1   *Title*: **Functional diversity of marine ecosystems after the Late Permian mass**

2   **extinction event**

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11   **Introductory paragraph**: The Late Permian mass extinction event was the most severe such

12   crisis of the past 500 million years and occurred during an episode of global warming. It is

13   assumed to have had significant ecological impact, but its effects on marine ecosystem

14   functioning are unknown and the patterns of marine recovery are debated. We analysed the fossil

15   occurrences of all known Permian-Triassic benthic marine genera and assigned each to a

16   functional group based on their inferred life habit. We show that despite the selective extinction

17   of 62-74% of marine genera there was no significant loss of functional diversity at the global

18   scale, and only one novel mode of life originated in the extinction aftermath. Early Triassic

19   marine ecosystems were not as ecologically depauperate as widely assumed, which explains the

20   absence of a Cambrian-style Triassic radiation in higher taxa. Functional diversity was, however,

21   significantly reduced in particular regions and habitats, such as tropical reefs, and at these scales

22   recovery varied spatially and temporally, probably driven by migration of surviving groups.

23   Marine ecosystems did not return to their pre-extinction state, however, and radiation of

24   previously subordinate groups such as motile, epifaunal grazers led to greater functional evenness

25   by the Middle Triassic.

26 **Main text**

27   The Late Permian extinction event, which occurred 252.28 ±0.08Ma (*1*), during a

28 period of climate warming (*2-3*), was the largest such crisis of the Phanerozoic in terms of

29 both diversity loss (*4-6*), and long term ecological impact (*7*). Local-scale, field-based studies

30 have suggested, however, that extinction magnitude and rate of subsequent recovery varied

31 with depositional setting (*8-12*), palaeolatitude (*10*, *13-14*) and region (*15-16*). The ecological

32 impact of past extinctions is, however, difficult to quantify and is arguably poorly understood

33 (*17*).

34   Here we use the ecospace model of Bambach et al. (*18*) to provide the first

35 quantitative analysis of the autecology of all known Permian-Triassic benthic marine genera.

36 This approach has been successfully applied to analysis of the Cambrian radiation, and to

37 compare the functional diversity of Palaeozoic and modern ecosystems (e.g. *19-20*), but has

38 not been used previously to quantify ecological change during extinction events. Our

39 analyses show that the Late Permian extinction event caused almost no loss of overall

40 functional diversity at the global scale, but did result in significant ecological shifts in benthic

41 marine communities from particular depositional settings, palaeolatitudes and regions.

42   Two complementary databases were constructed and analysed (available from

43 http://www.pangaea.de/, doi to be confirmed). Firstly, a database of all known marine

44 invertebrate genus-level occurrences from the Late Permian to the Middle Triassic, compiled

45 from the Paleobiology Database <www.pbdb.org> (PaleoDB), supplemented by additional

46 published data, along with locational, stratigraphic, lithological and environmental data. This

47 database comprises 22,263 recorded occurrences of 1420 genera. Occurrence data do not

48 capture Lazarus taxa, however, especially those that range-through, but do not occur within,

49 the study interval, and therefore underestimate the total number of genera known to have

50 existed in any particular time interval. Therefore, a second database comprising range-

51 through data of 1770 genera was compiled by ranging-through the occurrence database, and

52 supplementing these data with additional data from the PaleoDB and Sepkoski (*21*) [see

53 Supplementary Information].

54   The occurrences were binned into 12 unequal-duration time intervals equivalent to

55 Permian ages and Triassic sub-ages. Vetting of the data followed (*22*) [see Supplementary

56 Information]. Modes of life were inferred by using data from extant relatives, previous

57 publications and functional morphology, and each genus was assigned to a bin in the

58 ecospace model of (*18*) based on its tiering, motility and feeding habits [see Supplementary

59 Information]. Occurrences with sufficient geological information were assigned one of five

60 broad depositional settings along an onshore-offshore gradient: Inner Shelf (i.e. above fair

61 weather wave base), Middle Shelf (between fair and storm weather wave base), Outer Shelf

62 (between storm weather wave base and the shelf edge), Slope and Basin (beyond the shelf

63 edge), and Reefs (including build ups and bioherms). All occurrences were assigned to one of

64 the following palaeolatitudinal zones: Tropics (within 30°of the palaeoequator), northern

65 (>30°north) and southern (> 30°south). Finally, all occurrences were assigned to one of four

66 regions: Panthalassa, Boreal Ocean, Palaeotethys and Neotethys.

67   Aggregation of data within these bins was quantified using Green's coefficient of

68 dispersion (*23*). High Green coefficient values indicate dominance by one or two categories

69 within a particular stratigraphic bin, with values >0.5 considered to represent a significant bias

70 (*24*). In order to take into account variations in sampling intensity within and between the

71 different time bins and categories we applied the subsampling routine of Miller and Foote (*25*)

72 using a modified R script of Lloyd et al. (*26*) to standardise the functional richness based on the

73 number of occurrences. Subsampling quotas were set at 250 occurrences per bin for the global

74 analysis and 100 occurrences for the smaller scale analyses of palaeolatitude, region or

75 depositional setting. In each case, time bins with less than the specified quota of occurrences were

76 excluded from subsampling. This compromise avoids the degradation that may occur if the

77 quality of the poorest bin is used as the subsampling quota (*26*), but we recognise that higher

78 subsampling levels could reveal additional variability.

Global-scale changes in functional diversity

80 Global genus-level extinction is estimated at 62% (using range-through data) or 74%

81 (using occurrence data). There are often considerable differences between the range-through

82 and occurrence data, with the former providing lower extinction estimates for most modes of

83 life (Fig. 1). This difference is an unsurprising consequence of the poor quality Early Triassic

84 fossil record, which is due to a variety of factors including rock record biases, incomplete

85 sampling and poor preservation. Thus, while occurrence data indicate that as many as nine

86 modes of life completely disappeared across the P/Tr boundary (Fig.1), six of these are

87 recorded by the range-through data, implying that genera exhibiting those particular modes of

88 life have either been overlooked, were present at abundances that were too low to be

89 recorded by the fossil record, or existed at locations other than those that have been sampled

90 to date. Thus, at most, only three modes of life disappeared across the P/Tr boundary:

91 surficial, fast moving predators; semi-infaunal, stationary, unattached deposit feeders; and

92 deep infaunal, facultatively motile, unattached suspension feeders (Fig. 1).

93 Range-through data at the taxonomic resolution of families and superfamilies, which

94 have longer ranges than their constituent genera and may span an interval of time from which

95 no constituent genera have been recorded, show, however, that even this is an over-estimate

96 (Fig. 2a). The boundary-crossing family Erymidae demonstrates that at least one genus of

97 surficial, fast moving, predator must have been present somewhere. Likewise, deep infaunal,

98 facultatively motile, unattached, suspension feeders must have survived the extinction event,

99 as demonstrated by the boundary-crossing superfamily Pholadomyoidea. Thus, it would

100 appear that the greatest mass extinction event of the past 500 million years led to the loss of

101 just a single mode of life – that of semi-infaunal, stationary, unattached deposit feeders; a

102   consequence of the extinction of the rostroconchs. Subsampling to standardise the global

103   occurrence data also supports a lack of change in functional diversity across the P/Tr

104   boundary, despite the significant drop in generic richness (Fig. 2b). Therefore, overly

105   simplistic models suggesting that Early Triassic marine ecosystems functioned for millions of

106   years with primary producers only and no higher trophic levels (e.g. *27*) can be rejected.

107   The resistance of functional groups to global extinction, even those with few

108   constituent genera, is further demonstrated by the upward trajectory of functional diversity

109   since the start of the Phanerozoic (*18-20; 28*). Even though functional diversity was reduced

110   locally and regionally, for example in the tropics, because the Late Permian extinction did not

111   reduce functional diversity at the global scale an ecologically diverse group of marine

112   metazoan survivors were able to refill this vacant ecospace once conditions ameliorated (*29-*

113   *30*). This explains why relatively few classes, orders, or phyla originated in the early

114   Mesozoic, despite a return to levels of taxonomic diversity that were similar to the early

115   Palaeozoic (*29*). This may also explain why just one novel mode of life originated in the

116   Early Triassic; namely the erect, facultatively motile, attached suspension feeders, which

117   appeared with the evolution of motile crinoids in the Smithian (*31-32*; Fig. 2a). Globally, the

118   Early Triassic benthic ecosystem functioned much like a ship manned by a skeleton crew;

119   each post was occupied, but by only a few individual taxa.

120   The Late Permian extinction event was highly selective (Fig. 3; *29*), with the erect and

121   surficial, stationary, attached suspension feeders comprising 64% of the genera that

122   disappeared. Selection against these formally dominant groups led to increases in the relative

123   abundance at the global scale of most other groups during the Induan (Fig. 3). Despite

124   slightly increasing in relative abundance in the Olenekian, sessile epifaunal suspension

125   feeders never returned to the same level of dominance that characterised the Lopingian.

126   Instead, the appearance of motile crinoids (*31)* and the radiation of the 'modern biota',

127 including motile and infaunal bivalves (*34*), predatory arthropods (*35*), and grazing

128 gastropods (*36*), increasingly filled a diverse suite of lifestyles during the early Mesozoic (Fig.

129 3). By the Middle Triassic, functional evenness at the global scale had increased, due

130 especially to a radiation of the mobile grazing epifauna. Beginning even before the Late

131 Permian extinction event, surficial, slow moving grazers underwent a gradual, uninterrupted

132 increase in relative abundance through the entire study interval (Fig. 3). Apart from those

133 groups that originated after the extinction, this represents the most important change to the

134 functional landscape of benthic marine ecosystems during the earliest stages of the Mesozoic

135 Marine Revolution.

136 **Latitudinal trends and regional biases**

137 Although the Late Permian extinction event eliminated just a single mode of life at the

138 global scale, at smaller scales functional diversity loss was more pronounced. Prior to the

139 extinction event, equatorial palaeolatitudes, as expected, housed the greatest ecological and

140 functional diversity (Fig. 4a). Following extinction, however, raw and subsampled data

141 record similar levels of functional diversity in tropical and northern palaeolatitudes during the

142 Induan, and especially in the Dienerian (Fig. 4a). This low gradient of functional diversity

143 between the tropics and northern belt during the Induan may reflect the cosmopolitan nature

144 of Induan benthic faunas (*5*) and implies relatively greater ecological impact in the tropics.

145 Greater ecological impact in the tropics may be a consequence of climate warming, including

146 concomitant factors such as expansion of hypoxic dead zones, reduced circulation, reduced

147 nutrient cycling, and temperature rise itself, as well as the loss of reef ecosystems.

148 By the Anisian, raw and subsampled data show that tropical functional diversity had

149 exceeded that recorded at low palaeolatitudes during the Lopingian, and a steep functional

150 gradient between the tropics and higher latitudes had been re-established (Fig. 4a). Greater

151 tropical functional diversity during the Middle Triassic is probably due to migration from

152   higher latitudes of taxa with lifestyles that were not previously recorded in the tropics. In

153   many time bins, however, occurrences are not distributed evenly between palaeolatitudes, but

154   are biased towards the tropics (Green coefficients > 0.5; Fig. 4a). The Spathian and Anisian

155   record the greatest such bias, being dominated by well-studied sections from Europe and

156   South China (*37-39*), and the 'global' record of Spathian-Anisian recovery is therefore really

157   a 'tropical' record.

158   Raw functional diversity decreases from the Changhsingian to the Griesbachian in all

159   regions except the Boreal Ocean, which records an earlier decline, with minima being

160   recorded at different times within the Early Triassic (Fig. 4b). Results of subsampling suggest,

161   however, that except for Panthalassa these trends may be an artefact of sampling biases (Fig.

162   4b). The timing and patterns of recovery of functional diversity also apparently vary between

163   regions, although there are too few post-Griesbachian occurrences in Neotethys and the

164   Boreal Ocean for robust subsampling. A return to greater functional diversity occurred sooner

165   in Panthalassa than in Palaeotethys, although relative differences during the Middle Triassic

166   may be due to sampling problems because the regional occurrence data are strongly biased

167   towards Palaeotethys during the Anisian (Green coefficients >0.5; Fig. 4b). Indeed, the

168   widely held view that post-extinction recovery did not occur until the Anisian (e.g. *27*) is

169   likely due to this regional bias and the 'global' signal is evidently just a Palaeotethyan signal.

170   **Functional diversity in reefs and shelf settings**

171   Although most Early Triassic occurrences are from the inner shelf, there is no major

172   sampling bias between depositional settings through the study interval (Green coefficients

173   <0.5; Fig. 4c). It is well known that reefs disappeared during the earliest Triassic (e.g. *40*),

174   but our raw and subsampled data demonstrate for the first time that the major loss of

175   functional diversity in reef ecosystems occurred significantly before the late Changhsingian

176   mass extinction horizon (Fig. 4c). During the Wuchiapingian, metazoan reefs were globally

the most important habitat in terms of functional richness, recording 19 of the 23 known

modes of life (i.e. 83%), from 74 localities in UK, Russia, Germany, Greece, China,

Greenland, Lithuania and Pakistan. Only four modes of life are, however, recorded in

Changhsingian reefs, from a total of 36 localities from China, Russia, Tajikistan, Greece and

Thailand. These data imply that reef ecosystems underwent precipitous collapse, and/or a

major contraction, prior to climate warming in the latest Changhsingian. This may have been

due to Lopingian sea-level fall or to a currently unknown episode of climatic or

oceanographic change, possibly related to the earliest phases of Siberian Trap volcanism (*41*).

The subsequent rebuilding of reefs began locally in the Smithian (*42*) and Spathian, involving

organisms such as sponges (*42*), cementing bivalves (*43*) and *Tubiphytes* (*44*). Metazoan

reefs of the Anisian were as functionally rich as their Wuchiapingian predecessors (Fig. 4c),

although reefs were not common until after the Illyrian following the appearance and

radiation of the Scleractinia.

During the Early Triassic 'reef gap', basin and slope settings gradually lost functional

richness, whereas shelf seas, especially the inner and outer shelf, were functionally the most

diverse settings (Fig. 4c). By the Middle Triassic, inner shelf settings housed greater

functional richness than the re-emerging reefs. The 'habitable zone' hypothesis (*10*) predicts

that nearshore, wave-aerated settings should house greater diversity in the earliest Triassic

and although our inner shelf data support this hypothesis, the outer shelf data imply that even

if deeper settings were taxonomically depauperate functional diversity was still maintained, at

least in the Griesbachian (Fig. 4c).

Even though Early Triassic shelf settings were functionally diverse, the loss of erect

and deep infaunal taxa led to a reduction in occupied tiers. This restriction of benthic animals

to within a few centimetres above and below the sediment-water interface is the most

dramatic such shift of the entire Phanerozoic (*45*), and characterises the immediate extinction

202 aftermath worldwide (*14; 46*). It would have significantly impacted nutrient cycling and

203 secondary production, with bioturbation depths in most ecosystems returning to levels not

204 recorded globally since the Cambrian. Genera identified as being 'deep infaunal' reappear

205 first in the Smithian of eastern Panthalassa, but are represented by small-sized taxa such as

206 *Sinbadiella pygmaea* (*47*), which probably could not burrow that deeply. Full ecosystem

207 function would not have been restored until larger bioturbators reappeared. The earliest

208 reappearances of the erect tier are also represented by relatively small-sized animals: in the

209 inner shelf by bryozoans in the Dienerian (*48*); and in slope and basin settings by the crinoid

210 *Holocrinus* in the Smithian (*49*).

211   Despite the significant worldwide loss of species richness, the Late Permian

212 extinction event did not significantly reduce functional diversity of benthic marine

213 ecosystems at the global scale. As a consequence, few higher taxa and only one new mode of

214 life originated in the extinction aftermath. At smaller scales, however, significant changes in

215 functional diversity did occur in particular regions and depositional settings. Ecological

216 changes during this critical time in Earth history are more complex than simple models have

217 hitherto suggested, and supposed 'global' patterns may reflect biases in regional data,

218 especially in the post-extinction recovery interval.

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356 WJF and RJT are equally responsible for the project design, interpretation, and writing. WJF

357 compiled the databases and undertook the analyses.

358

359 **Fig 1:** The percentage of genera that became extinct within the Changhsingian in each

360 individual mode of life, for (**a**) range-through and (**b**) occurrence data. The numbers of

361 genera recorded in the Changhsingian (bold) and surviving into the Griesbachian (grey) are

362 reported above each respective bar. Error bars represent one standard error in each direction

363 [supplementary information]. 1 = erect, stationary, attached, suspension feeder; 2 = surficial,

364 fast moving, deposit feeder; 3 = surficial, fast moving, predator; 4 = surficial, slow moving,

365 suspension feeder; 5 = surficial, slow moving, deposit feeder; 6 = surficial, slow moving,

366 grazer; 7 = surficial, slow moving, predator; 8 = surficial, facultatively motile, unattached,

367 suspension feeder; 9 = surficial, facultatively motile, attached, suspension feeder; 10 =

368 surficial, facultatively motile, attached, deposit feeder; 11 = surficial, stationary, unattached,

369 suspension feeder; 12 = surficial, stationary, attached, suspension feeder; 13 = semi-infaunal,

370 slow moving, suspension feeder; 14 = semi-infaunal, facultatively motile, attached,

371 suspension feeder; 15 = semi-infaunal, stationary, unattached, deposit feeder; 16 = semi-

372   infaunal, stationary, attached, suspension feeder; 17 = shallow infaunal, slow moving,

373   suspension feeder; 18 = shallow infaunal, slow moving, miner; 19 = shallow infaunal, slow

374   moving, predator; 20 = shallow infaunal, facultatively motile, unattached, suspension feeder;

375   21 = shallow infaunal, facultatively motile, unattached, miner; 22 = shallow infaunal,

376   facultatively motile, attached, suspension feeder; 23 = shallow infaunal, facultatively motile,

377   attached, other; 24 = deep infaunal, facultatively motile, unattached, suspension feeder; 25 =

378   deep infaunal, facultatively motile, attached, other. Images of fauna are not to scale.

379

380   **Fig 2:** Diversity curves for generic and functional richness across the studied interval. (**a**)

381   Generic richness of raw range-through data (filled squares) and occurrence data (filled

382   circles); and number of modes of life occupied using generic range-through (open triangles),

383   generic occurrence data (open squares), and range-through data for higher taxonomic levels

384   (open circles). (**b**) Subsampled generic and functional richness using occurrence data. Median

385   generic richness (open circles) and median number of modes of life occupied (filled squares).

386   Error bars represent 5th and 95th percentiles. The Lopingian and Middle Triassic epochs are

387   shaded, bold vertical line shows the Permian/Triassic boundary.

388

389   **Fig 3:** Relative abundance of genera in each mode of life across the studied interval. Colours

390   indicate changes in abundance of >0.1%: increases (red), decreases (blue) and no change

391   (yellow) from the previous time bin. Wuchiapingian abundances are unshaded. 1 = erect,

392   facultatively motile, attached suspension feeder. 2 = erect, stationary, attached suspension

393   feeder; 3= surficial, fast moving suspension feeder; 4 = surficial, fast moving deposit feeder;

394   5 = surficial, fast moving predator; 6 = surficial, slow moving suspension feeder; 7 = surficial,

395   slow moving deposit feeder; 8 = surficial, slow moving grazer; 9 = surficial, slow moving

396   predator; 10 = surficial, facultatively motile, unattached suspension feeder; 11 = surficial,

397   facultatively motile, attached suspension feeder; 12 = surficial, facultatively motile, attached

398   deposit feeder; 13 = surficial, stationary, unattached suspension feeder; 14 = surficial,

399   stationary, attached suspension feeder; 15 = semi-infaunal, slow moving suspension feeder;

400   16 = semi-infaunal, facultatively motile, unattached predator; 17 = semi-infaunal,

401   facultatively motile, attached suspension feeder; 18 = semi-infaunal, stationary, unattached

402   deposit feeder; 19 = semi-infaunal, stationary, attached suspension feeder; 20 = shallow

403   infaunal, slow moving suspension feeder; 21 = shallow infaunal, slow moving miner; 22 =

404   shallow infaunal, slow moving predator; 23 = shallow infaunal, facultatively motile,

405   unattached suspension feeder; 24 = shallow infaunal, facultatively motile, unattached miner;

406   25 = shallow infaunal, facultatively motile, attached suspension feeder; 26 = shallow infaunal,

407   facultatively motile, attached other; 27 = deep infaunal, facultatively motile, unattached

408   suspension feeder; 28 = deep infaunal, facultatively motile, unattached suspension feeder; 29

409   = deep infaunal, facultatively motile, attached other. Images of fauna are not to scale.

410

411   **Fig. 4.** Permian-Triassic functional richness in different (**a**) palaeolatitudes, (**b**) regions, and

412   (**c**) environments. Raw data (open circles) and subsampled medians (filled squares). Error

413   bars represent 5th and 95th percentiles. Green coefficient values >0.5 indicate bias in the data

414   within that time bin. The Lopingian and Middle Triassic epochs are shaded. The Permian/

415   Triassic boundary is marked with a thick line.

a

b

Lopingian | Induan | Olenekian | Anisian | Ladinian

Wuchiapingian
Changhsingian
Griesbachian
Dienerian
Smithian
Spathian
Aegean
Bithynian
Pelsonian
Illyrian
Fassanian
Longobardian
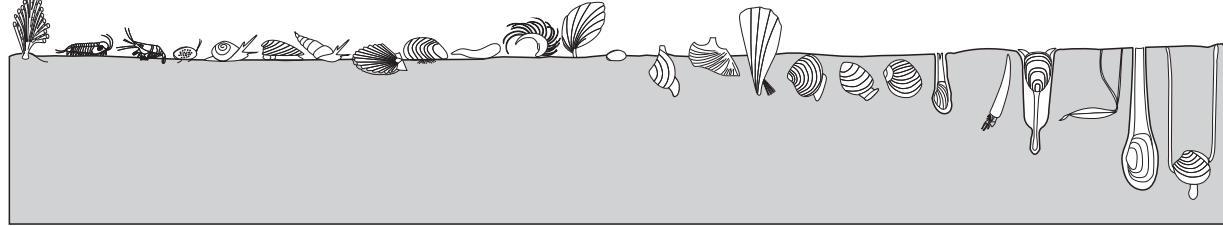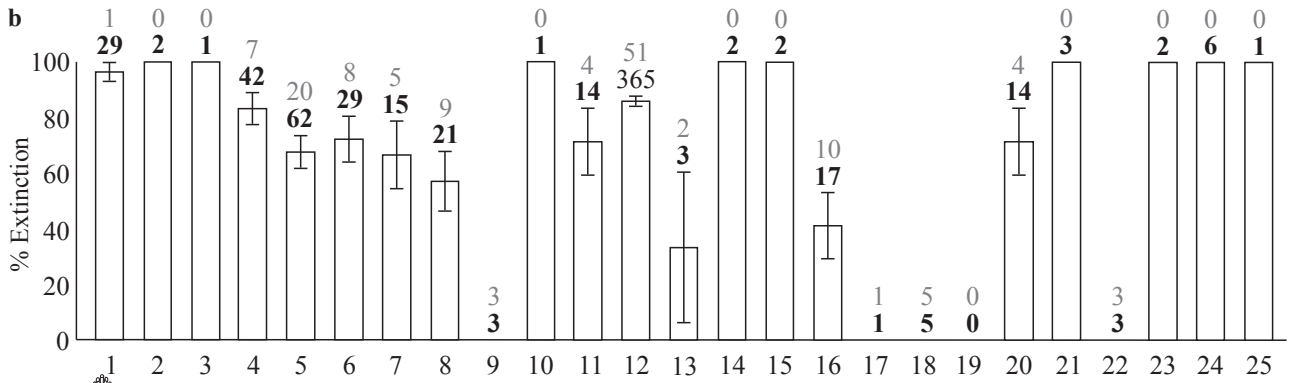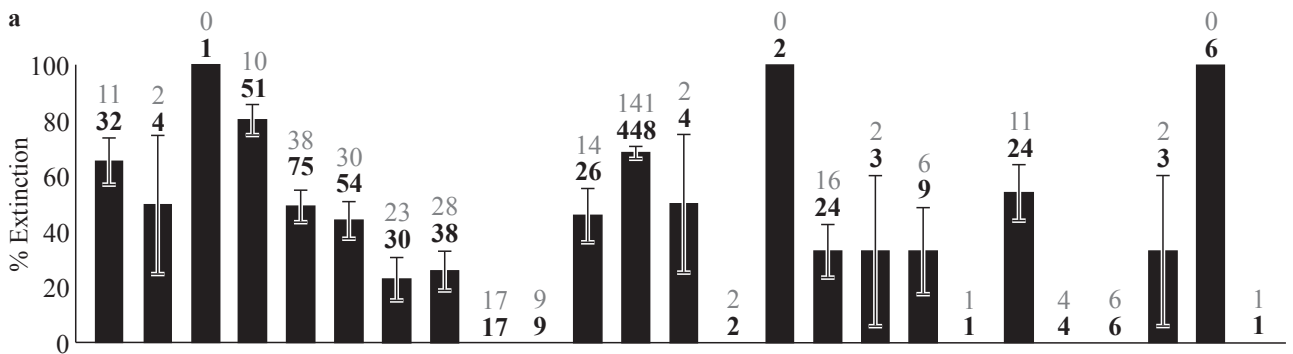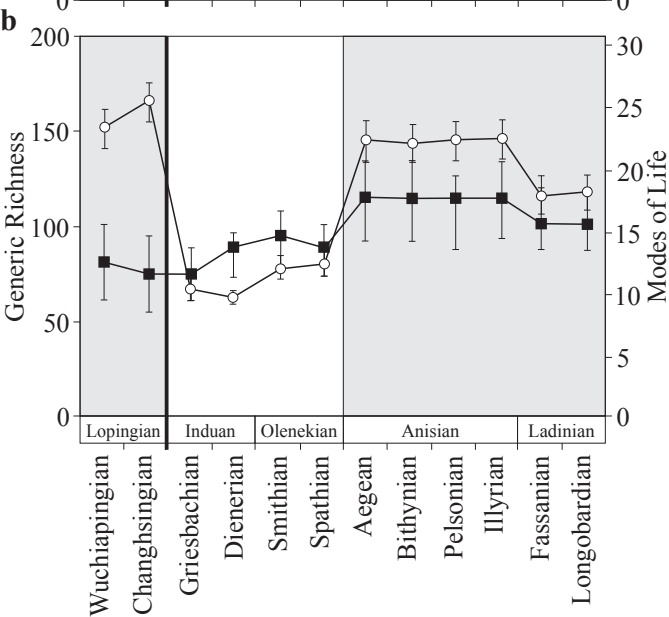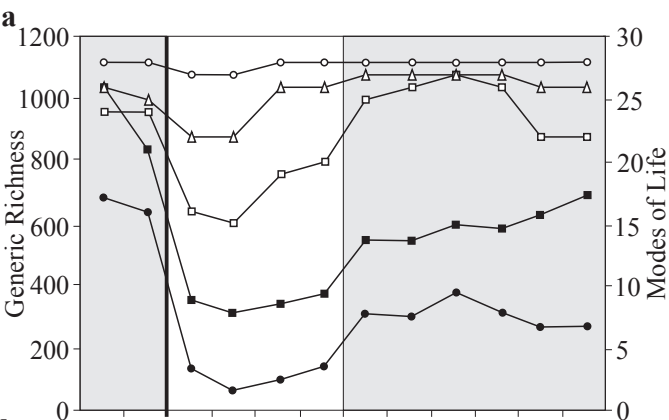
Relative abundances
○ 0.1-1% ○ 2-5% ○ 6-10% ○ 11-20% ○ 21-50% ○ >50%

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Lon																													
Fas																													
Ill																													
Pel																													
Bit																													
Aeg																													
Spa																													
Smi																													
Die																													
Gri																													
Cha																													
Wuc																													

a

Tropics

Northern, >30°N

Southern, >30°S

Green coefficient

Lopingian | Induan | Olenekian | Anisian | Ladinian

Wuchiapingian
Changhsingian
Griesbachian
Dienerian
Smithian
Spathian
Aegean
Bithynian
Pelsonian
Illyrian
Fassanian
Longobardian

b

Palaeotethys

Panthalassa

Neotethys

Boreal Ocean

Green coefficient

Lopingian | Induan | Olenekian | Anisian | Ladinian

Wuc
Cha
Gri
Die
Smi
Spa
Aeg
Bit
Pel
Ill
Fas
Lon

c

Inner Shelf

Middle Shelf

Outer Shelf

Basin and Slope

Reefs

Green coefficient

Lopingian | Induan | Olenekian | Anisian | Ladinian

Wuc
Cha
Gri
Die
Smi
Spa
Aeg
Bit
Pel
Ill
Fas
Lon