Report

Current Biology

Flourishing Sponge-Based Ecosystems after the End-Ordovician Mass Extinction

Highlights

- A new exceptionally preserved fossil fauna is reported from Zhejiang, China
- Sponges dominated seafloor ecology after the end-Ordovician mass extinction
- These post-extinction sponge faunas were as diverse as modern communities
- Sponges may have assisted in post-extinction ecosystem recovery

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In Brief

Botting et al. document post-extinction sponge-dominated communities from uppermost Ordovician rocks of South China. More than 75 sponge species represent multiple lineages that survived the Late Ordovician mass extinction. Sponges also flourished after other mass extinctions and may have facilitated ecosystem recovery by stabilizing sediment.

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Current Biology
Report

Flourishing Sponge-Based Ecosystems after the End-Ordovician Mass Extinction

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SUMMARY

The Late Ordovician (Hirnantian, approximately 445 million years ago) extinction event was among the largest known, with 85% species loss [1]. Post-extinction survival faunas are invariably low diversity, especially benthic communities [2], but ecological structure was restored relatively rapidly [1]. This pattern, however, reflects organisms with robust skeletons, as only one exceptionally preserved Hirnantian fossil biota was previously known [3, 4]; in particular, almost no Hirnantian sponges have been recorded. Our study reveals an extraordinarily diverse, sponge-dominated community thriving immediately after the Hirnantian extinction in Zhejiang, South China. Several contemporaneous sites preserve a total diversity of over 75 sponge species, many with preserved soft tissues, in pronounced contrast to normal survival and early recovery faunas. This diversity is unprecedented for any Hirnantian fossil group, and the fauna provides a unique window into a post-extinction ecosystem. The sponges are often large and structurally complex and represent numerous different lineages that survived the extinction. Layers with abundant sponge remains were deposited after other mass extinctions [5, 6], suggesting a general pattern of sponge abundance during collapse of Phanerozoic marine ecosystems. It is possible that the conditions of ecological collapse increase the particulate food sources for sponges, while they themselves are relatively unaffected by the crises. Furthermore, the abundance of sponges in the Hirnantian sequence of South China may have aided post-extinction ecosystem recovery by stabilizing the sediment surface, allowing sessile suspension feeders such as brachiopods, corals, and bryozoans to recover rapidly.

RESULTS

The Late Ordovician mass extinction (Hirnantian Age, approximately 445 million years ago) was extremely severe at low taxonomic levels but less dramatic in terms of shaping global marine ecology [1, 2]. The extinction was related to an initial extinction phase during the abrupt onset of an ice age in the early Hirnantian and a second phase corresponding to its end at the beginning of the *Metabolograptus persculptus* Biozone [7, 8], coinciding with the glacial maximum [9]. A subsequent interval of severely suppressed diversity continued through the Ordovician–Silurian boundary. The glacial interval is marked by the globally recognized *Hirnantia* fauna of brachiopods in shallow water [1]. Following post-glacial sea level rise and the extinction of this community, the Ordovician–Silurian boundary interval is normally marked by low-diversity faunas consisting mainly of planktonic graptolites, due primarily to a major sea level rise that resulted in global deposition of anoxic black mudstones [10].

The only previous record of sponges from uppermost Ordovician strata is a moderately diverse fauna of offshore species dated to the late Hirnantian *Metabolograptus persculptus* Biozone of the Kaochiapien Formation in Beigong, Anhui Province, China [11]. This was described as a unique occurrence, and it was suggested that the sponge community was a deep-water community that had been forced inshore by deep-water anoxia in the aftermath of the second extinction phase [11].

This report reveals a new, exceptionally preserved, sponge-dominated fauna from the Hirnantian Wenchang Formation in Anji County, Zhejiang Province. Several sections spread over approximately 10 km preserve the same 10-m-thick mudstone interval (representing sea level deepening), which has been dated on the basis of graptolites as being in the mid to upper part of the *M. persculptus* Biozone of the Hirnantian (Figures 1 and S2), immediately following the final pulse of the end-Ordovician mass extinction event. These assemblages lived after the second extinction pulse but before significant benthic recovery during the earliest Silurian [1, 14–16]. The Anji sponge faunas therefore lived during the post-extinction crisis interval.

In addition to approximately 2,000 sponges and abundant graptolites, a single articulated eurypterid, preserved with appendages (Figure 2A), four nautiloid shells, and other rare mollusks including a gastropod were recovered. A basal sandy

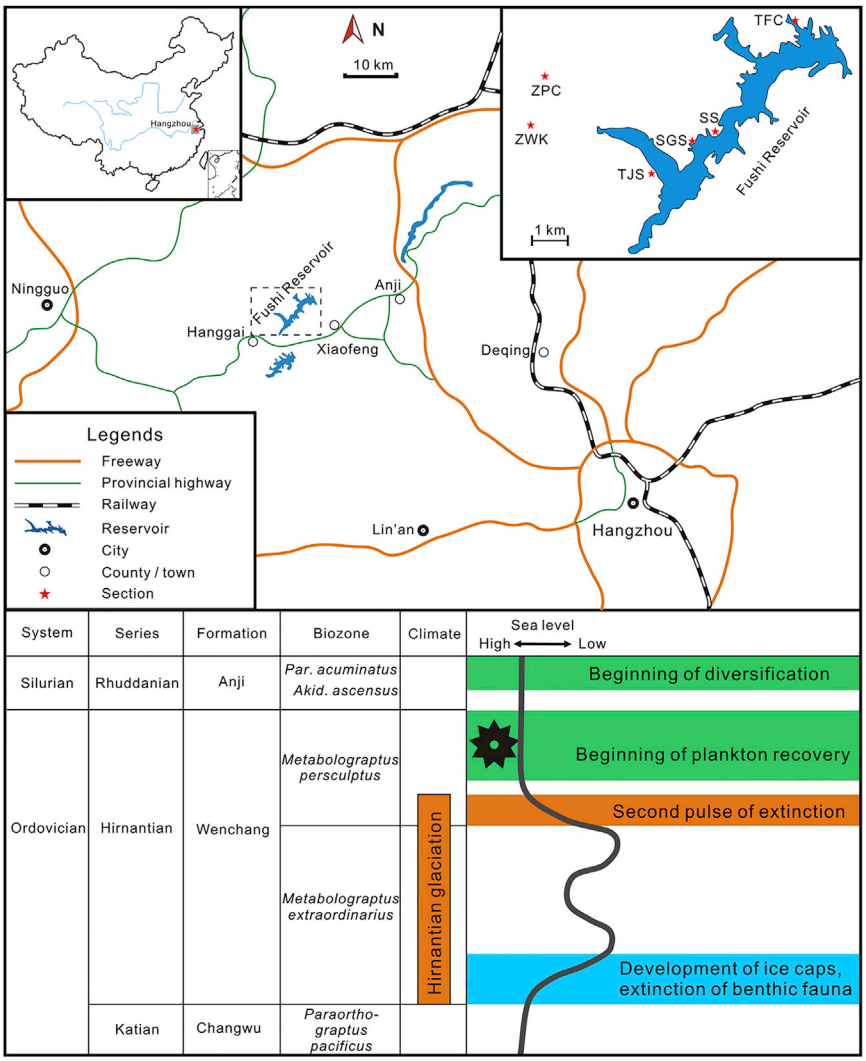

Figure 1. Regional Map and Stratigraphy, Showing the Position of the Anji Area and Anji Fauna in Northern Zhejiang Province, Southeast China

Lithostratigraphy is after reference [12]; sea level and bioevents are after reference [13]. The star indicates the approximate position of the sponge-bearing interval (Anji fauna). The inset map shows positions of the studied sections relative to the Fushi Reservoir (see Supplemental Information for details of sections). Abbreviations are as follows: ZWK, Zhuwukou; ZPC, Zhupingchang; TJS, Tianjiashan; SGS, Shangangshang; SS, Shuanshe; TFC, Tianfucun. See also Figure S2.

clay layer in some sections (Tianjiashan, Shangangshang, and Zhuwukou; Figure 3) yielded a transported, shallow water assemblage of low-diversity trilobites and brachiopods, equivalent to the *Hirnantia* fauna.

The total diversity of the Anji sponge assemblages exceeds 75 species: this total is preliminary and is likely to increase substantially with further collecting. The majority of species (Figure 2) are hexactine-bearing groups, but a wide range of major taxonomic groups are represented, including reticulosans (stem-group hexactinellids and siliceans [17]), protomonaxonids (early-branching sponges of uncertain position [18]), hexactinellids, and demosponges. All are delicate, thin-walled, spiculate sponges, and exceptional conditions were required to preserve articulated remains of these taxa.

Sponges are concentrated in the central part of the mudstone interval, representing the deepest-water conditions. Intensive sampling was conducted at several levels within productive sections (see Figure 1 and Supplemental Information for further detail). At two localities, Zhuwukou (ZWK) and Tianfucun (TFC), sponges are extremely abundant throughout the center of the exposed sections, except where interbedded sandstones become dominant near the base or top; at a third section, Shangangshang (SGS), sponges are apparently limited to a meter-thick interval in the center. In the remaining sections, Shuanshe (SS) and Tianjiashan (TJS), sponges are preserved only in narrow bands or as isolated specimens. Alpha diversity therefore varies dramatically between sections, with the lowest-diversity samples representing sparser populations or less favorable taphonomic conditions.

Some of the lowest beds (e.g., sample TFC-1; Figure 3) and the most condensed sections (TJS) have yielded articulated spicule skeletons only. However, the most productive levels (particularly SGS, samples ZWK-2, 2a, and 3, and sample TFC-2; Figure 3) yield a high proportion of sponges with soft-tissue remains. Both skeletons and soft tissues are primarily preserved as pyrite replacements, weathered to a range of iron oxides (see Supplemental Information). Spicules are often preserved as molds with pyritized axial canals, although most of the detail is lost after weathering. Non-biomineralized tissue preservation is also present in the single eurypterid specimen (Figure 2A).

Many of the sponges show adaptations that increase height above the seafloor: either a tall, slender growth form (Figures 2C and 2K), or possession of extensive parietal gaps (gaps through the body wall; Figures 2H–2J) that reduce the amount of material required to construct a skeleton to a given height. The most abundant species (Figure 2K) is a cylindrical reticulosan that forms dense assemblages, often of similar growth stage. This species occurs as part of a diverse assemblage but is dominant at most horizons in the most productive beds. The most diverse assemblages appear to be in the levels with highest sponge abundance, but, as many species are rare, this may be partly a preservational or sampling artifact.

Taxonomic overlap between samples is remarkably low (Table S1). Of the preliminary estimate of 75 species, 56 occur in only one sample level, 12 are present in two samples, and only seven were recovered from more than two sites; some of these, though, were found very widely. Among the shared species,

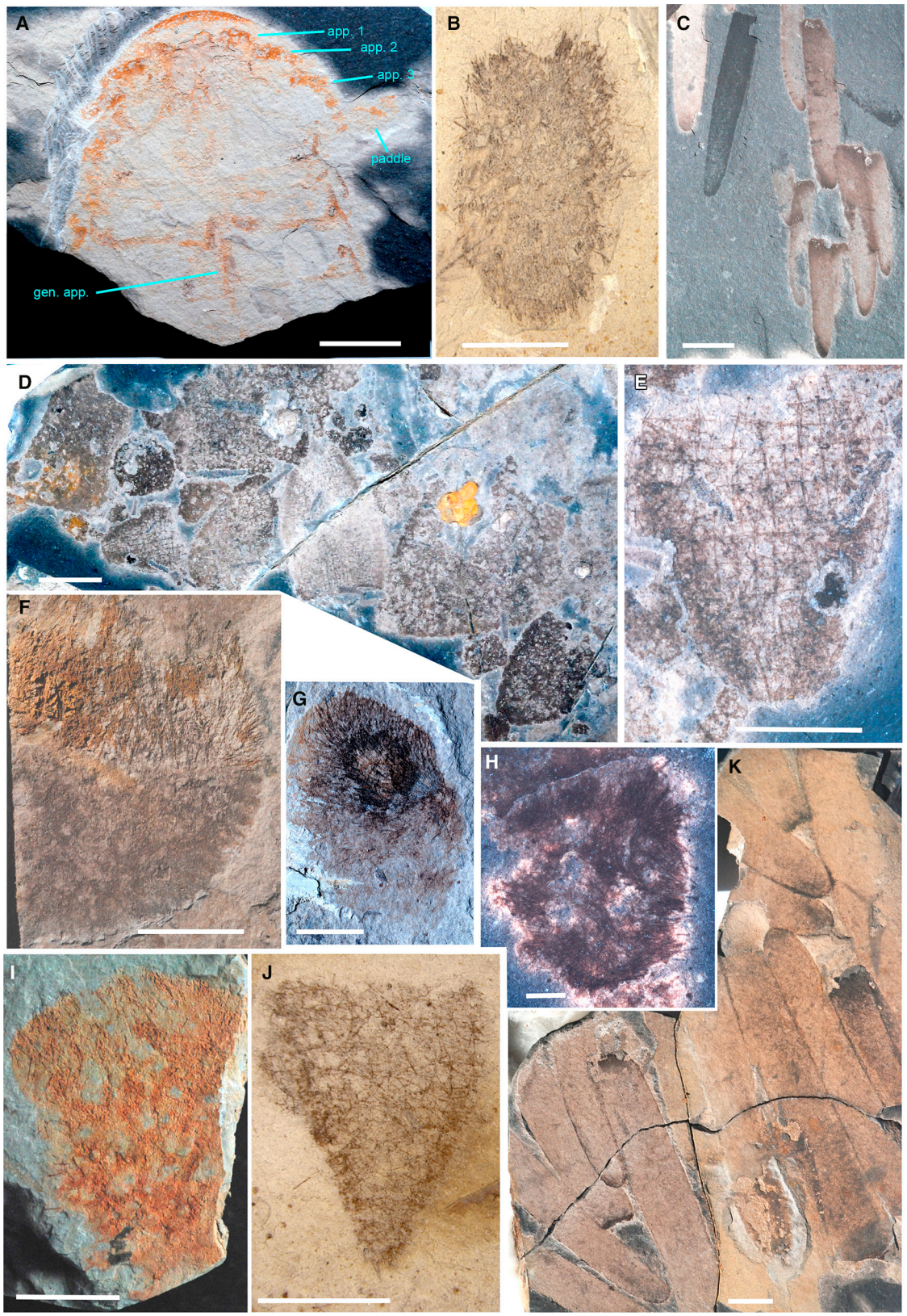

Figure 2. Fossils of the Hirnantian Anji Fauna of Zhejiang, China

(A) NIGP164906, Hughmilleriid eurypterid (app., appendage; gen. app., genital appendage; paddle, swimming appendage).

(B) NIGP164907, undescribed monaxonid sponge of uncertain affinity.

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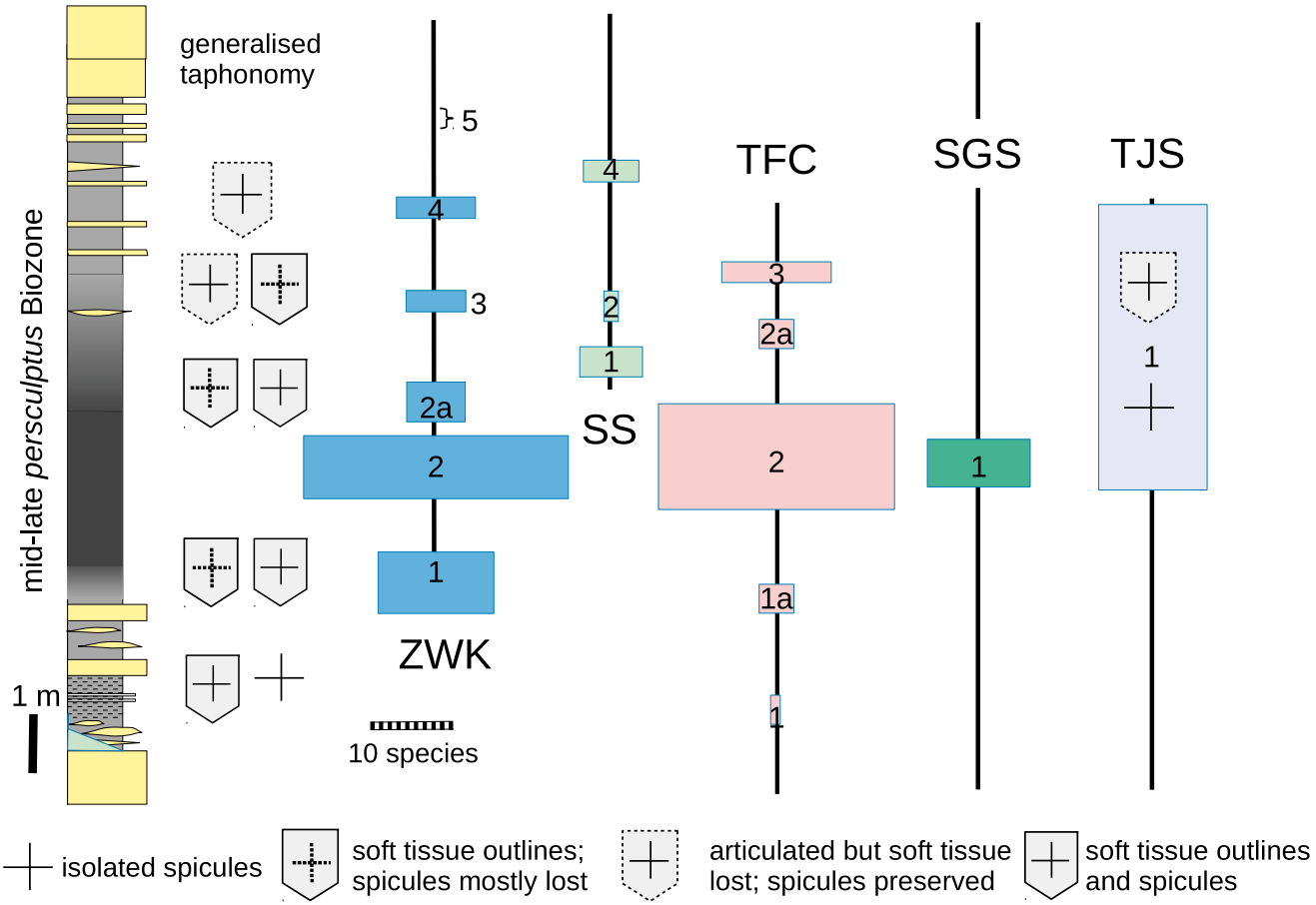

Figure 3. Composite Stratigraphic Log, with Indication of the Taphonomic Mode at Different Levels, and the Relative Positions and Diversities of the Sponge-Bearing Sections

The green clay layer containing a transported shelly assemblage is indicated by the green wedge at the base of the black mudstone interval. The diversity of each numbered sample is represented by the width of each box; box height denotes stratigraphic thickness. See also Figure S1 and Table S1 for matrix of the taxa shared between samples.

there is no preference for species shared between levels within one section or between sections at the same level (Table S1). There is also virtually no overlap of the Anji sponge fauna with the illustrated species from southern Anhui [11].

DISCUSSION

Sponges are extraordinarily diverse and abundant in the Anji assemblages, in direct contrast to the depauperate, stunted assemblages of shelly taxa typical of the post-extinction interval [2, 14], although the pattern is complex [19]. The Anji sponges are often large and structurally complex, and their diversity is equivalent to the total known modern sponge diversity in the richest areas of the Southern Ocean, even comparing with much larger areas of 3° by 3° [20]. The diversity is also substantially higher than that of the entire Burgess Shale complex (middle Cambrian, Canada) after a century of collecting [21].

The timescales recorded by the Anji fauna are geologically short, consistent with the observed distribution patterns representing ecological rather than evolutionary changes through

(C) NIGP164908, multiple specimens of the most abundant species, current aligned, and showing different stages of oxide weathering after original pyrite replacement of soft tissues.
(D) NIGP164909, mass assemblage of articulated sponges, including several species.
(E) Detail of (D), showing a complete specimen of *Cyathophycus* sp.
(F) NIGP164910, complex hexactinellid-like sponge with pronounced marginalia.
(G) NIGP164911, *Lenica*-like protomonaxonid.
(H) NIGP164912, hexactinellid-like sponge with palisade of pentactines resembling some modern Rossellidae.
(I) NIGP164913, reticulosan with parietal gaps and marginalia.
(J) NIGP164914, skeletal preservation of reticulosan with thin wall of fine hexactine derivatives.
(K) NIGP164915, mass assemblage of undescribed reticulosan with full soft-tissue preservation.
Scale bars of (A), (C), (I), and (K) represent 10 mm. Scale bars of (B), (D), (E)–(G), and (J) represent 5 mm. Scale bar of (H) represents 2 mm. See also Figure S3.

the sections. The duration of the *M. persculptus* Biozone was approximately 600,000 years [22]; the narrow mudstone interval in Anji, which represents a small part of the biozone, we estimate to have been deposited in less than 100,000 years and perhaps as little as 10,000 years based on the large thickness (over 360 m) of the Hirnantian Stage in the area. A short duration is consistent with the rapid sedimentation required for exceptional fossil preservation.

The abundant soft-tissue preservation, observed in the eurypterid as well as numerous sponges, makes the Anji fauna a Konservat-Lagerstätte. Such deposits preserve a relatively complete view of ancient ecosystems, in that many organisms that would normally have decayed are preserved. Interpreting the completeness of the assemblage is, however, difficult because various biases can operate against different elements of the living community. In the Anji fauna, preservation was mainly through pyritization following rapid burial by anoxic mud flows; this type of preservation frequently preserves a large proportion of the benthic community [23, 24]. The preservation of sponge soft tissues, together with eurypterid appendages, implies that many other organisms, including arthropods, should have been preserved if they had originally been present. The absence of any benthic fossils except sponges is thus likely to be a real ecological signal, and the lack of trace fossils combined with visible undisturbed sediment laminations further indicates the absence of mobile benthos. The dominance and extreme abundance of the sponges in this assemblage therefore appears to be a direct reflection of the local post-extinction ecology.

The presence of many distinct sponge lineages demonstrates that these communities represent diverse survivors from pre-extinction faunas rather than rapid radiation by a few surviving groups into empty post-extinction ecospace. Although earlier Late Ordovician non-lithistid sponges remain poorly known [25, 26], there is no suggestion of any significant diversity loss immediately preceding the Anji fauna, and the observed alpha and beta diversities are comparable with that observed in earlier Ordovician [27] and modern tropical [28] faunas. The range of morphologies and complex co-occurrence patterns also indicate well-developed tiering and ecological structure within the community. The distribution of present-day sponge species is notoriously patchy [29], related to abiotic factors as well as ecological interactions with other taxa [30]. These patterns are distinct from that of a normal survival fauna, in which a consistent low-diversity assemblage is recognizable over very wide distances, as with the *Hirnantia* fauna [31]. Instead, the offshore sponge community appears to have been largely unaffected by the mass extinction, except for the remarkable abundance of individuals.

The observed pattern of high alpha and beta diversity, seen across several sites covering 10 km, is strengthened by comparison with the contemporaneous assemblage from Anhui Province [11], 100 km away. The combined data demonstrate that sponge-dominated faunas were not confined to the Anji area but remained diverse during the late Hirnantian of, at least, this region of South China. Abundance of sponges also appears to be a more general pattern during mass extinctions: anomalously high abundances of sponge remains (often forming spiculite layers) within otherwise depauperate post-extinction crisis communities have been reported from sections on several continents spanning the Frasnian–Famennian [5] and end-Triassic [6, 32–34] extinction events. The diversity of these sponge faunas is currently unknown, but high abundance appears to be a general pattern. For the end-Permian mass extinction, the most severe extinction event of the Phanerozoic [35, 36], sponge remains (e.g., spiculite layers) occurred in upper Permian strata, but even these vanished or were greatly reduced in spicule size and abundance during the most severe crisis phase, at the Permian–Triassic boundary [36–38]. In modern oceans, intervals of high sponge abundance have also followed recent El Niño events [39], suggesting high tolerance of severe temperature anomalies and the opportunistic ability to thrive during ecological crises. The presence of exceptionally abundant sponges during mass extinction intervals might therefore be regarded as a direct symptom of ecological collapse.

There are further implications for the end-Ordovician extinction and for the subsequent recovery. Some fossil groups began to re-diversify early in the Rhuddanian (earliest Silurian), and paleocommunity structure in brachiopods, in particular, rapidly reverted to replicate that seen before the extinction, at least in some regions [14]. Despite high taxonomic losses, and changes in the dominant brachiopod groups, ecological changes were not as dramatic as might be expected [2], and community types were reestablished during the Rhuddanian for many groups such as brachiopods and corals [14]. This is difficult to explain if the ecosystem was redeveloping in a radically altered, low-diversity ecosystem.

Recognition of sponge-dominated benthic ecology during the Late Ordovician extinction interval has major implications for the initial stages of ecological recovery in offshore settings. In particular, sponges are regarded as ecosystem engineers [40] in that their disarticulated skeletons help to stabilize the seafloor, and they substantially structure offshore benthic ecosystems, raising the total diversity. Many of the most abundant Ordovician and Silurian fossil groups were sessile suspension feeders that required a firm substrate for attachment, including many rhynchonelliform brachiopods, bryozoans, and corals. Even where direct attachment is not necessary (e.g., certain successful Silurian brachiopod lineages), a stabilized sediment surface provides a lower risk of burial by resuspension of particles and reduces disturbance by burrowing organisms. There are also other potential ecological effects of high sponge abundance, such as the concentration of available organic matter into localized areas, in a manner reminiscent of the "Savannah Hypothesis" as applied to the Ediacaran [41]. In that case, it was argued that the evolution of large individual organisms in contrast to homogeneous microbial mats promoted the rise of burrowing and motility.

The flourishing of sponges through the low-diversity post-extinction interval therefore provided a means of stabilizing the offshore seafloor sufficiently to facilitate colonization by sessile suspension-feeding groups and also potentially aided redevelopment of motile scavengers and detritivores. Early reestablishment of brachiopod and tabulate ecology has been previously recognized [14], and sponges should thus be considered as potential facilitators of the revival of at least deeper-shelf ecosystems following the Late Ordovician ecological crisis. In contrast, reestablishment of diversity and of ecosystems after the end-Permian extinction (in which even sponges were severely affected) was

gradual [35]: the slow recovery from this event may have been exacerbated by the lack of sponges and spicule mats, suggesting that sponges may have played a pivotal role in recovery from biotic crises more widely throughout the Phanerozoic.

EXPERIMENTAL PROCEDURES

Field collections were made by hand from multiple horizons within sections exposing the mudstone interval. The studied sections are SGS, ZWK, TFC, SS, TJS, and Zhupingchang (ZCP). Specimens were imaged with a Nikon D80 DSLR camera and 105 mm macro lens and with a Leica M125 stereomicroscope and DFC450c digital imaging system. Figured specimens are deposited in the Nanjing Institute of Geology and Palaeontology Type and Figured Collection (NIGP).

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, three figures, and one table and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.12.061.

AUTHOR CONTRIBUTIONS

J.P.B. wrote the manuscript with contributions from L.A.M. and Y.Z. L.A.M. performed the biostratigraphy. X.M. and Y.Z. constructed Figure 1. J.P.B., L.A.M., Y.Z., X.M., J.M., L.W., J.Z., Y.S., and X.F. contributed substantially to fieldwork, organized by Y.Z.

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