

UC Santa Cruz

UC Santa Cruz Previously Published Works

Title

Conservation evidence from climate-related stressors in the deep-time marine fossil record.

Permalink

<https://escholarship.org/uc/item/4x00n29w>

Journal

Philosophical Transactions of the Royal Society B Biological Sciences, 374(1788)

ISSN

0962-8436

Author

Clapham, Matthew E

Publication Date

2019-12-23

DOI

10.1098/rstb.2019.0223

Peer reviewed

Conservation Evidence from Climate-Related Stressors in the Deep-Time Marine Fossil Record

Matthew E. Clapham

Department of Earth and Planetary Sciences, University of California Santa Cruz, Santa Cruz, CA 95064, USA. ORCID 0000-0003-4867-7304

Keywords: Climate change; mass extinctions; ocean acidification; paleontology; conservation paleobiology

1 Main Text

1 Summary

1 Conservation of marine species requires the ability to predict the effects of climate-related stressors
2 in an uncertain future. Experiments and observations in modern settings provide crucial information,
3 but lack temporal scale and cannot anticipate emergent effects during ongoing global change. By
4 contrast, the deep-time fossil record contains the long-term perspective at multiple global-change
5 events that can be used, at a broad scale, to test hypothesized effects of climate-related stressors. For
6 example, geologically-rapid carbon cycle disruption has often caused crises in reef ecosystems, and
7 selective extinctions support the hypothesis that greater activity levels promote survival. Geographic
8 patterns of extinction and extirpation were more variable than predicted from modern physiology,
9 with tropical and temperate extinction peaks observed at different ancient events. Like any data
10 source, the deep-time record has limitations, but also provides opportunities that complement the
11 limitations of modern and historical data. In particular, the deep-time record is the best source of
12 information on actual outcomes of climate-related stressors in natural settings and over evolutionary
13 timescales. Closer integration of modern and deep-time evidence can expand the types of hypotheses
14 testable with the fossil record, yielding better predictions of extinction risk as climate-related
15 stressors continue to intensify in future oceans.

1 Introduction

1 Terrestrial and marine ecosystems are in the midst of an extinction crisis [1]. Human activities
2 have caused and continue to cause population declines through overharvesting, habitat degradation
3 and fragmentation, and introduction of invasive species. Anthropogenic carbon dioxide emissions
4 also trigger wide-ranging environmental disruption (often called “global change”) that increases
5 extinction risk for species on land and in the ocean. In marine ecosystems, these climate-related
6 stressors of warming, ocean deoxygenation, and ocean acidification will continue to intensify in the
7 coming decades, also elevating the extinction risk for vulnerable organisms.

1 To protect species from extinction, it is crucial to identify organisms that are currently at risk
2 or may be at risk in the future. This is an extremely challenging goal, given multiple and potentially
3 synergistic stressors and the need to extrapolate into an uncertain future. Unsurprisingly, given the
4 urgency of climate change and ocean acidification as some of the factors that might increase
5 extinction risk in the oceans, a tremendous amount of research seeks to constrain the effects of
6 climate-related stressors on marine organisms. This research brings together a range of methods:
7 experimental manipulations in the laboratory and with mesocosms [e.g., 2,3], observations of “natural

laboratories” such as low-pH vent sites [e.g., 4,5], and analysis of large databases [e.g., 6,7]. Although climate-related stressors are not the only causes of increased extinction risk, they could be significant contributors that must therefore be considered when assessing conservation needs.

Experimental and observational studies of modern species provide valuable insights into the effects of climate-related stressors on marine organisms, but also have limitations. The scale of the problem is especially challenging: marine global change involves multiple stressors acting on hundreds of thousands of species, throughout the entire ocean and over decades to centuries of evolutionary time (figure 1). Experimental manipulations, and even natural laboratories, can only provide information at small spatial and temporal scales, and in many cases in controlled but artificial conditions [3,8]. Outcomes may depend on the rate of change [9,10], making extrapolations to longer timescales more difficult. Analyses of large databases can assess many species at global spatial scales, but studies using data only from the modern and historical record will rarely be able to evaluate changes over evolutionary timescales.

The deep-time fossil record (pre-Quaternary, or older than about 2.5 million years) can fill that gap by providing unparalleled scale for evaluating biological impacts of climate-related stressors. Focusing on the marine record, there have been multiple “natural experiments” of geologically-rapid global change, with different rates and magnitudes, over the past 300 million years [11] (figure 2). Some were catastrophic mass extinctions while others had only minimal taxonomic losses. They capture a spectrum of climate-related stressors, from ocean anoxic events to hyperthermals with abrupt ocean warming and acidification. That spectrum of events can test the importance of traits under different climate scenarios and can reveal general principles that apply across a range of perturbations. Although the nature of the deep-time fossil record also limits some inferences, and events in deep time are not exact analogues to modern ecosystems or environmental change, Earth history is the only way to assess the biological impacts of climate-related stressors across myriad taxa, in natural ecosystems, and over evolutionary timescales.

Evidence from the deep-time record has been incorporated into conservation biology in limited areas, most notably in reef conservation [12,13], but there is unrealized potential for wider use. Quaternary fossil records can provide baseline conditions for natural ecosystems, but both the Quaternary and deep-time records have uses beyond setting pre-anthropogenic baselines [14,15]. Paleontological studies have included exploratory analyses of extinction selectivity that investigated a variety of traits: feeding, motility, and other life-habit attributes; geographic range, paleolatitudinal distribution, and habitat preference; and physiological traits such as buffering of calcification [16,17]. Other studies have quantified selective taxonomic losses that potentially reflect physiological differences, but with the primary goal of evaluating potential environmental “kill mechanisms” during extinctions [18]. These investigations contribute significantly to reconstructions of environmental and biotic change during mass extinctions, but I suggest that the deep-time fossil record is best placed to contribute to conservation biology through more targeted testing of hypotheses generated from experiments or observations in modern settings.

Not all hypotheses can be tested with the deep-time fossil record, however. To take advantage of the fossil record, testable hypotheses must make predictions that can be evaluated at broader temporal and spatial resolution and with extinct organisms that might be only distantly related to extant species. Functional trait-based hypotheses have been promising [19], especially for traits that can be inferred from shell morphology and for traits that can be generalized at higher taxonomic levels (using taxonomy as a proxy for suites of traits that are not or not-easily measurable in fossils). Hypotheses that make predictions, for example, about geographic patterns of risk or about expectations for range shifts, may also be well-suited for testing at deep-time global change events.

Case studies: testing functional trait predictions

In today’s oceans, reef-building corals are thought to be among the organisms most vulnerable to warming and acidification [20]. This assessment stems in part from the observation that corals are already suffering during bleaching events when ocean heat waves cause widespread mortality [21]. The vulnerability of reef-building corals likely results from their sensitive functional, especially physiological, traits, such as the delicate symbiosis with photosynthetic algae and the rapid

62 calcification of large skeletons. However, although concern over the future of corals and coral reef-
63 building is warranted, there is continuing uncertainty because some corals may have potential for
64 evolutionary adaptation, may respond to future multistressor global change in ways that cannot be
65 predicted from current responses, or may be rescued by more resilient species or populations [12].

66 The deep-time fossil record has demonstrated that reef ecosystems, and the corals or
67 hypercalcified sponges that built them, are especially vulnerable to global environmental change.
68 Although only one event, the Permian-Triassic extinction 250 million years ago, caused total
69 extinction of corals, reef-building organisms typically suffered disproportionate losses during
70 hyperthermal extinctions [22] (figure 2). Even when taxonomic losses were minimal, such as during
71 the Paleocene-Eocene Thermal Maximum (PETM), rapid environmental change resulted in decreased
72 reef volume [22]. Although assessing rates over short timescales is challenging in deep time [23], reef
73 crises appear to have been more severe at hyperthermals with more rapid carbon cycle perturbations
74 (Permian-Triassic and Triassic-Jurassic extinctions, PETM) than at those with more protracted
75 warming (Cretaceous ocean anoxic events) [22]. It appears that evolutionary potential, rescue by
76 more resilient populations, and other mechanisms were not sufficient to prevent major reef declines
77 and sometimes widespread extinction during deep-time hyperthermals. These outcomes lend support
78 to some of the more pessimistic projections for future reefs and create more urgency for minimizing
79 the rate of ocean warming and acidification and limiting non-climate stressors to reef ecosystems.

80 In the younger parts of the deep-time record, a greater proportion of fossil taxa belong to still-
81 living genera or families, which enables more nuanced functional inferences even though most or all
82 fossil species are now extinct. Among corals, this can allow feeding mode, the presence of symbiosis,
83 and even reproductive strategy to be inferred in 50 million-year-old species from their living
84 relatives, testing the importance of those functional traits during time periods that included the PETM
85 and other hyperthermal events [24]. During those time periods, fossil coral species with a broader
86 range of feeding options and mixed reliance on photosymbiosis tended to be more likely to survive, a
87 pattern of selectivity that differed from background extinctions in other time periods [24]. Studies of
88 ancient hyperthermals can complement the focused investigations of extant corals, providing a
89 valuable perspective on actual outcomes during environmental stress over long timescales.

90 Functional traits are likely important predictors of survival not just among corals, but among
91 all marine organisms. For example, more-active organisms might have physiological traits and
92 mechanisms that enable them to cope with elevated CO₂ levels [25], and may also be less vulnerable
93 to ocean warming [9]. The underlying physiological traits that cause these different responses to CO₂
94 or temperature stress may be impossible to measure in fossils, but Peck et al. [9] developed a
95 motility- and feeding-based activity quotient that can be generalized even to extinct species. Using
96 this quotient, there was no clear relationship between activity levels and extinction risk over a 150
97 million-year interval from the Permian to Jurassic, except at three extinctions (Guadalupian,
98 Permian-Triassic, Triassic-Jurassic) when higher levels of activity promoted survival among benthic
99 marine invertebrates [26] (figure 2). However, the relationship between activity and extinction was
100 less clear when including marine vertebrates, perhaps because of vulnerability at different life stages.
101 Sharks preferentially survived the Permian-Triassic and Triassic-Jurassic mass extinctions relative to
102 invertebrates, but bony fishes and invertebrates had similarly elevated extinction rates at the Triassic-
103 Jurassic [27]. These findings suggest that the relevance of activity level, in a broad sense, operates
104 both over the short timescales of experimental work [9,25] and over evolutionary timescales in
105 ancient hyperthermal extinctions.

106 Although the deep-time record enables testing of hypothesized links between functional traits
107 and extinction risk during global change, there are limitations to the conclusions, just as there are also
108 limitations in controlled laboratory experiments, observations from modern ecosystems, or any type
109 of study. One limitation is that functional traits are often inferred from taxonomic relationships, and
110 at broad taxonomic levels, rather than being directly measurable. For example, activity levels were
111 categorized mostly at the level of taxonomic order or even class, assigning the same value to all
112 epifaunal brachiopods [26] even though there undoubtedly were physiological differences among
113 brachiopod species. Analyses of the deep-time record are also typically performed with data binned
114 into time intervals that are several million years long. This binning is not a major issue when
115 extinction rates are high, because the signal from the event will outweigh background selectivity, but

116 it can be potentially difficult to attribute selectivity to environmental stresses when extinction rates
117 are similar to background levels. As in all studies, the limitations must be considered when applying
118 interpretations in a different context and translating deep-time findings to the modern ocean, but the
119 scale of the record provides complementary strengths that can benefit conservation studies.

121 Case studies: testing geographic predictions

122
123 In contrast to functional traits, which must be inferred from morphology or extrapolated from
124 living relatives, the paleogeographic location of fossil occurrences can be observed directly. This
125 enables testing of hypotheses that use geographic distribution to predict vulnerability to climate-
126 related stressors. For example, are organisms that inhabit the tropics at greater risk of extinction from
127 climate-related stressors [28]? In modern oceans, many tropical organisms have only a small buffer
128 between maximum environmental temperatures and their physiological thermal limits [10,28].
129 Perhaps physiological plasticity is instead important for survival during global change [29]. If that is
130 the case, could organisms inhabiting more variable habitats, at temperate latitudes for example, be
131 less vulnerable?

132 These hypotheses are challenging to test solely in the modern, but events in deep time provide
133 natural rates and patterns of global change that can be used to investigate the responses of organisms
134 over evolutionary timescales. At the Triassic-Jurassic extinction, marine invertebrates with a tropical
135 preference were more likely to go extinct [30], providing support for the hypothesis of greater risk in
136 the tropics (figure 2). However, tropical extinction rates were lower than at temperate latitudes during
137 the Permian-Triassic extinction, suggesting more complex spatial patterns from multiple stressors,
138 such as the combination of elevated temperature and reduced oxygen [31]. Overall, the relationship in
139 deep time between climate-driven stress and the geographic pattern of extinction is complicated and
140 variable [32].

141 The combination of paleogeographic data with general circulation models or Earth-system
142 models can provide powerful tools for testing hypothesized effects of climate-related stressors.
143 Taxonomic losses during the Permian-Triassic extinction may have been more severe at latitudes
144 where the combined effects of warming and deoxygenation were most severe, consistent with the
145 importance of metabolic oxygen supply and demand during global change events [31]. During the
146 PETM, calcareous nannoplankton disappeared from the tropics and became restricted to higher
147 latitudes with lower carbonate saturation state, suggesting that temperature rather than ocean
148 acidification was a key control on their distribution [33].

149 However, several factors complicate the interpretation of deep-time geographic distribution
150 data. For one, global change events in deep time are represented by fossiliferous rocks preserved and
151 exposed at some geographic locations, but missing from others. Ancient terrestrial environments
152 typically have sparser geographic records while rocks from ancient marine environments tend to be
153 geographically more widespread, because marine sedimentary basins tend to be deeper, longer-lived,
154 and less susceptible to later erosional destruction [34]. As a result, reconstructions of geographic
155 distribution must be done with care, especially when attempting to infer absences, and even more so
156 when inferring the absence of organisms that would have been rare.

157 The interpretation of geographic extinction patterns can also be confounded by non-random
158 distribution and/or sampling of taxonomic groups that had different extinction rates. For example,
159 corals tended to be especially vulnerable to climate-related stressors and also had predominantly
160 tropical distributions in the past, as today. On the other hand, fossil ostracods had comparatively low
161 extinction rates during the Permian-Triassic crisis, and are most often collected by dissolving
162 limestone rocks that predominantly form in the tropics; as a result, the vast majority of Permian-
163 Triassic ostracods are also known from the ancient tropics. Although geographic patterns of
164 extinction may not be as clear after disentangling taxonomic selectivity, consistent with complex
165 impacts of climate-related stressors, the deep-time record has tremendous potential.

167 Applicability of the deep-time record

168

169 The case studies demonstrate situations where the deep-time record can reveal the biological
170 consequences of climate-related stressors, but how can that be applied to answer conservation
171 questions? Can the deep-time fossil record help guide applied species or ecosystem management
172 decisions? Or can it help inform restoration strategies and best practices for conservation
173 interventions? In these areas, the deep-time record is likely of little relevance. The deep-time record
174 also cannot document human impacts on ecosystems or assess the societal consequences of
175 biodiversity loss. However, I argue that the deep-time fossil record can nevertheless provide
176 important guidance for conservation biology. There are several hundred thousand marine species
177 [35], but only a tiny fraction of those species have had their conservation status formally assessed.
178 Similarly, although experiments have documented the risks to selected marine species from warming
179 or acidification, it will be impractical to perform multistressor experiments at the scale needed to
180 evaluate all species. As a result, the vulnerability of the vast majority of marine species remains only
181 loosely constrained, especially the vulnerability to climate-related stressors.

182 As demonstrated by the case studies, the deep-time fossil record is best positioned to refine
183 assessments of vulnerability to climate-related stressors at broad scales. But predictions of extinction
184 risk are not a simple binary (either known or unknown); instead, our assessments occupy a spectrum
185 of varying degrees of confidence from complete ignorance to complete certainty. Experimental or
186 observational studies in modern settings have the potential to substantially increase the certainty of
187 extinction risk predictions, but only for a few species. Conversely, the enormous scope of the deep-
188 time record can increase the certainty of extinction risk predictions for a huge number of species,
189 albeit likely providing more incremental knowledge gains than possible from controlled experiments.
190 Nevertheless, even incremental improvements in certainty are valuable, especially when helping to
191 refine the extinction risk of unstudied or understudied groups.

192 Applied conservation decisions require that scientific knowledge be translated into actionable
193 tasks, which often can be challenging to synthesize from basic research. However, this challenge
194 applies not only to evidence from the deep-time fossil record, but also to many experimental or
195 observational studies on modern organisms. Nonetheless, these basic research studies provide crucial
196 guidance for understanding the fundamental mechanisms that govern vulnerability to climate-related
197 stressors. Evidence from the deep-time record, or from experiments or observations, will not always
198 translate to specific actions, but decision-making is ultimately strengthened by incorporating diverse
199 evidence from sources with different strengths.

200 Many marine species lack data on their conservation status, but forecasting future risk is even
201 more difficult given the complexity of environmental and biological systems. Are there emergent
202 behaviors, which cannot be extrapolated from experiments or historical observations, over
203 evolutionary timescales or as conditions change beyond thresholds? Experimental or observational
204 studies can propose hypotheses but are not, on their own, conclusive predictions of the future. The
205 deep-time record, because it contains the actual responses to climate-related stressors over
206 evolutionary timescales, is the best and perhaps only way to approach these questions. Did a
207 taxonomic group that is hypothesized to be vulnerable actually suffer greater extinction in the past?
208 Was a functional trait that promoted survival in an experiment actually a significant predictor of
209 survival during real global change events? Patterns of taxonomic, functional, or geographic
210 selectivity that occurred consistently at multiple deep-time global change events are likely to
211 represent important and general processes governing vulnerability to climate-related stressors. These
212 patterns can also yield insights that would be unavailable from modern evidence alone. For example,
213 the deep-time fossil record strongly implies that such responses are not likely to be adequate to save
214 reef ecosystems over the short term, given continued environmental change at current rates, although
215 reefs will recover over geological timescales. Time is the most significant limitation of studies of the
216 extant fauna, but the long-term perspective of the deep-time record, its greatest strength, fills that gap
217 and provides complementary evidence to investigate the response to climate-related stressors.

218 219 **Conclusion: toward a closer integration of modern and deep-time evidence**

220
221 Deep-time natural experiments are best placed to test hypotheses over evolutionary
222 timescales. For example, do findings from experiments or observations actually apply over realistic

223 scales of global change? Ancient global change events can be used to test the importance of
224 functional traits, for example supporting predictions that more active organisms are generally less
225 vulnerable to climate-related stressors. The deep-time record is also well-placed to test geographic
226 controls, for example indicating that the relationship between geographic distribution and extinction
227 risk is more complicated than predicted from experiments on modern taxa. Deep-time studies provide
228 the big-picture view, documenting outcomes across multiple taxonomic or functional groups and
229 potentially across multiple events. This perspective can help reveal the general principles underlying
230 vulnerability of marine organisms to climate-related stressors.

231 But what can be done to expand the utility of the deep-time record and increase the
232 applicability of its findings? Progress toward this objective will be maximized if both biologists and
233 paleobiologists think about approaches that bridge the temporal and spatial scales between
234 experimental studies and deep-time data.

235 One goal might be to increase the number of hypotheses that are testable with deep-time data.
236 This will require greater willingness on the part of biologists to make predictions that can be
237 generalized to the broader taxonomic, functional, or geographic scales available in deep time.
238 Experimental and observational studies typically ask highly-focused questions, and there may be a
239 reluctance to generalize their outcomes because responses can be species-specific, contingent on the
240 combination of stressors, or otherwise nuanced. While those concerns are valid, it is still valuable to
241 synthesize results of individual studies to generate more broadly-applicable and testable predictions.
242 Average differences in the predicted vulnerability of different taxonomic, functional, or geographic
243 groups, even if there is variability among responses within each group, can be tested thanks to the
244 vast scope of the deep-time record.

245 A parallel goal might be to increase the ability of the deep-time fossil record to test
246 hypotheses. This will require paleobiologists to think creatively about methods for testing
247 hypotheses, especially ways to bridge the gap in scales between high-resolution but short-timescale
248 modern data and long-timescale but coarse-resolution fossil data. For example, continued integration
249 of multiple types of information – paleobiological, modeling, isotopic, and others – will expand the
250 types of questions that can be answered in deep time. Other techniques, such as sclerochronology (the
251 sampling of shell growth increments for geochemical and biological information), can provide a
252 high-resolution archive for testing hypotheses at timescales comparable to some studies of modern
253 organisms. These and other methods can help translate deep-time data to modern settings and
254 questions.

255 Experiments, observations, historical data, the Quaternary fossil record, and deep-time events
256 all provide pieces of information to inform conservation questions. Each method has different
257 strengths and limitations – the deep-time record is not unique in that respect – and some types of data
258 are better suited to particular types of questions. Deep time allows us to ask and answer the question
259 “what actually happened?” when organisms were faced with climate-related stressors. The
260 combination of this unique and powerful ability with the precision and nuance of modern studies can
261 open exciting possibilities for conservation biology. A core principle of geology is uniformitarianism
262 (“the present is the key to understanding the past”), but in a time of rapid environmental disruptions
263 that are unprecedented in the historical record, Earth’s deep-time past may actually be the key to
264 understanding our future [36].
265

266 Acknowledgments

267 I thank the contributors to the Paleobiology Database. This is Paleobiology Database publication #3XX.
268
269

270 References

- 271 1. Barnosky AD *et al.* 2011 Has the Earth’s sixth mass extinction already arrived? *Nature* **471**, 51–57.
272 (doi:10.1038/nature09678)
- 273 2. Collard M, Dery A, Dehairs F, Dubois P. 2014 Euechinoidea and Cidaroidea respond differently to
274 ocean acidification. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*
275 **174**, 45–55. (doi:10.1016/j.cbpa.2014.04.011)

- 276 3. Queirós AM *et al.* 2015 Scaling up experimental ocean acidification and warming research: from
277 individuals to the ecosystem. *Global Change Biology* **21**, 130–143. (doi:10.1111/gcb.12675)
- 278 4. Crook ED, Cohen AL, Rebolledo-Vieyra M, Hernandez L, Paytan A. 2013 Reduced calcification and
279 lack of acclimatization by coral colonies growing in areas of persistent natural acidification. *Proceedings of*
280 *the National Academy of Sciences* **110**, 11044–11049. (doi:10.1073/pnas.1301589110)
- 281 5. Kroeker KJ, Micheli F, Gambi MC, Martz TR. 2011 Divergent ecosystem responses within a benthic
282 marine community to ocean acidification. *Proceedings of the National Academy of Sciences* **108**, 14515–
283 14520. (doi:10.1073/pnas.1107789108)
- 284 6. Sunday JM, Bates AE, Dulvy NK. 2011 Global analysis of thermal tolerance and latitude in
285 ectotherms. *Proceedings of the Royal Society B: Biological Sciences* **278**, 1823–1830.
286 (doi:10.1098/rspb.2010.1295)
- 287 7. Stuart-Smith RD, Edgar GJ, Bates AE. 2017 Thermal limits to the geographic distributions of
288 shallow-water marine species. *Nature Ecology & Evolution* **1**, 1846–1852. (doi:10.1038/s41559-017-0353-x)
- 289 8. De Boeck HJ *et al.* 2015 Global Change Experiments: Challenges and Opportunities. *BioScience* **65**,
290 922–931. (doi:10.1093/biosci/biv099)
- 291 9. Peck LS, Clark MS, Morley SA, Massey A, Rossetti H. 2009 Animal temperature limits and
292 ecological relevance: effects of size, activity and rates of change. *Functional Ecology* **23**, 248–256.
293 (doi:10.1111/j.1365-2435.2008.01537.x)
- 294 10. Nguyen KDT, Morley SA, Lai C-H, Clark MS, Tan KS, Bates AE, Peck LS. 2011 Upper temperature
295 limits of tropical marine ectotherms: global warming implications. *PLoS ONE* **6**, e29340.
296 (doi:10.1371/journal.pone.0029340)
- 297 11. Clapham ME, Renne PR. 2019 Flood Basalts and Mass Extinctions. *Annual Review of Earth and*
298 *Planetary Sciences* **47**. (doi:10.1146/annurev-earth-053018-060136)
- 299 12. Pandolfi JM. 2015 Incorporating Uncertainty in Predicting the Future Response of Coral Reefs to
300 Climate Change. *Annual Review of Ecology, Evolution, and Systematics* **46**, 281–303. (doi:10.1146/annurev-
301 ecolsys-120213-091811)
- 302 13. Pandolfi JM, Kiessling W. 2014 Gaining insights from past reefs to inform understanding of coral reef
303 response to global climate change. *Current Opinion in Environmental Sustainability* **7**, 52–58.
304 (doi:10.1016/j.cosust.2013.11.020)
- 305 14. Willis KJ, Birks HJB. 2006 What Is Natural? The Need for a Long-Term Perspective in Biodiversity
306 Conservation. *Science* **314**, 1261–1265. (doi:10.1126/science.1122667)
- 307 15. Dietl GP, Flessa KW. 2011 Conservation paleobiology: putting the dead to work. *Trends in Ecology &*
308 *Evolution* **26**, 30–37. (doi:10.1016/j.tree.2010.09.010)
- 309 16. Clapham ME, Payne JL. 2011 Acidification, anoxia, and extinction: A multiple logistic regression
310 analysis of extinction selectivity during the Middle and Late Permian. *Geology* **39**, 1059–1062.
311 (doi:10.1130/G32230.1)
- 312 17. Dunhill AM, Foster WJ, Azae S, Sciberras J, Twitchett RJ. 2018 Modelling determinants of
313 extinction across two Mesozoic hyperthermal events. *Proceedings of the Royal Society B: Biological Sciences*
314 **285**, 20180404.
- 315 18. Knoll AH, Bambach RK, Payne JL, Pruss S, Fischer WW. 2007 Paleophysiology and end-Permian
316 mass extinction. *Earth and Planetary Science Letters* **256**, 295–313. (doi:10.1016/j.epsl.2007.02.018)
- 317 19. Polly PD *et al.* 2011 History matters: ecometrics and integrative climate change biology. *Proceedings*
318 *of the Royal Society B: Biological Sciences* **278**, 1131–1140. (doi:10.1098/rspb.2010.2233)
- 319 20. Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL. 2011 Projecting Coral Reef Futures Under Global
320 Warming and Ocean Acidification. *Science* **333**, 418–422. (doi:10.1126/science.1204794)
- 321 21. Baker AC, Glynn PW, Riegl B. 2008 Climate change and coral reef bleaching: An ecological
322 assessment of long-term impacts, recovery trends and future outlook. *Estuarine, Coastal and Shelf Science* **80**,
323 435–471. (doi:10.1016/j.ecss.2008.09.003)
- 324 22. Kiessling W, Simpson C. 2011 On the potential for ocean acidification to be a general cause of ancient
325 reef crises. *Global Change Biology* **17**, 56–67. (doi:10.1111/j.1365-2486.2010.02204.x)
- 326 23. Kemp DB, Eichenseer K, Kiessling W. 2015 Maximum rates of climate change are systematically
327 underestimated in the geological record. *Nature Communications* **6**, 9890. (doi:10.1038/ncomms9890)
- 328 24. Weiss AM, Martindale RC. 2019 Paleobiological Traits That Determined Scleractinian Coral Survival
329 and Proliferation During the Late Paleocene and Early Eocene Hyperthermals. *Paleoceanography and*
330 *Paleoclimatology* (doi:10.1029/2018PA003398)
- 331 25. Melzner F, Gutowska MA, Langenbuch M, Dupont S, Lucassen M, Thorndyke MC, Bleich M. 2009
332 Physiological basis for high CO₂ tolerance in marine ectothermic animals: pre-adaptation through lifestyle and
333 ontogeny? *Biogeosciences* **6**, 2313–2331.

- 334 26. Clapham ME. 2017 Organism activity levels predict marine invertebrate survival during ancient
335 global change extinctions. *Global Change Biology* **23**, 1477–1485. (doi:10.1111/gcb.13484)
- 336 27. Vázquez P, Clapham ME. 2017 Extinction selectivity among marine fishes during multistressor global
337 change in the end-Permian and end-Triassic crises. *Geology* **45**, 395–398. (doi:10.1130/G38531.1)
- 338 28. Vinagre C, Leal I, Mendonça V, Madeira D, Narciso L, Diniz MS, Flores AAV. 2016 Vulnerability to
339 climate warming and acclimation capacity of tropical and temperate coastal organisms. *Ecological Indicators*
340 **62**, 317–327. (doi:10.1016/j.ecolind.2015.11.010)
- 341 29. Hofmann GE, Todgham AE. 2010 Living in the now: physiological mechanisms to tolerate a rapidly
342 changing environment. *Annual Review of Physiology* **72**, 127–145. (doi:10.1146/annurev-physiol-021909-
343 135900)
- 344 30. Kiessling W, Aberhan M, Brenneis B, Wagner PJ. 2007 Extinction trajectories of benthic organisms
345 across the Triassic–Jurassic boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* **244**, 201–222.
346 (doi:10.1016/j.palaeo.2006.06.029)
- 347 31. Penn JL, Deutsch C, Payne JL, Sperling EA. 2018 Temperature-dependent hypoxia explains
348 biogeography and severity of end-Permian marine mass extinction. *Science* **362**, eaat1327.
349 (doi:10.1126/science.aat1327)
- 350 32. Reddin CJ, Kocsis ÁT, Kiessling W. 2019 Climate change and the latitudinal selectivity of ancient
351 marine extinctions. *Paleobiology* **in press**.
- 352 33. Gibbs SJ, Bown PR, Ridgwell A, Young JR, Poulton AJ, O’Dea SA. 2016 Ocean warming, not
353 acidification, controlled coccolithophore response during past greenhouse climate change. *Geology* **44**, 59–62.
354 (doi:10.1130/G37273.1)
- 355 34. Holland SM. 2016 The non-uniformity of fossil preservation. *Philosophical Transactions of the Royal
356 Society B: Biological Sciences* **371**, 20150130. (doi:10.1098/rstb.2015.0130)
- 357 35. Costello MJ, Chaudhary C. 2017 Marine Biodiversity, Biogeography, Deep-Sea Gradients, and
358 Conservation. *Current Biology* **27**, R511–R527. (doi:10.1016/j.cub.2017.04.060)
- 359 36. Doe BR. 1983 The past is the key to the future. *Geochimica et Cosmochimica Acta* **47**, 1341–1354.
360 (doi:10.1016/0016-7037(83)90293-4)

361
362

363 Figure captions

364 **Figure 1.** The phenomenon of global change involves multiple climate-related stressors (depicted
365 schematically by multiple arrows for each axis) that operate over a range of spatial, temporal, and
366 taxonomic scales. Investigations that use the modern and historical record (yellow box) are mostly
367 conducted at spatial and taxonomic scales but are fundamentally limited in temporal scale. The deep-
368 time fossil record (blue box) reveals actual outcomes over evolutionary timescales, mostly at broad
369 spatial and taxonomic scales. Together, these methods provide complementary information on the
370 biotic response to climate-related stressors.

371
372 **Figure 2.** Global change events in Earth’s deep-time history, caused by carbon cycle disruption,
373 ocean warming and deoxygenation, and in some cases acidification. Geologically-rapid perturbations
374 of the carbon cycle caused extinction events (red circles), including the Guadalupian, Permian-
375 Triassic (P-T), and Triassic-Jurassic (T-J). Extinction rates are for marine invertebrates, from the
376 Paleobiology Database. Carbon release also led to ocean anoxic events when the duration was more
377 prolonged, especially in the Jurassic and Cretaceous periods, and Cenozoic hyperthermals such as the
378 Paleocene-Eocene Thermal Maximum (PETM) when the rate of carbon release was more rapid.
379 Climate-related stressors caused reef crises when rates of global change were more rapid, while
380 climate-driven extinctions in the Permian and Triassic resulted in selective survival of more active
381 groups. The Triassic-Jurassic extinction and PETM led to selective extinction or extirpation in the
382 tropics, but extinctions were greater at temperate latitudes during Permian-Triassic extinction.



