predator consuming a pelagic prey.[104] Cannibalism was rarely included amongst the feeding interactions, as the taxa lacked evidence of cannibalistic behavior.

The size of prey compared to consumer, in terms of body length, was also considered, if the size of both was known, as predators tend to feed within a certain interval of prey sizes.[96] The size used was the largest known to ensure that adults rather than juveniles formed the basis of the network model. Like Dunne et al.,[12] we assumed that a predator could eat prey within a size interval smaller than itself.[104,105] This is a common approach to understanding predator-prey interactions because it reflects nature, as opposed to an ecology whereby ''everyone eats everyone else''.

Inherent errors of characterizing trophic interactions were counter-balanced by creating trophic species, and by assigning a level of uncertainty to each trophic interaction (see subsection *Uncertainty analysis*). Once all trophic links were established, species were grouped into trophic species so that all species with the same resources and consumers were grouped as one. Grouping trophic species can reduce variations of a methodological and statistical origin due to a heterogeneous resolution of the taxa,[106] or to insufficient sampling.[91] Using trophic species can also highlight the major energy and nutrient flows between the main ecological species types.[17] Our trophic species model was thus based on a list of 106 trophic species and 1405 trophic links instead of 202 taxa and 3930 trophic links.

Creating the trophic network

Three empirical trophic network models were built. The first two were models of the Fezouata fauna based on the trophic species interaction data (a species network and a trophic species network). A third was built using the species interactions with the intention of conducting an uncertainty analysis (see subsection *Uncertainty analysis*). These networks are composed of nodes (S) representing species and links (L) between the nodes representing the trophic interactions between these species.[16,107]

Niche model and network properties

The fauna of the Lower Fezouata Shale was modeled using the cascade model,[108] the nested-hierarchy model,[109] and the niche model[85] for comparison with the empirical networks created with the interaction data. To do so, we conducted 1000 model simulations for each model and network. It was then compared to the empirical models, but only the niche model was used for further analysis, as it was found to be the most effective at accurately predicting trophic networks.[74] These models are useful to compare networks of different sizes and complexity, since many properties are scale-dependent, rendering a direct comparison of property values potentially misleading.[70,77] The description and results of the cascade and nested-hierarchy models are presented in the Supplementary Items (Figures S1 and S2).

The niche model is the model most frequently used to build trophic networks.[16] It is a generative model based on only two empirical parameters: the number of species and connectance.[12,16,85] This model assigns food links based on an arbitrary niche formation axis.[85] It associates each species to a niche value which determines which other species it can eat within a given niche range. In contrast to the cascade model and our empirical network reconstruction, species can eat others of a higher value if said species remain within their resource range. Species with similar niches will often eat the same resources.[85] The niche model also allows for cannibalism and looping and creates a higher trophic overlap, which corrects some of the cascade model's limitations.[74] It however makes trophic networks interval, meaning that they would be well explained by one single dimension, which does not fully correspond to many empirical trophic networks.[110,111] We used this model to simulate networks using the connectance (C) and number of nodes (S) calculated from the corresponding empirical networks amongst the species and trophic species networks of the Lower Fezouata Shale.

For all empirical and simulated networks, 15 properties were calculated (Box 1) (See Table 2 for empirical values and means of the niche model; Figures S1 and S2 for their distributions). As was done by Dunne et al.,[12] these included the proportion of top species, those with no consumers, sometimes also referred to as apex consumers (Top), basal species, those without links to any resource species (Bas), and intermediate species, those with both consumers and resources (Int). We also calculated the proportion of herbivores, species that only consume basal species (Herb), and omnivores, species that consume others from more than one TL (Omn). The mean food chain lengths (ChLen), the standard deviation of those lengths (ChSD), and the log number of food chains (ChNum) were also calculated. Other measured properties included the mean trophic level (TL), the mean of the maximum trophic similarity of species, a measure of the extent to which species possess the same resources and consumers (MaxSim), the standard deviation of vulnerability (VulSD), generality (GenSD), and total links (LinkSD), which respectively represent the standard deviation of a species' number of consumers, number of resources, and number of consumers and resources together. Finally, the mean shortest food chain length between all species pairs (Path) and the mean clustering coefficient, the probability for two species linked to the same third one to also be linked together (Clust), were also calculated (See Julia code for calculation methods of the properties). The mean TL was calculated by averaging species' fractional trophic levels. These were obtained following Williams & Martinez[112] by assuming each prey occupies an equal proportion of a consumer's diet.

Contrary to Dunne et al.,[12] the proportion of cannibal species and species found in loops were not considered, because any value calculated for these properties would be too biased (close to 0) by the method used to establish trophic links. Indeed, as was mentioned earlier, cannibalism was rarely included amongst interactions because of a lack of information concerning most species in that regard. The presence of loops is also affected by our methodology as species were mainly restricted to consuming others smaller than them when size-related data was available.

Once all values of those properties were obtained, some of them for the trophic species network (Top, Int, Bas, Herb, Omn, and MaxSim) were compared to those of four extant marine trophic networks,[70] namely those of Benguela,[71] a small and a large

Caribbean reef,[72] and the NE US Shelf.[73] The other properties were not directly compared as they were not calculated in the same way. Property values for all four extant marine trophic networks were taken from Dunne et al. (2004)[70] and three of these networks were also used in Dunne et al. (2008).[12] Both articles omitted the method by which their network properties were calculated. By reverse-engineering their methods using the Cambrian fauna data from Dunne et al., (2008)[12] (results not shown here), we were able to determine which properties were calculated using the same methods as ours. Our methods for calculating network properties can be found in our code.

The property values of the Lower Fezouata network were then compared between each empirical network and its niche model counterpart using model errors (see model errors section).

Uncertainty analysis

As is always the case when working with trophic interactions, and especially for those of extinct animals, there is a certain amount of uncertainty. To account for this, an uncertainty analysis was conducted in the same manner as Dunne et al.[12] Each trophic interaction was assigned a level of certainty: level 3 was a certain link, level 2 was a probable link, and level 1 was a possible link. A certain link (level 3) would be deduced from direct evidence or proven interactions. As no fossilized direct evidence of feeding was found in the Fezouata Shale, these are quite few and only include the feeding interactions of zooplankton on phytoplankton and bacterioplankton. A possible interaction (level 1) is one that could technically be possible but doesn't necessarily possess specific evidence to give supplementary support (such as a predator trilobite technically being able to eat some other reasonably smaller trilobite), while a probable interaction (level 2) does possess such evidence (ex: trilobite tracks intersecting worm burrows or tracks which then stop there). Then, an analysis to detect systemic bias caused by link uncertainty was performed. Briefly, a permutation analysis consisting of randomly removing 10%, 25%, and 50% of low-certainty (level 1) links from the trophic network was performed, and any disconnected taxa were removed to create a single connected trophic network. One hundred permuted networks per removal level were generated for a total of 300 trophic networks with low-certainty links removed. To facilitate comparisons, the analysis was repeated by removing the same number of links from each network, but with all links available for removal regardless of certainty level.

The 15 network metrics (Box 1 in main text) were calculated for each of the 600 permuted trophic networks. The mean value of each metric for each method and magnitude of link removal was then visually compared (Figure 2 in main text). Discrepancies in values for trophic networks with random vs. low-certainty links removed could indicate systemic bias caused by uncertainty. For each metric with visible discrepancies in values, the full distribution of calculated metric values was compared between the two removal methods to determine if the change in mean value was due to increased removal of random or low-certainty links. If removing increasing numbers of low-certainty links, but not random links, leads to large changes in a metric value, uncertain links could be introducing systemic bias into the dataset. If removing random links leads to large changes in metric values, the metrics are likely sensitive to link removal *per se* rather than the removal of particular links, indicating that uncertain links are probably not introducing systematic bias.

To determine whether trophic networks are sensitive to uncertainty at a particular TL, trophic roles were assigned to each species in the full trophic network for each fossil assemblage, according to their previously assigned links. The permutation analysis described above was then repeated, by removing 10%, 25%, and 50% of low-certainty links and the same number of random links involving species assigned to basal, herbivore, omnivorous, and top trophic roles. We generated 100 permutated trophic networks for each trophic role/removal percentage/removal type combination and visually compared the mean and the full distribution of metrics as described above.

QUANTIFICATION AND STATISTICAL ANALYSIS

Software

The trophic networks were built using the Julia programming language,[92] version 1.189.2, using the EcologicalNetworks.jl package,[93,113] version 0.5.2

The uncertainty analysis was conducted using the R software,[94] version 4.5.3. and the Julia programming language,[92] version 1.12.2, with the EcologicalNetworks.jl package,[93,113] version 0.5.2.

Model errors

To compare the properties of the Lower Fezouata network with their niche model counterpart, a model error (ME) (here calculated as a percent error[114]) was calculated. To do so, the value from the empirical model was subtracted from the niche model values and standardized (divided) by the empirical value:

$$ME = \frac{x_{niche} - x_{empirical}}{x_{empirical}}$$

A distribution of model errors was therefore obtained (Figure 1 in main text, see Figure S3 for the distribution of MEs for the original species trophic network). The mean, mode, and median of those errors was also calculated. The mode was calculated using values rounded to three decimals. An ME is regarded as meaningfully different if smaller than -1 or higher than 1. In the case of a negative ME, the model tends to underestimate the actual value of the property, while a positive ME value indicates an overestimation by the model.[12]