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Main Manuscript for

Decreasing Phanerozoic extinction intensity as a consequence of Earth surface oxygenation and metazoan ecophysiology

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Classification: Physical Sciences/Earth, Atmospheric, and Planetary Sciences

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Main Text
Figure Captions

1 **Abstract**

2 The decline in background extinction rates of marine animals through geologic time is an
3 established but unexplained feature of the Phanerozoic fossil record. There is also
4 growing consensus that the ocean and atmosphere did not become oxygenated to near-
5 modern levels until the mid-Paleozoic, coinciding with the onset of generally lower
6 extinction rates. Physiological theory provides us with a possible causal link between
7 these two observations – predicting that the synergistic impacts of oxygen and
8 temperature on aerobic respiration would have made marine animals more vulnerable to
9 ocean warming events during periods of limited surface oxygenation. Here, we evaluate
10 the hypothesis that changes in surface oxygenation exerted a first-order control on
11 extinction rates through the Phanerozoic using a combined Earth system and
12 ecophysiological modeling approach. We find that although continental configuration, the
13 efficiency of the biological carbon pump in the ocean, and initial climate state all impact
14 the magnitude of modeled biodiversity loss across simulated warming events,
15 atmospheric oxygen is the dominant predictor of extinction vulnerability, with metabolic
16 habitat viability and global ecophysiotype extinction exhibiting inflection points around
17 40% of present atmospheric oxygen. Given this is the broad upper limit for estimates of
18 early Paleozoic oxygen levels, our results are consistent with the relative frequency of
19 high-magnitude extinction events (particularly those not included in the canonical Big
20 Five mass extinctions) early in the Phanerozoic being a direct consequence of limited
21 early Paleozoic oxygenation and temperature-dependent hypoxia responses.

22

23 **Significance Statement**

24 The decline in extinction rates through geologic time is a well-established but enigmatic
25 feature of the marine animal fossil record. We hypothesize that this trend is driven largely
26 by secular changes in the oxygenation of the atmosphere and oceans, as physiological
27 principles predict that marine animals would have been more vulnerable to ocean
28 warming during intervals of geological time with limited atmospheric oxygenation. We

29 test this at a global oceanographic scale by combining models of ocean biogeochemistry
30 and animal physiology. We show that atmospheric oxygen exerts a first-order control on
31 the simulated extinction vulnerability of marine animals, highlighting its likely
32 importance in controlling extinction trends through geologic time.

33

34 **Introduction**

35 One of the most striking and poorly understood features of the marine fossil record is a
36 long-term decline in apparent extinction rates through the Phanerozoic (1–7). First
37 revealed by analyses of stratigraphic range compilations ~40 years ago (1), this decline
38 has been a persistent feature in subsequent analyses using expanded databases (8) and
39 improved extinction rate and richness metrics since then (e.g. (2–7); Figs. 1, S1).
40 Declining genus-level extinction rates are a consistent feature of Phanerozoic analyses
41 using a broad range of different richness and extinction rate metrics ((7); Fig. S2, Table
42 S1), and are not substantially altered by varying temporal binning or controlling for
43 species/genus ratio (Figs. S1-2, Table S1; *Materials and Methods*). In particular, the
44 Cambrian and Ordovician Periods stand out as intervals of especially high faunal
45 turnover ((6, 7, 9); Figs. S1-2), to the point that the early Paleozoic is often treated
46 separately from the rest of the Phanerozoic in quantitative analyses of extinction (e.g. (7,
47 10, 11)). Changes in the distribution of lineage ages and geographic range sizes, area of
48 continental shelf environments, intensity of species interactions, frequency of geological
49 triggers, stabilization of Earth’s climate, and rock-area sampling biases have all been
50 proposed as drivers of this trend (10–14). However, despite the long history of study and
51 numerous proposed explanations, no consensus has been reached regarding the drivers of
52 much higher early Paleozoic extinction rates vs. those of the later Paleozoic, Mesozoic
53 and Cenozoic.

54 Secular trends in the oxygenation of the ocean and atmosphere are an
55 underexplored factor that may help explain changing extinction intensity through time. A
56 growing body of geochemical proxy evidence suggests that Earth’s surface did not
57 become oxygenated to near-modern levels until the early-mid Paleozoic (Fig. 1) (15–20)

58 and the most recent generation of long-term carbon cycle models support only limited
59 early Paleozoic oxygenation (21–23). While early Paleozoic marine oxygen
60 concentrations were self-evidently above minimum thresholds for aerobic metazoan
61 metabolism (at least, in the shallow ocean), modern observations clearly show that
62 variations in dissolved oxygen exert a strong control on marine biodiversity (24–26).
63 Moreover, experimental respirometry, metabolic theory, and ecophysiological modeling
64 have demonstrated that the synergistic effects of oxygen and temperature on capacity for
65 aerobic respiration significantly influence the metabolic viability of marine habitat (27–
66 32). Following the principle of oxygen and capacity limited thermal tolerance (OCLTT –
67 see Pörtner (28) for review), the critical partial pressure of oxygen (pO_2) required to
68 sustain resting metabolism increases exponentially with temperature, and the increase in
69 oxygen supply required for ecologically sustainable populations results in a further
70 steepening of this exponential relationship (Fig. 2; (33)). Meta-analyses investigating the
71 sensitivity of modern marine ectotherms to climate-related stressors and the vulnerability
72 of their fossil representatives to extinction further suggest that physiological traits of
73 modern marine animals can be generally scaled to extinction sensitivity to ancient climate
74 perturbations (34).

75 Seawater pO_2 would have been dramatically lower in an early Paleozoic Earth
76 system with limited surface oxygenation, leading to the prediction that marine ectotherms
77 would have been substantially more vulnerable to temperature-dependent hypoxia, and
78 therefore climate-driven extinction, due to reduced thermal safety margins in poorly
79 oxygenated ancient oceans (Fig. 2; (35)). This logic further leads to the implication that
80 dissolved oxygen was likely important to the structure of marine ecosystems at
81 concentrations well above critical hypoxic thresholds that have previously been invoked
82 for the evolution of early animals (36, 37), as is observed at regional scales in modern
83 marine environments (29–31, 38). Recent advances in Earth system modeling provide an
84 opportunity to test this hypothesis at the planetary-scale and to explicitly distinguish the
85 role of changes in surface oxygenation through the Phanerozoic from variations in
86 continental configuration, biological carbon cycling and climate state.

87 Our approach is two-fold – incorporating both Earth system and ecophysiological
88 modeling. First, using an Earth system model of intermediate complexity (cGENIE (39) –
89 see *Materials and Methods* and *Supplementary Information*) and an ensemble
90 experimental approach, we generate a suite of three-dimensional realizations of potential
91 marine environmental conditions. These Earth system model experiments span a range of
92 scenarios for atmospheric O₂ and CO₂ concentrations (Fig. 3a) in order to address
93 uncertainty associated with reconstructions of these variables through geologic time (e.g.
94 Fig 1b). Atmospheric CO₂ concentrations are varied to force global climate in our
95 experiments and solar forcing is kept constant for each ensemble (Fig. 3). Simulating the
96 potential three-dimensional structure of past oceans in these experiments is critical: in the
97 upper ocean, oxygen and temperature both decrease with depth, but have opposite
98 gradients with respect to latitude (33, 38). Temperature gradients decrease towards the
99 poles, while subsurface oxygen gradients increase. Because aerobic habitability for
100 marine animals involves the synergistic combination of oxygen and temperature (29, 34,
101 35, 38), elucidating the spatial complexity of the environmental landscape of ancient
102 oceans is required to appropriately understand biological responses to environmental
103 perturbations.

104 We additionally identify key boundary conditions that have significantly changed
105 through Earth history and may offer alternative explanations for the trends in extinction
106 rates observed in the fossil record. 1) Continental configuration, which affects latitudinal
107 habitat (i.e. continental shelf) distribution, as well as ocean circulation (and resulting
108 temperature and oxygen gradients), and could therefore have modulated the susceptibility
109 of animals to extinction (33, 40, 41). 2) The efficiency of the biological carbon pump in
110 the ocean, which exerts a control on the distribution of oxygen in the upper water column
111 (42) and has been previously identified as important in differentiating earlier Paleozoic
112 vs. Mesozoic-Cenozoic ocean redox conditions (17). 3) Climate state, which directly
113 impacts ocean surface temperatures (and by extension dissolved marine oxygen) and
114 therefore influences how close animals at a given latitude are living to their physiological
115 limits (29, 38).

116 Utilizing model ocean temperatures and dissolved oxygen concentrations from
117 this suite of 3D realizations, we then employ the recently developed Metabolic Index (29,
118 33, 38) in order to evaluate the proportion of modern marine ectotherms (based upon
119 available experimental respirometry data) that could survive in these simulated
120 environments. While we do not attempt to directly simulate taxonomic diversity, the
121 Metabolic Index provides us with a means to mechanistically assess the physiological
122 ecotypes (herein, ecophysiotypes) that can contribute to biodiversity. We apply a
123 probabilistic representation of temperature-dependent hypoxia responses (Fig. 2) to
124 define ‘metabolic habitat viability’, a global metric describing the percentage of feasible
125 ecophysiotypes that can live anywhere in the shelf environments of our 3D ocean models.
126 Following other paleoecological modeling approaches (e.g. (41)), we focus our analyses
127 on shelf environments because they constitute the majority of the Phanerozoic fossil
128 record and host the majority of marine biodiversity in the modern, although we provide
129 complimentary simulations for the entire global ocean.

130 Finally, we estimate global extinction sensitivity across a range of atmospheric O₂
131 concentrations to link our ecophysiological models more directly to the trends we observe
132 in the geologic record. We model ‘global ecophysiotype extinction’ as the predicted loss
133 of ecophysiotypes across a nominal warming event of ~5°C (as defined by mean
134 temperature change in the equatorial surface ocean; Fig. S3, Table S2). These warming
135 events are represented by Earth system models separated by two doublings of
136 atmospheric CO₂, and are designed to mimic relatively extreme (but not infrequent)
137 examples of climate variability known to have occurred throughout Earth history (43,
138 44). We performed this extinction sensitivity estimate for all scenarios of atmospheric O₂
139 and for each ensemble (continental configuration, biological pump efficiency; Figs. 3,
140 S3) across multiple baseline climate states. We further explore the consistency of our
141 results across different thresholds for minimum habitat area (number of equal area ocean
142 model cells) and tolerances for proportional habitat loss, as well as across deviations from
143 the distributions of physiological tolerances observed in modern marine ectotherms.
144 Thus, by combining ecophysiology and ensemble Earth system modeling, we evaluate the
145 vulnerability of marine ectotherms to warming events at a range of atmospheric O₂ levels

146 in a framework that is neutral to the selective advantage of different ecophysiotypes and
147 explores the relative impacts of other aspects of Phanerozoic Earth system evolution on
148 marine animal ecophysiology.

149

150 **Results**

151 *Metabolic habitat viability*

152 Metabolic habitat viability – the total number of ecophysiotypes that can live in
153 the shelf environments of each ancient ocean realization – is shown in Figure 4 for our
154 ensemble of simulations employing an Ordovician continental configuration and Figure
155 S4 for all other Earth system model ensembles. In all ensembles, metabolic habitat
156 viability exhibits a positive relationship with atmospheric O₂ and a negative relationship
157 with global temperature, resulting in a sigmoidal relationship between atmospheric O₂
158 and metabolic habitat viability for a given climate state. While our primary analyses
159 focus on shelf environments, very similar trends are observed when the entire ocean is
160 considered as potential habitat for marine animals (Figs. S5-6). Using entire 3D ocean
161 models often results in slightly higher estimates of metabolic habitat viability because
162 cooler and (at higher atmospheric O₂ levels) well-oxygenated deep ocean environments
163 may act as refugia, despite being unlikely diversity hotspots for other reasons such as
164 food supply (45, 46). The latitudinal distribution of viable ecophysiotypes is similar
165 between continental configurations (Figs. 3, S3), with more ecophysiotypes generally
166 able to inhabit cooler polar regions of the surface ocean. Identifying oceanographic and
167 tectonic drivers of regional differences in viable ecophysiotype biogeography between
168 continental configurations is an interesting avenue for future research, but this would
169 require tuning model ensembles to precisely equivalent climate states and is therefore
170 beyond the scope of this study.

171 Changes in metabolic habitat viability between cooler and warmer climate states
172 allow us to begin linking ecophysiology to extinction sensitivity under different scenarios
173 of atmospheric oxygenation (Fig. 4). The percentage change in metabolic habitat viability

174 between colder and warmer ocean simulations increases as atmospheric oxygen decreases
175 from modern levels (100% preindustrial atmospheric levels, PAL), reaching maximum
176 values at atmospheric O₂ concentrations reconstructed for the early Paleozoic (<40-50%
177 PAL – grey envelope in Figs. 4, S4). Furthermore, because extinction is expected to track
178 the proportional rather than absolute loss of ecophysiotypes (33, 40), differences in
179 metabolic habitat viability would therefore be amplified to result in high levels of
180 warming-driven extinction at lower levels of atmospheric oxygenation reconstructed for
181 the early Paleozoic (e.g. 20% PAL). In such cases, the number of viable ecophysiotypes
182 in any low-O₂ scenario is much lower, leading to greater proportional change despite a
183 similar absolute change in metabolic habitat viability to that predicted at higher O₂ levels
184 (e.g. 80% PAL). Our analyses thus demonstrate that the expected proportional loss of
185 ecophysiotypes during a global warming event would be substantially higher under the
186 limited surface oxygenation scenarios hypothesized for the early Paleozoic than for
187 modern (or, more broadly, post-mid-Paleozoic) levels of oxygenation.

188

189 *Sensitivity of global extinction simulations*

190 When we simulate the impacts of warming events on the extinction of marine
191 animals, the general trend of greater predicted extinction at lower atmospheric oxygen
192 levels is a common feature of all ensemble experiments (Figs. 5, S7-12). There is
193 variation in the absolute magnitude of simulated global ecophysiotype extinction between
194 the different continental configurations tested in our ensembles. However, we do not
195 observe any time-dependent trends in extinction sensitivity between progressive
196 continental reconstructions and the most striking feature of the results remains the non-
197 linear increase in global ecophysiotype extinction with declining oxygenation (Figs. 5,
198 S7-12). Below 10% PAL O₂, the relationship between modeled extinction and
199 atmospheric oxygen is less predictable. However, the initial pool of viable pre-extinction
200 ecophysiotypes in these simulations is very small at low O₂ levels (Figs. 3, 4, S4-6),
201 suggesting that this inconsistency may partially be a product of sample size (as supported
202 by wider envelopes in Figures 5, S7-8, S11) and the limited experimental respirometry

203 data for animals that live in low-oxygen environments (47). We find that modeled
204 extinction is high at low atmospheric oxygen levels for the Ordovician configuration
205 regardless of the efficiency of the biological pump (Fig. S7), suggesting that despite its
206 role in controlling the distribution of oxygen in the upper water column this factor is of
207 secondary importance compared to atmospheric O₂. A shallower remineralization depth
208 does slightly reduce simulated extinction sensitivity at low atmospheric O₂ (~5-20%
209 PAL), although the same caveat of small initial ecophysiotype population size applies.

210 Increasing the baseline temperature in our extinction simulations (i.e. testing for
211 any initial climate state dependence of extinction susceptibility), results in increased
212 predicted global ecophysiotype extinction for all three continental configurations (Fig.
213 S8). A corresponding decrease in modeled ecophysiotype extinction is generally observed
214 at cooler baseline temperatures. Cool, low O₂ (<20% PAL) Ordovician simulations are a
215 minor exception to this general rule, suggesting that continental configuration may exert a
216 second-order control on the climate state dependence of extinction vulnerability. The
217 impact of initial climate state on simulated ecophysiotype extinction appears less
218 dramatic than the impact of atmospheric oxygen, particularly in light of the apparent
219 inflection in modeled extinction observed around upper estimates for early Paleozoic O₂
220 levels. However, we note that pre-extinction climate state impacts modeled
221 ecophysiotype extinction more than any other Earth system boundary condition explored
222 in this study.

223 Altering the assumptions of our ecophysiological modeling approach does not
224 dramatically impact the observed relationship between predicted extinction and
225 atmospheric oxygen. In our primary analyses, we define ecophysiotype extinction as only
226 occurring when no cells in our simulated shelf environments are viable for an
227 ecophysiotype, or (equivalently) when 100% of metabolically viable habitat area is lost.
228 Increasing the minimum number of inhabited ocean cells required to survive a warming
229 event or decreasing the proportional habitat loss required for extinction moderately
230 increases modeled global ecophysiotype extinction (Figs. S9-10). The differences in the
231 shape of these responses highlight the importance of these parameters and the second-

232 order effects of continental configuration. However, the overall trend of decreasing
233 extinction intensity with increased atmospheric O₂, with an apparent inflection point
234 generally around 40% PAL, is consistent across all of these simulations. Similar trends
235 are observed when investigating the impacts of varying the distributions used to
236 parameterize physiological responses (A_o – the inverse of the hypoxic threshold; and E_o –
237 the temperature-dependency of the hypoxic threshold). While varying the distributions of
238 A_o and E_o does impact the magnitude of simulated global ecophysiotype extinction and
239 the steepness of the inflection around 40% PAL O₂ (Fig. S11), the overarching trends of
240 increasing predicted extinction with decreasing atmospheric oxygen (down to at least
241 20% PAL O₂) are not impacted. The size of the synthetic population of ecophysiotypes
242 (*Materials and Methods*) has no noticeable effect on the analyses illustrated in Figure 5
243 (Fig. S12).

244

245 **Discussion**

246 Using a coupled Earth system and ecophysiological modeling approach, our analyses
247 suggest that oxygenation of the shallow ocean (as modulated by atmospheric oxygen
248 levels) is the dominant factor in governing the vulnerability of marine animals to
249 extinction during warming events. These results remain consistent when complex
250 oceanographic relationships between temperature and seawater oxygenation and
251 uncertainties in ocean circulation, biological pump efficiency, climate state, and habitat
252 area thresholds are taken into account. Critically, the relationship we observe between
253 simulated global ecophysiotype extinction and atmospheric oxygen is non-linear, with an
254 apparent inflection point around 40% PAL O₂ (Fig. 5). This broadly coincides with the
255 upper limit of estimates for early Paleozoic atmospheric oxygen (Fig. 1; (15, 17)),
256 supporting the hypothesis that relatively low atmospheric oxygen levels created boundary
257 conditions under which high-magnitude extinction events were more likely to occur as a
258 product of climate variability.

259 While atmospheric oxygen is the primary control on extinction sensitivity in our
260 simulations, our analyses show that other factors modulate the response to varying
261 degrees. This is unsurprising considering how these factors affect the three-dimensional
262 oxygen-temperature landscape of the ocean. In particular, our analyses indicate that
263 continental configuration may play an important secondary role in governing
264 ecophysiotype extinction vulnerability at the global scale (Fig. 5), although this is
265 difficult to clearly separate from minor climatic differences between ensembles. Notably,
266 we do not observe time-correlative trends between the three continental configurations
267 that could help explain the secular extinction rate observations from the fossil record. In
268 other words, we do not find that extinction sensitivity in the polar-biased and relatively
269 compact continental configuration of the Ordovician is particularly different from that of
270 the more evenly latitudinally distributed and dispersed configuration of the Paleocene
271 when compared to the differences associated with changing atmospheric O₂. The
272 efficiency of the biological pump (simulated here as a difference in prescribed
273 remineralization depths in the ocean) is also thought to have changed through the
274 Phanerozoic (17). However, we find that the differences in simulated extinction
275 sensitivity are minimal and (if anything) in opposition to the influence of changes in
276 atmospheric oxygenation (Fig. S7). This is likely because both continental configuration
277 and carbon remineralization depth mainly change oxygen distributions in the deeper
278 ocean, whereas most animals are living (and dying) in the surface ocean, which is closely
279 coupled to the O₂ concentration of the atmosphere. Finally, while the habitat area
280 thresholds we used to define simulated extinction and specific parameterization of
281 physiological traits do impact the slope and magnitude of the observed relationship
282 between atmospheric oxygen and extinction (in expected directions; Figs. S9-11), the first
283 order trends remain consistent regardless of how we parametrize our ecophysiological
284 extinction model.

285 We additionally find that an important climate state-dependence exists for
286 ecophysiological extinction sensitivity. Marine animals are expected to be living closer to
287 their thermal limits as defined by oxygen and capacity limited thermal tolerance in
288 warmer environments based on observations from modern tropical marine habitats (Fig.

289 2; (29, 38)), with implications for broader areas of the ocean in ancient greenhouse
290 climates. We provide further model support for this hypothesis by demonstrating
291 increased simulated extinction magnitudes in warmer climate states (Fig. S8). Very warm
292 early Paleozoic sea surface temperatures have been reconstructed using geochemical
293 paleothermometry (48–50), suggesting that this phenomenon could also provide some
294 explanatory power for the frequency of high magnitude extinctions. However, while
295 recent advances in paleothermometry have shown considerable potential in constraining
296 Ordovician climate dynamics (50), there is still currently limited consensus on directional
297 trends in early Phanerozoic sea surface temperatures, especially in the earliest Paleozoic
298 (51–53). In contrast, reconstructions of atmospheric oxygen are increasingly consistent,
299 even if the absolute concentrations are poorly constrained (Fig. 1). This discussion should
300 not be framed as a question of oxygen *versus* temperature; inherent to the concept of
301 temperature-dependent hypoxia is that both interact to determine aerobic safety margins
302 (Fig. 2; (29, 34, 38)). We therefore suggest that atmospheric oxygen can confidently be
303 established as a first-order control on early Phanerozoic extinction rates, and that
304 potentially high sea surface temperatures through the same time interval may have
305 amplified the effect of limited surface oxygenation. Changes in the latitudinal focus of
306 fossil sampling through the Phanerozoic may also bias extinction rate estimates slightly
307 towards environments with warmer baseline temperatures in the early Paleozoic when
308 well-sampled paleocontinents were mainly situated at low latitudes (54). However, the
309 lack of similarly high long-term extinction rates across other intervals with low-latitude
310 sampling biases indicates that this cannot fully explain the trends we seek to explain here
311 and that atmospheric oxygen (potentially compounded by warm global climate) is a more
312 probable first-order driver.

313 The plausibility of temperature-dependent hypoxia as a driver of high early
314 Paleozoic extinction rates is supported by links between sea-level changes, ocean
315 deoxygenation and extinctions during this interval of geologic time. The Cambrian-
316 Ordovician biomere-style extinction events are a major component of the
317 characteristically high early Paleozoic extinction rates (9). These events, predominantly
318 observed in the trilobite fossil record (e.g. (55)), have long been recognized as associated

319 with sedimentological evidence of sea-level change, possible thermocline migration and
320 ocean anoxia (56, 57). Stable isotope geochemistry provides further evidence that the
321 biomere events were linked to major marine carbon and sulfur cycle perturbations,
322 consistent with ocean warming and deoxygenation (58–61). Similar inferences of ocean
323 anoxia and rapid sea-level change have been made for the early-middle Cambrian
324 Botomian extinction event (62). In contrast, multiple Mesozoic and Cenozoic
325 hyperthermals (including the Paleocene-Eocene Thermal Maximum and Cretaceous
326 Oceanic Anoxic Event 2) that exhibit similar broad patterns of environmental change (43,
327 63–65) do not correlate with global marine extinctions of comparably high magnitude
328 (Fig. 1; (9)). Our analyses demonstrate that the effects of changing atmospheric
329 oxygenation on the thermal safety margins of marine ectotherms (Fig. 2) may account for
330 this discrepancy in extinction magnitude between events with similar signatures of
331 environmental change. Our simulations of metabolic habitat viability also offer a
332 potential mechanism for the high origination rates observed through the early Paleozoic
333 (6, 7) – particularly if simple logistic models of extinction and subsequent recovery (i.e.
334 origination; e.g. (4, 66)) can be broadly applied to the Phanerozoic fossil record.
335 However, we focus upon warming driven extinction events because fewer assumptions
336 regarding the evolutionary advantages of different ecophysiotypes (and how they relate to
337 the rate at which physiological diversity increases in cool climate states) are required for
338 these models, which simply simulate the instantaneous loss of viable ecophysiotypes.

339 Our combined Earth system and ecophysiological modeling approach provides a
340 methodological advance in moving from simple correlation to more mechanistic
341 understanding of how environmental change impacted marine ecosystems through Earth
342 history. The use of physiology as a conceptual bridge between the fossil and geochemical
343 records is of clear appeal for establishing a mechanistic understanding of animal-
344 environment interactions from the geologic record (67). However, the power of Earth
345 system models in simulating the ecophysiological responses of marine animals to deep-
346 time environmental change is only recently being explored (e.g. (33, 41)). We apply
347 simple assumptions about the diversification of ecophysiotypes (i.e. that ecophysiotypes
348 proliferate in times of stability and become inviable during warming events) to test the

349 hypothesis that limited atmospheric oxygenation would increase physiological
350 vulnerability to ocean warming events on geologic timescales. For increasingly accurate
351 models of animal-environment interactions through the Phanerozoic (for example, ones
352 that directly simulate latitudinal gradients in taxonomic diversity), other key variables
353 involved in these interactions will need to be incorporated. At the organism-scale,
354 physiological traits including vulnerability to ocean acidification, food supply limitation
355 and possible variations in physiological responses are all likely important variables. For
356 example, the different buffering capacities of marine animal groups have previously been
357 invoked to explain differential extinction selectivity (68, 69). Meta-analytical approaches
358 also suggest that sensitivity to climate related stressors correlates with genus survival
359 across ancient extinction events in higher-level taxonomic groups (34), further indicating
360 that differences in physiological tolerances between marine clades may be an important
361 consideration when applying ecophysiological principles to Earth history. While we
362 demonstrate that our results are consistent across a range of deviations from mean
363 modern physiological responses, it will hopefully become feasible to begin linking
364 physiological traits more directly to extinct animal groups based on phylogenetic and
365 adaptive principles as the availability of experimental respirometry data characterizing
366 temperature-dependent hypoxic responses of marine ectotherms increases. At the
367 macroecological scale, migration (as applied in Saupe et al. (41)), species interactions,
368 and resource competition also play key roles in governing population and species
369 responses to environmental change. As model frameworks for deep-time animal-
370 environment interactions develop in terms of both ecophysiological and biogeochemical
371 realism, the temporal-spatial resolution of paleontological and geochemical databases
372 will also be critical to the explanatory power of these methodologies, as will techniques
373 addressing the limitations and biases inherent to the geologic record (4–6, 13, 54, 70–72).

374

375 **Conclusions**

376 Using a novel ensemble Earth system and ecophysiological modeling framework, we
377 demonstrate that atmospheric oxygen levels likely exerted a first-order control on

378 extinction vulnerability through the Phanerozoic. Our model analyses illustrate that the
379 theoretical predictions of oxygen and capacity limited thermal tolerance are expected to
380 have globally significant implications, resulting in dramatically increased extinction of
381 marine animals under varying climatic conditions during geological periods with limited
382 surface oxygenation. While warmer initial climate states increase the magnitude of our
383 simulated extinctions, and continental configuration and the strength of the biological
384 pump also have minor impacts on our predictions, the trend of increased extinction
385 vulnerability with early Paleozoic levels of atmospheric oxygen is dominant across all of
386 our simulations. We therefore argue that the exceptional frequency of high-magnitude
387 extinction events in the early Paleozoic was primarily a consequence of limited surface
388 oxygenation and temperature-dependent hypoxia responses in marine animals.

389

390 **Materials and Methods**

391 *Quantitative paleobiology*

392 We performed a series of quantitative paleobiological analyses to evaluate evidence for
393 declining extinction rates through the Phanerozoic. We adapted methods from Kocsis et
394 al. (7) to generate new reconstructions and statistical analyses of extinction rates through
395 the Phanerozoic specifically for marine ectotherms, using an updated download from the
396 Paleobiology Database (PBDB) and omitting endothermic and/or exclusively air-
397 breathing higher-level marine taxa (marine mammals, marine reptiles and turtles). We
398 generated reconstructed extinction rates using three richness metrics (classical
399 rarefaction, raw occurrences and shareholder quorum subsampling) and four extinction
400 rate metrics (second-for-third substitution, corrected three-timer, gap-filler and per-
401 capita). We applied these metrics to generate reconstructions for all genera both at stage
402 resolution and using the PBDB ~10 million year bins. To investigate the potential impact
403 of changing species to genus ratios through the Phanerozoic (e.g. (73)), we further
404 conducted the same analyses on filtered datasets, generating reconstructions all genera,
405 genera with a single accepted named species, genera with 2 species, genera with 3

406 species, and genera with 4 or more accepted named species (Fig. S1). For shareholder
407 quorum subsampling analyses we used a quorum level of 0.5 to accommodate lower
408 sampling intensity in filtered datasets (as supported by Boag et al. (32)) and remain
409 within the >0.4 quorum range suggested by previous authors (7). Figure 1 is a summary
410 of the top-right panel of Figure S1, including all genera at stage resolution. We further fit
411 cross-validated LOESS models to our reconstructed extinction rates to evaluate whether
412 early Paleozoic decreases in extinction rates were a major feature of the full Phanerozoic
413 record (Fig. S2). Finally, we generated Spearman's correlation coefficients to investigate
414 the statistical significance of temporal declines in extinction rates across all of our
415 treatments (Table S1). Adapted code from Kocsis et al. (7) and filtered Paleobiology
416 Database download are available at [https://github.com/richardstockey/cGENIE-](https://github.com/richardstockey/cGENIE-metabolic_index_extinction)
417 [metabolic_index_extinction](https://github.com/richardstockey/cGENIE-metabolic_index_extinction) and are assigned a DOI: 10.5281/zenodo.5143583

418

419 *Earth system modeling*

420 cGENIE is an Earth system model of intermediate complexity, designed for the spatially-
421 explicit biogeochemical characterization of global-scale paleoceanographic problems
422 (39). We create a range of 3D realizations of ocean environmental conditions by running
423 ensembles of model experiments. The experiments in each ensemble are run for 10,000 or
424 20,000 years (depending on the time required for dissolved marine O₂ and seawater
425 temperature to reach steady state), with a range of assumptions regarding atmospheric
426 pCO₂ specific to each continental configuration based upon changing solar luminosity
427 and albedo (Fig. 3), and a range of atmospheric pO₂ scenarios based upon the range of
428 estimates from geochemical proxy data and biogeochemical box modeling (Fig. 1). We
429 apply this ensemble treatment to three ancient continental configurations, chosen for their
430 relatively even temporal spread across the Phanerozoic and history of use in previous
431 paleoclimate studies – a Paleocene configuration (~55 Ma) (43), a Permian configuration
432 (~251 Ma) (74), and an Ordovician configuration (~450 Ma) (based on the 8 PAL CO₂
433 FOAM simulation of Pohl et al. (75) – see *Supplementary Information*). For each of these
434 ancient configurations, we apply age-appropriate solar luminosity (76). Finally, in the

435 Ordovician continental configuration, we explore the possible influence of postulated
436 Phanerozoic changes in organic matter remineralization depth in the ocean (17, 42) –
437 testing ~1/3 modern, or specifically 200m, e-folding depth (42).

438 We extract the mean annual ocean temperature and ocean oxygen concentration
439 during the last simulated year for each ocean grid cell and generate corresponding
440 seawater oxygen partial pressure (pO_2) values (following the methods of Hofmann et al.
441 (77)). Changing solar luminosity and continental configuration results in different mean
442 sea surface temperatures for the same atmospheric CO_2 assumption. We therefore
443 identify the pCO_2 values for each continental configuration that create comparable
444 climate simulations (Table S2 and *Supplementary Information*). These climate scenarios
445 are compared using the mean equatorial ($3.2^\circ S$ to $3.2^\circ N$, 0-80m depth) surface ocean
446 temperature for each model (Figs. 4, S4-6, Table S2).

447 The code for the version of the ‘muffin’ release of the cGENIE Earth system
448 model used in this paper is tagged as v0.9.19 and is assigned a DOI:
449 10.5281/zenodo.4473048. Configuration files for the specific experiments presented in
450 the paper can be found in the directory: genie-userconfigs/MS/stockeyetal.PNAS.2021.
451 Details on the experiments, plus the command line needed to run each one, are given in
452 the readme.txt file in that directory. All other configuration files and boundary conditions
453 are provided as part of the code release.

454 A manual detailing code installation, basic model configuration, tutorials covering
455 various aspects of model configuration and experimental design, plus results output and
456 processing, is assigned a DOI: 10.5281/zenodo.4469678.

457

458 *Ecophysiological simulations of animal-environment interactions*

459 We combine our ensemble Earth system modeling experiments with a probabilistic
460 ecophysiological model of extinction vulnerability. The Metabolic Index, as defined by
461 Deutsch et al. (29) and Penn et al. (33), is configured here to calculate the proportion of

462 modern marine ectotherms (based on described temperature-dependent hypoxia
 463 responses) that can inhabit each ocean cell in the cGENIE Earth system model.

$$464 \quad \text{Metabolic habitat viability} = \sum_{\min(A_o, E_o, \phi_{\text{crit}})}^{\max(A_o, E_o, \phi_{\text{crit}})} A_o \frac{pO_2}{\exp\left[\frac{-E_o}{k_B} \left(\frac{1}{T} - \frac{1}{T_{\text{ref}}}\right)\right]} > \phi_{\text{crit}}$$

465 (Eqn. 1)

466 At the individual organism scale, A_o is the inverse of the hypoxic threshold of the
 467 organism (the minimum required seawater pO_2 (P_{crit}) to sustain resting aerobic
 468 metabolism), E_o is the temperature-dependency of the hypoxic threshold and ϕ_{crit} is the
 469 multiplicative increase in oxygen supply that is required to support ecologically
 470 sustainable populations (calculated based on biogeographic distribution, relative to
 471 experimental respirometry measurements of resting metabolism). In our modeling
 472 approach, these variables are parametrized by probability density functions based on
 473 observations from laboratory experiments and species distributions (Fig. 2; following
 474 Penn et al. (33)). Seawater temperature and pO_2 are environmental variables generated
 475 through the Earth system modeling approach described above (Fig. 3). All other variables
 476 are constant (k_B is the Boltzmann constant, T_{ref} is a reference temperature of 15°C). In
 477 our analyses, we simulate 1000 ecophysiotypes, sampled from probability distributions of
 478 A_o , E_o and ϕ_{crit} , and map which cells (if any) in each cGENIE ocean model are habitable
 479 for each ecophysiotype (see Figure S12 for exploration of the number of ecotypes used).

480 Metabolic habitat viability, as defined here, quantifies the proportion of these
 481 modeled ecophysiotypes that can live in the non-polar shelf environments (defined as any
 482 cell adjacent to continental land mass in the top 3 layers of the cGENIE ocean, or
 483 <283.8m water depth) of each global ocean model. See Figures S5-6 for sensitivity
 484 analyses using the entire global ocean model, rather than shelf environments alone. Polar
 485 environments (>70°N and <70°S) are excluded from all analyses due to the coarse model
 486 resolution of polar ocean environments (e.g. in a Paleocene northern polar ocean) in
 487 cGENIE and to reduce local non-linear responses to sea ice extent.

488 We further simulate extinction as the global loss of ecophysiotypes between two
489 CO₂ scenarios at the same O₂ level. Specifically, we evaluate the proportional loss of
490 ecophysiotypes between baseline climate states (relatively cool, approximately pre-
491 industrial mean equatorial surface ocean temperatures – *Supplementary Information*) and
492 equivalent model scenarios that have undergone ~5°C equatorial warming (Table S2;
493 modeling a nominal hyperthermal event of roughly the same magnitude as the Paleocene-
494 Eocene Thermal Maximum (43)) at each atmospheric O₂ level. Global ecophysiotype
495 extinction is thus defined as the proportion of ecophysiotypes that were viable in shelf
496 environments of the colder baseline simulation but are no longer viable in any continental
497 shelf cell of the warmer ocean simulation. Sensitivity analyses exploring the number of
498 viable cells required to survive a simulated warming event, and the proportional habitat
499 loss required to drive extinction, are shown in Figures S9-10. Additional sensitivity
500 analyses exploring deviations from the distributions of A_o and E_o defined in Penn et al.
501 (33) are shown in Figure S11. In these analyses, “low” and “high” distributions have
502 mean values defined by the 25th and 75th percentiles of the distributions used in our
503 primary analyses, and half of the variance of those distributions. In plots of global
504 ecophysiotype extinction in shelf environments, we summarize the distribution of results
505 from 100 different simulated populations of 1000 randomly sampled ecophysiotypes to
506 illustrate the range of sampling-related uncertainty in our probabilistic approach to
507 ecophysiological modeling. All plots of single ecotype populations (i.e. those with points
508 rather than envelopes – Figs. 4, S4-6) use the same randomly sampled population.

509 R scripts to reproduce the ecophysiological analyses and associated figures are
510 available at https://github.com/richardstockey/cGENIE-metabolic_index_extinction and
511 are assigned a DOI: 10.5281/zenodo.5143583

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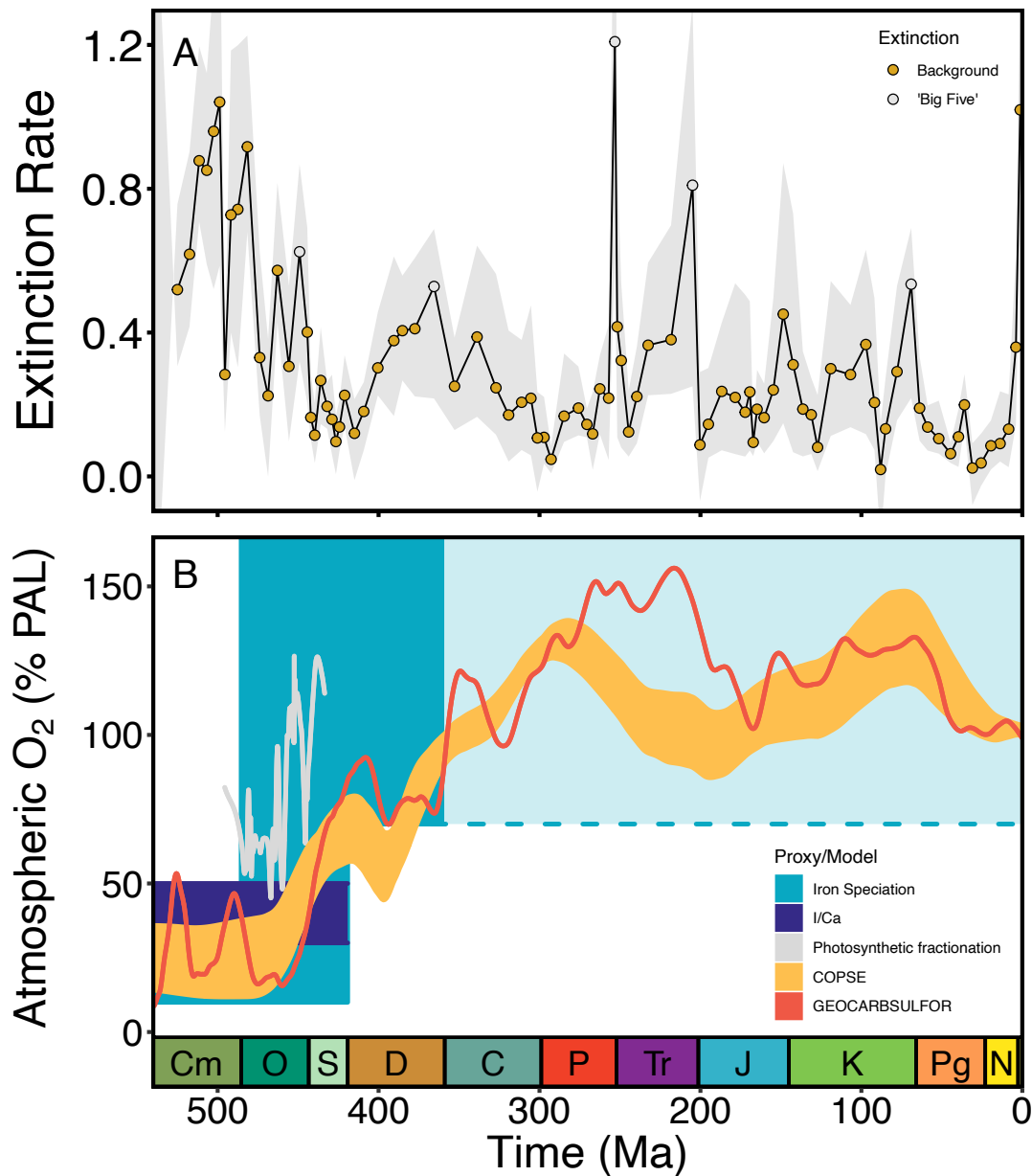
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692 **Figures**

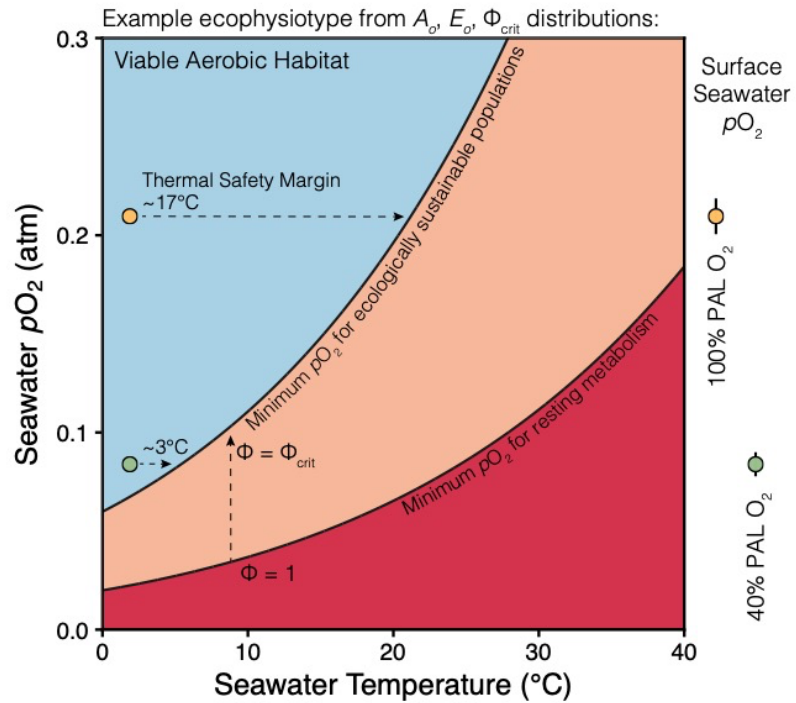
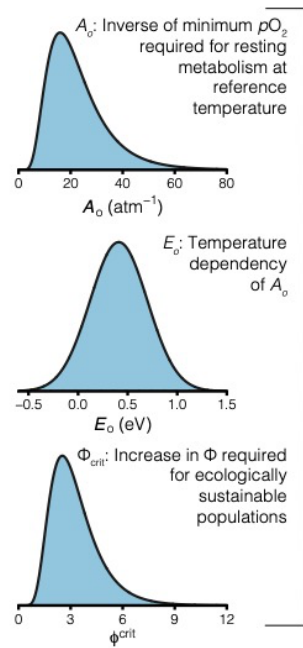
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 695 Figure 1: Trends in atmospheric oxygen and extinction rates through the Phanerozoic. A) Genus-level
 696 extinction rates for marine ectotherms (adapted from Kocsis et al. (7), *Materials and Methods*) – line
 697 and points represent mean values, envelope represents maximum and minimum estimates from all 12
 698 methodological approaches (3 treatments: raw, classical rarefaction and Shareholder Quorum
 699 Subsampling-standardized, for each of 4 metrics: average per capita rates, corrected three-timer rates,
 700 gap-filler rates and second-for-third substitution rates). B) Reconstructions of atmospheric oxygen
 701 from biogeochemical models (21, 22, 78) and geochemical proxy records (15, 17).

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Metabolic Index parameters:

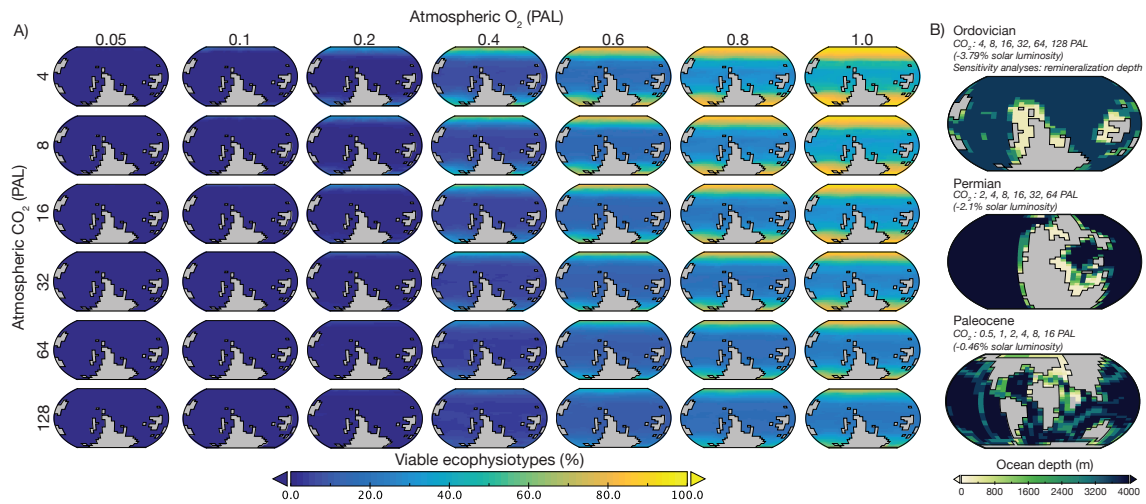


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Figure 2: Schematic of ecophysiological model based on the Metabolic Index (Equation 1). The frequency distributions of three key ecophysiological parameters – A_o , E_o and Φ_{crit} – are illustrated to the left. The implications of these parameters for the ecophysiological modeling framework employed in this study are illustrated for an example ecophysiotype on the right, based on the median values of these distributions. The minimum seawater pO_2 required for resting metabolism increases at an exponential rate, primarily due to temperature effects on metabolic rate. The minimum seawater pO_2 required for sustainable populations on ecological timescales also increases exponentially with temperature (faster than the minimum pO_2 required for resting metabolism), as the product of an exponential function defined by A_o , E_o and Φ_{crit} (see *Materials and Methods*, Equation 1 for full details). At a given temperature, the thermal safety margin of a hypothetical ecophysiotype is predicted to decrease with decreasing seawater pO_2 (either due to a change in equilibrium oxygen levels resulting from decreasing atmospheric oxygen, or a decrease in saturation resulting from biogeochemical processes such as organic carbon remineralization). Surface seawater pO_2 distributions (far right) are taken from Earth system model analyses presented in this study (8 PAL CO_2 Ordovician configuration; points represent mean values, and error bars 2 SD).

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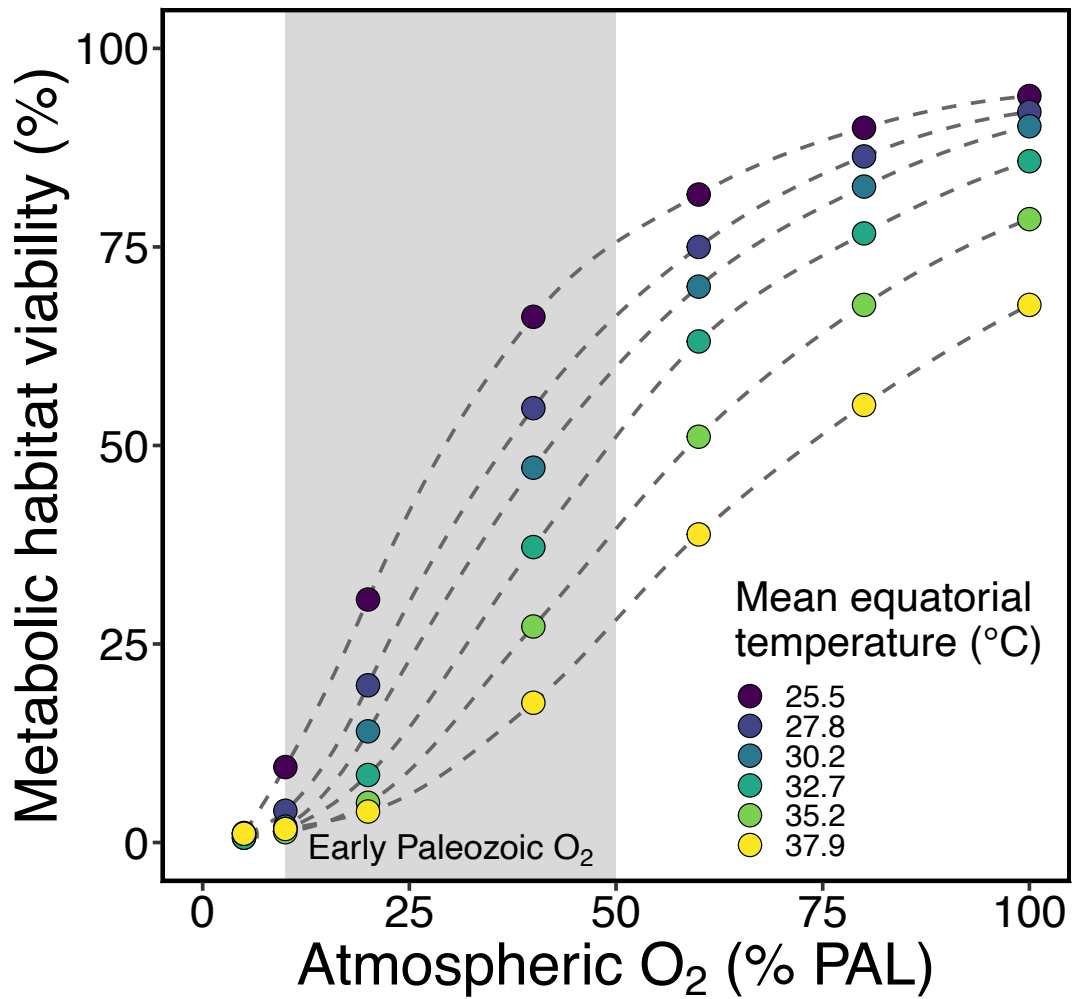


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721 Figure 3: Ensemble Earth system modeling approach using cGENIE. A) Example of ensemble O₂-CO₂
 722 Earth system modeling experiment using Ordovician continental configuration with modern
 723 remineralization depth. Color scale illustrates the proportion of the modeled ecophysiotypes that can
 724 live in each cell of the surface ocean (top 0-80m layer of the 16 layer cGENIE ocean is illustrated
 725 here). B) Sensitivity analyses performed in this study. Variations in continental configuration,
 726 remineralization depth and CO₂ forcing are detailed here. The atmospheric O₂ levels investigated in
 727 each ensemble experiment are the same. We present full surface ocean models here for ease of visual
 728 comparison, although main text analyses use only non-polar shelf environments (as illustrated in Fig.
 729 S3).

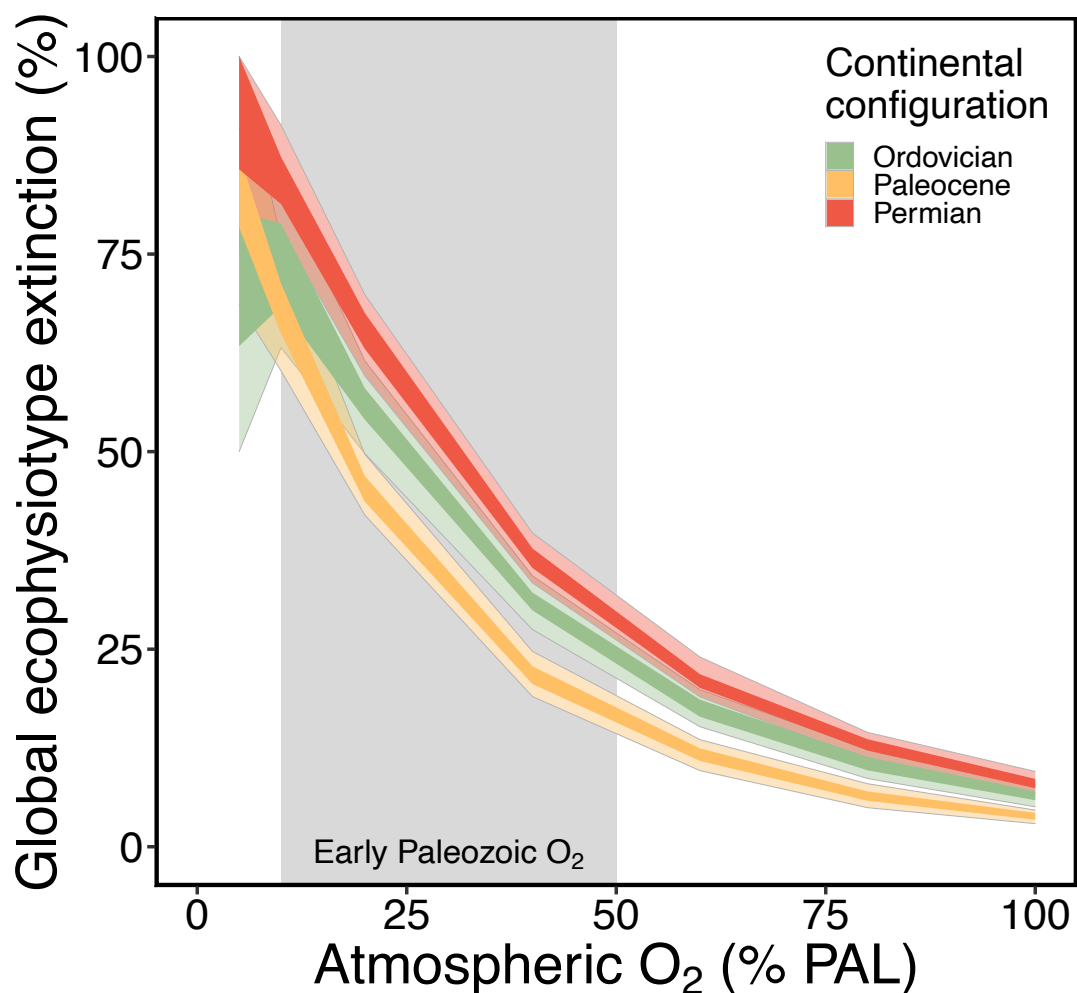
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732
 733 Figure 4: Metabolic habitat viability for the ensemble O₂-CO₂ Earth system modeling experiment with
 734 an Ordovician continental configuration and modern remineralization depth. Metabolic habitat
 735 viability is calculated as the proportion of the ecophysiotypes modeled that can live in shelf
 736 environments of each three dimensional ocean model produced using cGENIE (*Materials and*
 737 *Methods*). Circles represent individual experiments and are color coded by mean equatorial sea surface
 738 temperature (-3.2°S to 3.2°N, 0-80m depth), as a product of atmospheric CO₂ forcing.

739



740
 741 Figure 5: Global ecophysiotype extinction predicted to result from a ~5°C warming event from an
 742 approximately pre-industrial baseline sea surface temperature at different atmospheric O₂ levels,
 743 illustrating sensitivity analyses evaluating the influence of continental configuration on predicted
 744 extinction. Global ecophysiotype extinction is defined as the proportion of ecophysiotypes that were
 745 viable in the shelf environments of the colder baseline simulation but are no longer viable in any cell
 746 of the shelf environments of the warmer ocean simulation (*Materials and Methods*). Baseline CO₂
 747 levels used: 1 PAL – Paleocene; 8 PAL – Permian; 8 PAL – Ordovician. Darker envelopes represent
 748 25th-75th percentiles of 100 simulation results, lighter envelopes represent 5th-95th percentiles.