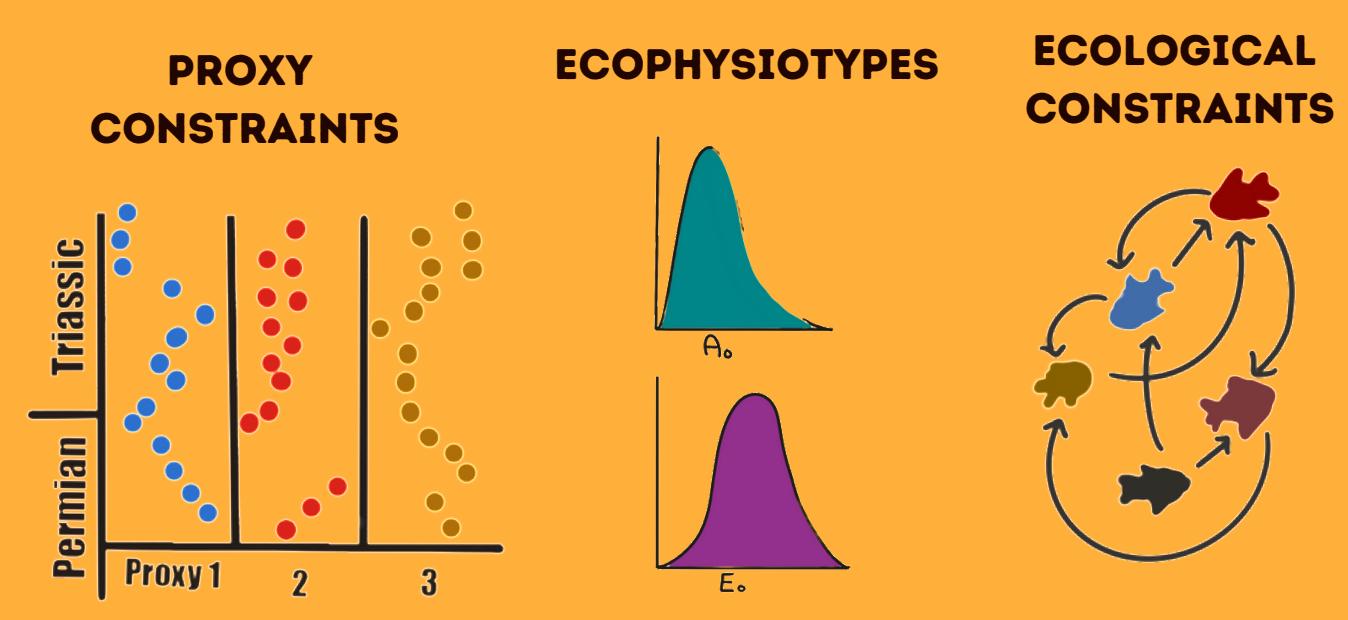


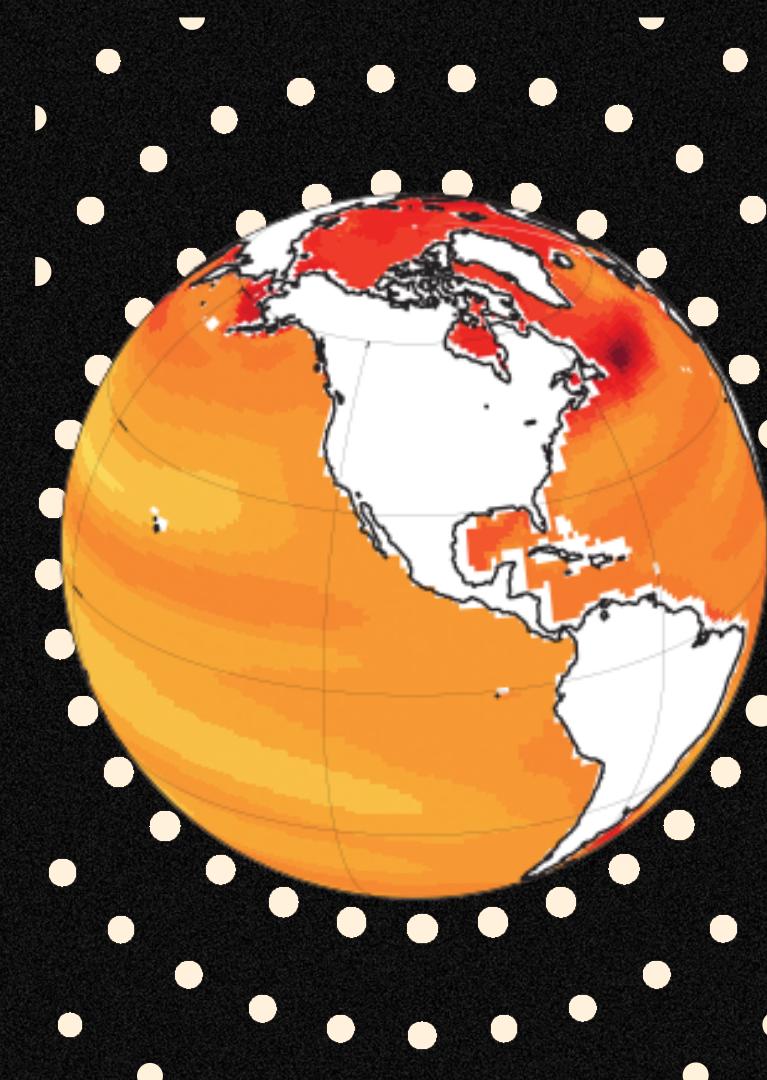
1 Selectivity of mass extinctions: patterns, processes, and future directions  
2  
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Geological evidence can reveal the physical and chemical changes that trigger mass extinctions, but differences in **biological traits** between victims and survivors provide key insights into actual **kill mechanisms**.

Species ecophysiological traits and ecological interactions can be incorporated into Earth system models, constrained by geological and geochemical proxies, to simulate extinction patterns for comparison with selectivity in the fossil record.



Mass extinctions are a critical source of information to project and mitigate biological responses to anthropogenic climate change.



15 IMPACT STATEMENT

16 Mass extinction events represent the greatest catastrophes in the history of animal life and only  
17 five major extinction events have occurred across the past 550 million years. Geological evidence  
18 can reveal the physical and chemical processes that caused environmental change, but  
19 differences in morphological, ecological, and physiological traits between extinction victims and  
20 survivors provide our best record of actual kill mechanisms. In recent years, this field has  
21 advanced both through the compilation of experimental data on organismal traits, enabling new  
22 insights into extinction patterns, and through the development of mechanistic models for biological  
23 response to environmental change, enabling incorporation of physiological tolerance into climate  
24 models to predict extinction pattern. Ultimately, mass extinction events are a critical source of  
25 data to calibrate the magnitude and rate of biological response to climate change over timescales  
26 longer than those of experiments and field studies. In this way, integration of information from the  
27 fossil record is becoming essential to the task of predicting and mitigating taxonomic losses due  
28 to current environmental change.

29

30 ABSTRACT

31 A central question in the study of mass extinction is whether these events simply intensify  
32 background extinction processes and patterns *versus* change the driving mechanisms and  
33 associated patterns of selectivity. Over the past two decades, aided by the development of new  
34 fossil occurrence databases, selectivity patterns associated with mass extinction have become  
35 increasingly well quantified and their differences from background patterns established. In  
36 general, differences in geographic range matter less during mass extinction than during  
37 background intervals, while differences in respiratory and circulatory anatomy that may correlate  
38 with tolerance to rapid change in oxygen availability, temperature, and pH show greater evidence  
39 of selectivity during mass extinction. The recent expansion of physiological experiments on living  
40 representatives of diverse clades and the development of simple, quantitative theories linking  
41 temperature and oxygen availability to the extent of viable habitat in the oceans have enabled the  
42 use of Earth system models to link geochemical proxy constraints on environmental change with  
43 quantitative predictions of the amount and biogeography of habitat loss. Early indications are that  
44 the interaction between physiological traits and environmental change can explain substantial  
45 proportions of observed extinction selectivity for at least some mass extinction events. A  
46 remaining challenge is quantifying the effects of primary extinction resulting from the limits of  
47 physiological tolerance *versus* secondary extinction resulting from the loss of taxa on which a  
48 given species depended ecologically. The calibration of physiology-based models to past  
49 extinction events will enhance their value in prediction and mitigation efforts related to the current  
50 biodiversity crisis.

51

52 KEYWORDS

53 Physiology, Ecology, Earth system models, Extinction, Fossil, Biodiversity, Oxygen, Temperature,  
54 Climate

55

56 SOCIAL MEDIA SUMMARY

57 The selectivity of taxonomic loss shows that climate change played an important role in several  
58 mass extinctions.

59  
60     1. INTRODUCTION  
61     Earth is currently undergoing a biodiversity crisis on a scale unprecedented in the history of the  
62     human species (Barnosky *et al.* 2011; Dirzo *et al.* 2014; McCauley *et al.* 2015), but crises of  
63     similar or greater magnitude have occurred at least five times across the 600-million-year history  
64     of animal life (Fig. 1A) (Barnosky *et al.* 2011; Raup & Sepkoski 1982). All major mass extinction  
65     events are associated with evidence of rapid environmental change. In some cases, such as the  
66     end-Permian (252 million years ago [Mya]) and end-Triassic (201 Mya) mass extinctions, there is  
67     evidence for rapid and pronounced climate warming (Blackburn *et al.* 2013; Bond & Sun 2021;  
68     Burgess *et al.* 2014; Kiessling & Simpson 2011; Payne & Clapham 2012). By contrast, the Late  
69     Ordovician (443 Mya) and Late Devonian (372 Mya) extinctions occurred in association with  
70     climate cooling (Finnegan *et al.* 2011; Joachimski & Buggisch 2002). The end-Cretaceous  
71     extinction (66 Mya) was associated with an asteroid impact event whose aftermath resembled the  
72     consequences of a hypothetical global thermonuclear war (Pollack *et al.* 1983; Turco *et al.* 1983).  
73     Due to the magnitude and global scale of the current “Sixth” extinction, these events from Earth’s  
74     past provide historical reference points for predicting the long-term magnitude, ecological impact,  
75     and recovery timescale from the current crisis or other, potential, human-mediated catastrophes.  
76  
77     While mass extinctions have been identified in the fossil record based largely on the magnitude  
78     of diversity loss across many higher taxa (Newell 1963, 1967; Raup & Sepkoski 1982), causal  
79     inference has relied more on geological and geochemical evidence of potential triggers (Alvarez  
80     *et al.* 1980; Finnegan *et al.* 2011; Svensen *et al.* 2009) and patterns of extinction selectivity  
81     interpreted to reflect proximal kill mechanisms (Finnegan *et al.* 2012; Jablonski 1986; Jablonski  
82     & Raup 1995; Knoll *et al.* 1996, 2007; Penn *et al.* 2018; Sheehan & Hansen 1986; Smith & Jeffery  
83     1998; Valentine & Jablonski 1986). Selectivity patterns have been assessed with respect to a  
84     wide range of traits (Fig. 1B-E), including geographic range (Dunhill & Wills 2015; Jablonski 1986;  
85     Kiessling & Aberhan 2007; Payne & Finnegan 2007), body size (Allen *et al.* 2019; Friedman 2009;  
86     Jablonski & Raup 1995; Longrich *et al.* 2012; Monarrez *et al.* 2021; Payne & Heim 2020),  
87     abundance (Lockwood 2003; Payne *et al.* 2011), larval ecology (Valentine & Jablonski 1986), diet  
88     (Wilson 2013), functional ecology (Bambach *et al.* 2002; Hughes *et al.* 2021; Payne *et al.* 2016b),  
89     environmental breadth (Jablonski & Raup 1995), respiratory and circulatory anatomy (Clapham  
90     2017; Knoll *et al.* 1996, 2007), and shell mineralogy (Clapham & Payne 2011; Kiessling &  
91     Simpson 2011).  
92  
93     Extinction selectivity provides our most direct evidence of proximal kill mechanisms (Raup 1986),  
94     but to date most testing of observed extinction patterns against hypothesized kill mechanisms has  
95     been semi-quantitative, focused on establishing consistency between predicted and observed  
96     directions of selectivity under various hypothesize kill mechanisms. Recently, advances in  
97     paleontological databases, geochemical proxies, physiological experiments, and Earth system  
98     and ecosystem models have enabled the comparison of observed and predicted extinction  
99     patterns within quantitative, self-consistent frameworks (Fig. 2) (Penn *et al.* 2018). Although  
100    quantitative model-data comparison between observed and predicted extinction patterns is still in  
101    its early days, the door for direct comparison of past and future biotic response to climate change  
102    is now open, increasing the value of the fossil record in the mitigation of the current biotic crisis.

103

## 104      2. PATTERN

105 Analyses of selectivity for individual mass extinction events date back many decades (Jablonski  
106 2005). Studies synthesizing and comparing selectivity patterns across all major mass extinctions  
107 (and intervening background intervals) have emerged more recently, alongside publicly available  
108 databases of fossil occurrences and other traits (Alroy 1999; Kiessling & Simpson 2011; Monarrez  
109 *et al.* 2021; Payne *et al.* 2016b; Payne & Finnegan 2007; Payne & Heim 2020; Peters 2008; Smith  
110 *et al.* 2018).

111

112 Geographic range is one of the traits most commonly hypothesized to correlate with extinction  
113 risk due to its influence on the extent to which populations of a given taxon may avoid a regional  
114 disturbance or have broad enough physiological tolerance limits or ecological capacities to survive  
115 a global one. Analyses of fossil data have confirmed that widely distributed taxa survive  
116 preferentially during background intervals (Fig. 1C) (Jablonski 1986, 2005; Payne & Finnegan  
117 2007). Broader geographic range is also significantly associated with survival during at least some  
118 major mass extinction events (Finnegan *et al.* 2016; Jablonski & Raup 1995), but the strength of  
119 this association (i.e., the change in odds or probability of extinction per unit change in geographic  
120 range) is greatly reduced relative to background intervals (Fig. 1C) (Kiessling & Aberhan 2007;  
121 Payne & Finnegan 2007). Due to the consistency of the association and the expectation of  
122 selectivity on total geographic range under most extinction scenarios, these patterns have rarely  
123 yielded direct insight into kill mechanisms. By contrast, the biogeography of extinction can be  
124 more informative. For example, end-Cretaceous echinoid extinction was significantly more severe  
125 in areas proximal to the Chicxulub impact site (Smith & Jeffery 1998), and differences in extinction  
126 intensity across latitude often correspond with expectations due to climate change (Finnegan *et*  
127 *al.* 2012; Penn *et al.* 2018; Reddin *et al.* 2019, 2021). Quantifying the expected magnitude of  
128 spatial gradients in extinction intensity and differences in such gradients across higher taxa (or  
129 functional groupings) is the key to linking these findings with hypothesized kill mechanisms, and  
130 one that is already being partially realized (Penn *et al.* 2018).

131

132 The extinctions of large mammals during the Pleistocene (0.0117 Ma) and of large, non-avian  
133 dinosaurs during the Maastrichtian (66 Ma) have long prompted speculation that large-bodied  
134 animals are at systematically higher risk of extinction during times of environmental change  
135 (Brown 1995; Raup 1986; Wallace 1889). Analyses of the fossil record reveal a more  
136 heterogeneous relationship, and one that may differ across taxa and habitats. For example,  
137 smaller body size is generally associated with greater extinction risk during background times for  
138 many classes of marine animals (Fig. 1D) (Monarrez *et al.* 2021; Payne & Heim 2020). By  
139 contrast, body size was not generally associated with extinction probability for terrestrial mammals  
140 until the Pleistocene (Alroy 1999; Smith *et al.* 2018). End-Cretaceous extinctions preferentially  
141 eliminated larger-bodied fish, lizards, and snakes (Friedman 2009; Longrich *et al.* 2012) but were  
142 unbiased in bivalves and gastropods (Jablonski & Raup 1995). End-Permian extinctions  
143 preferentially affected larger foraminifera and brachiopods (Schaal *et al.* 2016). Many taxon-size  
144 combinations have yet to be examined systematically. In marine animals, size selectivity changes  
145 between background and mass extinction in many classes but the direction and magnitude of the  
146 size bias during mass extinction differs among classes (Fig. 1D) (Monarrez *et al.* 2021; Payne &

147 Heim 2020). The differences in responses among classes remain to be explained. Because body  
148 size correlates with many ecological and physiological traits (Peters 1983), size bias on its own  
149 is insufficient to diagnose proximal kill mechanisms but may be useful in conjunction with other  
150 traits or in testing against predictions of specific kill mechanisms (Deutsch *et al.* 2022).

151  
152 Some mass extinction events exhibit selectivity patterns that can be mapped onto respiratory and  
153 circulatory anatomy, potentially reflecting underlying differences in susceptibility to metabolic  
154 stress from hypercapnia, anoxia, climate warming, or their interactive effects. For example, the  
155 end-Permian mass extinction preferentially affected heavily calcified marine animal genera with  
156 limited respiratory and circulatory systems (Fig. 1B), suggesting a role for hypercapnia and/or  
157 direct and indirect fitness effects of acidification on shell dissolution (Calosi *et al.* 2017) in driving  
158 the extinction (Knoll *et al.* 1996). At the same time, the lack of sophisticated oxygen supply  
159 mechanisms would also make these taxa more sensitive to temperature-dependent hypoxia  
160 (Deutsch *et al.* 2020; Endress *et al.* 2022) and metabolic differences among groups likely  
161 influence taxonomic selectivity patterns from changes in CO<sub>2</sub>, temperature, and O<sub>2</sub>. Similar  
162 patterns as seen in the end-Permian apply to other extinction events, including the end-Triassic  
163 mass extinction (Clapham 2017; Kiessling & Simpson 2011), consistent with shared kill  
164 mechanisms. By contrast, the end-Cretaceous mass extinction exhibits the opposite pattern, with  
165 taxa thought to be more sensitive to ocean acidification surviving preferentially (Kiessling &  
166 Simpson 2011), potentially reflecting differences in extinction patterns triggered primarily by  
167 volcanism *versus* impact events. The extent to which these patterns stand out from background  
168 extinction remains incompletely studied. A study controlling for differences between benthic  
169 *versus* planktonic and nektonic taxa indicates that many background intervals show the same  
170 selectivity, often of similar magnitude (Payne *et al.* 2016a). As discussed below, results of  
171 physiological experiments on living relatives of species in the fossil record are enabling  
172 quantitative prediction of biological response to past environmental changes inferred from  
173 geological and geochemical proxies. This is currently an area of rapid progress.

174  
175 Simultaneous analysis of extinction selectivity across multiple traits and time intervals enables  
176 quantitative comparison of selectivity patterns between background and mass extinction as well  
177 as among mass extinction events (Fig. 1E). Such analyses generally confirm that mass extinction  
178 events differ in selectivity from background patterns (Fig. 1C, E) (Finnegan *et al.* 2012; Kiessling  
179 & Simpson 2011; Monarrez *et al.* 2021; Payne *et al.* 2016b; Payne & Finnegan 2007) and that  
180 the pronounced size bias of the modern extinction makes it an outlier relative to major mass  
181 extinctions as well as recent background intervals (Fig. 1D) (Payne *et al.* 2016b; Smith *et al.*  
182 2018).

183  
184 Overall, selectivity patterns accord with geological and geochemical data, indicating that mass  
185 extinction events are typically associated with large and rapid environmental perturbations rather  
186 than intensification of background extinction processes (Alvarez *et al.* 1980; Finnegan *et al.* 2011;  
187 Hallam & Wignall 1997). Testing hypothesized kill mechanisms requires simultaneous  
188 consideration of selectivity across multiple variables because physiological and ecological traits  
189 are often linked in complex ways. For example, body size is related to the supply and demand of

190 oxygen (Deutsch *et al.* 2015, 2022) and food (Gearty *et al.* 2018) as well as to trophic level  
191 (Romanuk *et al.* 2011).

192

193

194 3. PROCESS

195

196 3. 1 *Introduction*

197

198 Understanding the causes of extinction selectivity in the fossil record requires additional  
199 information about the patterns of environmental change, the sensitivity of species to those  
200 changes, and disruptions in the ecological networks. The interpretation of extinction selectivity  
201 thus necessarily relies on geochemical reconstructions of climate, understanding of the ecological  
202 and physiological traits of living taxa and, increasingly, on models that incorporate all these  
203 aspects of ecological and Earth system dynamics into an internally consistent, quantitative  
204 framework (Fig. 2).

205

206 Patterns of extinction selectivity can arise simply from the fact that environmental changes can  
207 be highly variable in strength or even direction across space. Extinction selectivity could also arise  
208 from taxonomic or geographic differences in physiological sensitivity to environmental change,  
209 even if climate trends were globally uniform. In general, these factors are likely to be connected,  
210 as the tolerance limits of taxa to environmental conditions will shape the pre-extinction geographic  
211 distribution, which may confer greater or lesser sensitivity to environmental change in certain  
212 regions. Contemporary studies have advanced a mechanistic approach to investigating the  
213 causes of selectivity in mass extinctions by integrating many of these elements, from geochemical  
214 proxies of climate change, the modern diversity of ecophysiological traits, and the climate  
215 dynamics of Earth system models. In ocean studies, emphasis has been on integrating climate  
216 and physiological constraints (Penn *et al.* 2018; Stockey *et al.* 2021). Terrestrial studies, by  
217 contrast, have tended to focus on ecological (food web) mechanisms largely missing from marine  
218 analyses (Roopnarine 2006; Roopnarine & Angielczyk 2015). These dichotomous approaches  
219 have made significant advances in their respective domains, paving the way for more unified  
220 marine and terrestrial studies.

221

222 3.2 *Example: Metabolic Index*

223

224 One promising avenue for examining physiological kill mechanisms for ancient extinction events  
225 is the Metabolic Index, which was initially developed to test whether the biogeographic  
226 distributions of species are physiologically limited by O<sub>2</sub> supply and demand in the modern ocean  
227 (Deutsch *et al.* 2015). This ecophysiological model quantifies habitat viability for a species, in  
228 terms of its ability to carry out aerobic respiration, by taking a ratio of environmental oxygen supply  
229 to biological oxygen demand as a function of temperature and taxon-specific metabolic and O<sub>2</sub>  
230 supply traits (Eq. 1). The metabolic energy demands of water-breathing marine animals increase  
231 with water temperature and body size (Gillooly *et al.* 2001), raising corresponding biological O<sub>2</sub>  
232 requirements. Temperature and body size also impact the rates of organismal O<sub>2</sub> supply through  
233 diffusion, ventilation, and internal circulation (Deutsch *et al.* 2022; Endress *et al.* 2022), while

234 warmer water holds less ambient O<sub>2</sub>. The ratio of temperature and body size (B)-dependent rates  
235 of potential O<sub>2</sub> supply and organismal metabolic demand, termed the Metabolic Index ( $\phi$ ),  
236 quantifies the metabolic viability of a habitat for a given species:

237

$$\Phi = A_0 B^{-p} \exp \left( \frac{E_0}{k_B T} - \frac{1}{T_{\text{crit}}} \right)$$

Eq. 1

238

239 where  $A_0$  (atm<sup>-1</sup>) is the ratio of O<sub>2</sub> supply to resting demand rate coefficients, or hypoxia tolerance  
240 at a reference temperature and body size (B), with allometric scaling exponent  $\varepsilon$  and Arrhenius  
241 temperature sensitivity,  $E_0$  (eV), and  $pO_2$  and  $T$  are the oxygen partial pressure and temperature  
242 of ambient water, respectively (Fig. 3) (Deutsch *et al.* 2015, 2020). These physiological traits and  
243 their distributions across taxa can be estimated from critical oxygen thresholds in respirometry  
244 experiments conducted for diverse marine biota over the past half century (Chu & Gale 2017;  
245 Rogers *et al.* 2016). Critical oxygen thresholds define the Metabolic Index to be 1 (i.e.,  $\phi = 1$ ),  
246 allowing the traits to be estimated for organisms in a resting state under laboratory conditions. In  
247 the environment, O<sub>2</sub> requirements are elevated by more strenuous activities important for  
248 population persistence, such as growth, reproduction, feeding, defense, or motion. These  
249 additional energy demands require the O<sub>2</sub> supply to be raised by a factor,  $\phi_{\text{crit}}$ , corresponding to  
250 sustained metabolic scope (Peterson *et al.* 1990). Stable aerobic habitat barriers thus arise in  
251 ocean regions where the Metabolic Index falls below  $\phi_{\text{crit}}$ , while the geographic positions of these  
252 barriers depend on the species' traits (Deutsch *et al.* 2020). The habitability of any given parcel  
253 of water can therefore be determined from the temperature and oxygen partial pressure given the  
254 species values of  $A_0$ ,  $E_0$ , and  $\phi_{\text{crit}}$ . Earth system models can be populated with hypothetical  
255 species by drawing combinations of values from the trait distributions (Fig. 3). The promise of this  
256 framework for paleontological application is that trait distributions can be used to predict the  
257 patterns of biodiversity, providing a means for testing the model against the fossil record. Indeed,  
258 the observed tropical dip in marine species richness observed for diverse animal groups in the  
259 modern ocean (Chaudhary *et al.*, 2021) can be explained by aerobic habitat limitation implied by  
260 modern species Metabolic Index traits (Penn & Deutsch, 2022). Environmental temperature and  
261 oxygen concentration can be quantified using geochemical proxies for ancient events to calibrate  
262 Earth System models and body size can be measured from fossil specimens. In principle,  
263 ecological interactions can be further incorporated to model, allowing extinction cascades to be  
264 accounted for alongside direct, climate-driven habitat loss (Fig. 4).

265

266 During periods of climate warming, rising water temperatures can drive the metabolic O<sub>2</sub> demand  
267 above a supply declining from ocean deoxygenation, leading to the loss of available aerobic  
268 habitat, and eventually species extinctions at local and global scales (Penn *et al.* 2018; Reddin *et*  
269 *al.* 2020). At regional scales, such as in the California Current System, aerobic habitat changes  
270 have been linked to multi-decadal fluctuations of anchovy populations, including near-extirpation  
271 of larvae from portions of their range (Howard *et al.* 2020). At global scales, aerobic habitat loss  
272 under the climate change simulated for the end-Permian mass extinction predicted a geographic  
273 selectivity of extinction consistent with the fossil record (Fig. 5A): Extinction risk was greater for  
274 species inhabiting higher latitudes. This geographic selectivity arises because species previously  
275 occupying the tropics would already have been adapted to warm, low-O<sub>2</sub> conditions that became

276 more widespread, whereas polar habitat niches disappeared more completely (Penn *et al.* 2018).  
277 In contrast to the geographic selectivity predicted for warming, periods of global cooling, such as  
278 during the Late Ordovician, are expected to generate extinctions focused on the low latitudes  
279 (Saupe *et al.* 2020), consistent with the patterns observed for that mass extinction (Finnegan *et*  
280 *al.* 2012) and may also occur through aerobic habitat loss if accompanied by deoxygenation  
281 (Finnegan *et al.* 2016) or due to declining hypoxia tolerance in cold water in species with thermal  
282 optima (Boag *et al.* 2018; Endress *et al.* 2022). Aerobic habitat loss is also predicted to select  
283 against large-bodied species, with a strong variability within size classes that depends on a  
284 species' temperature sensitivity (Deutsch *et al.* 2022). Extinctions driven by aerobic habitat loss  
285 may also explain the amplified background extinction rates observed for the early Phanerozoic,  
286 because of dramatically lower atmospheric O<sub>2</sub> levels and thus species living closer to their  
287 ecophysiological limits (Stockey *et al.* 2021). Trait adaption to different past climate states  
288 (Bennett *et al.*, 2021) has the potential to buffer or amplify predicted extinction risks. The role of  
289 differences in ecophysiological traits across taxonomic groups in explaining observed patterns of  
290 extinction selectivity across higher taxa (Knoll *et al.* 1996, 2007) remains an open area of  
291 research.

292  
293 Primary extinctions driven by the loss of aerobic habitat have the potential to be amplified by  
294 secondary extinctions arising from food web effects (Fig. 4) or co-occurring environmental  
295 stressors that exacerbate direct aerobic habitat loss (Fig. 5J-O). Aerobically tolerant species could  
296 still be lost if they are ecologically tied to vulnerable ones, for example through the food web (Fig.  
297 4) or other critical interactions. Ocean acidification (Fig. 5M,N,O) has the potential to further  
298 deplete aerobic habitat through direct CO<sub>2</sub> effects on critical oxygen thresholds, but the magnitude  
299 and direction of this effect is uncertain and variable across limited available experimental studies  
300 (Fig. 3E) (Lefevre *et al.* 2015; Rosa *et al.* 2013). On its own, the magnitude of primary extinction  
301 from climate warming and associated physiological stresses depends on the amount of habitat  
302 loss beyond which a species can no longer sustain a viable population (i.e., the extinction  
303 threshold) (Penn *et al.* 2018; Penn & Deutsch 2022; Urban 2015), even if population decline takes  
304 a long time to occur. Extinction thresholds may vary across species, but the average value at the  
305 global ecosystem level has been estimated from comparison of end-Permian model simulations  
306 to the fossil record, and assuming a similar loss of habitat that drove extinctions in the past would  
307 apply in the modern ocean (Penn & Deutsch 2022). Calibration of this parameter from the fossil  
308 record has recently been used to project future extinction risk from climate changes resembling  
309 those of the end-Permian, which are arising today due to accelerating anthropogenic greenhouse  
310 gas emissions (Fig. 5).

311  
312

### 313       3.3 Example: Food Webs

314  
315 Terrestrial paleo-community dynamics are usually modeled according to trophic ecology and body  
316 size to investigate the role of food-web topology in the propagation of disruptions caused by  
317 environmental change. Models of extinction cascades suggest that responses can be complex,  
318 resulting from both bottom-up and top-down effects (Kaneryd *et al.* 2012), with debate about  
319 whether simple or complex communities are more susceptible to such cascades and whether

320 trophic *versus* other ecological interactions are most important (Donohue *et al.* 2017; Eklöf &  
321 Ebenman 2006). Explicit consideration of extinction cascades during mass extinctions has  
322 generally focused on the consequences of collapse in primary production (Tappan 1968; Vermeij  
323 2004). Bottom-up models predict extinction of smaller-bodied species in both the marine and  
324 terrestrial realms, due to the correlation of body size with trophic level, and exacerbated paleo-  
325 community instability post-extinction, which are consistent with investigations conducted on  
326 patterns of selectivity in relation to body size (de Visser *et al.* 2011; Dunne *et al.* 2002; Dunne &  
327 Williams 2009; Lotze *et al.* 2011; Roopnarine 2006; Roopnarine *et al.* 2007). Interestingly, the  
328 end-Cretaceous mass extinction, for which we have the strongest evidence for collapse of primary  
329 production, is associated with preferential extinction of larger-bodied species in some clades  
330 (Friedman 2009; Longrich *et al.* 2012) but not with the preferential extinction of smaller-bodied  
331 species, suggesting that physiology or other ecological factors (including top-down extinction  
332 cascades) were important in determining survivorship.  
333

334 Two challenges remain in the modeling of extinction via networks of ecological interactions. First,  
335 evidence that “primary” extinctions may often occur via environmental change that exceeds the  
336 physiological tolerance limits of species at many positions in the food web creates a need for  
337 further investigation of how food webs respond to such losses. Are extinction cascades more, or  
338 less, extensive when driven by primary extinctions occurring simultaneously at multiple trophic  
339 levels? Second, there is the challenge of integrating physiological and ecological models such  
340 that the full response of the marine or terrestrial ecosystem could be predicted in an integrated  
341 manner from the modeling of climate change to the loss of species that cannot physiologically  
342 tolerate the modified world, to the loss of species that depended on ecological interactions with  
343 species lost via primary extinctions (Fig. 4). Differences in timescale and level of biological  
344 organization at which physiological and ecological processes dominate add to this challenge.  
345

#### 346 4. APPLICATION TO THE SIXTH EXTINCTION

#### 347

348 Mass extinction events provide our best source of information regarding the response of the  
349 biosphere to planetary-scale environmental disruption and the timescales and mechanisms of  
350 subsequent recovery. This information may be particularly important for the oceans, where  
351 observing biological response to environmental change is challenging and where the fossil record  
352 is particularly complete and diverse. Since the industrial revolution, the oceans have experienced  
353 substantial changes in ocean biogeochemistry, mainly because of rapid injection of CO<sub>2</sub> into the  
354 atmosphere from anthropogenic sources. Under the accelerating future anthropogenic emissions  
355 scenario consistent with historical trends (Fig. 5C), the oceans are expected to warm by 4-5 °C  
356 and pH is expected to decrease, on average, by 0.44 pH units by the end of the 21<sup>st</sup> century, with  
357 changes increasing even further over the next few centuries (Fig. 5E, N) (Kwiatkowski *et al.* 2020).  
358 High temperatures are also expected to reduce the ocean’s oxygen content while also altering  
359 nutrient cycles (Sweetman *et al.* 2017). Unabated anthropogenic emissions could drive the  
360 oceans toward widespread oxygen deficiency over the rest of the 21<sup>st</sup> century and beyond (Fig.  
361 5H) (Breitburg *et al.* 2018).  
362

363 Such changes would have drastic consequences for marine ecosystems as evident from declining  
364 fish stocks, expansion of marine dead zones and reduced primary productivity across different  
365 parts of the globe (Fig. 5K) (Blanchard *et al.* 2012). Efforts are already underway to project  
366 changes in species' ranges and abundances in response to climate change on land and in the  
367 oceans (Chen *et al.* 2011; Cheung *et al.* 2009; Pinsky *et al.* 2020; Thuiller 2004). Extrapolating  
368 results from experiments and field observations over days or years to timescales of centuries,  
369 millennia, and beyond is challenging because different processes may dominate the biospheric  
370 response on different timescales, although there is emerging evidence that responses to some  
371 stresses are concordant across timescales (Reddin *et al.* 2020). Furthermore, the primary phase  
372 of extinction, dominated by physiology, may give way over time to a secondary phase of  
373 extinction, dominated by the effects of changing ecological interactions. Connecting the  
374 physiological and ecological processes driving extinction remains a research frontier.  
375

376 Studies from the fossil record show that the ecophysiological constraints on marine taxa due to  
377 global warming and ocean deoxygenation will exert a key role in determining their risk to extinction  
378 under current and future emissions scenarios. The fossil record can even be used to calibrate the  
379 Earth system models used to predict future extinctions and changes in geographic range, just as  
380 paleoclimate records are used to calibrate models providing climate projections (Zhu *et al.* 2022).  
381 Under a high emissions scenario (Fig. 5C) the marine biological richness could be reduced to  
382 65% of its current state due to global warming and oxygen loss from oceans by 2300 (Penn &  
383 Deutsch 2022). The combined climate-ecophysiological models indicate that the local loss of  
384 species is expected to be the highest in tropical to temperate regions where taxa are expected to  
385 undergo a significant loss of aerobic habitat at their warm/low-O<sub>2</sub> range boundaries. In contrast,  
386 in terms of global habitat loss and extinction risk, the equatorial taxa are expected to fare better  
387 overall in low oxygen and warmer oceans compared to polar species due to their higher tolerance  
388 limits to warm climates and opportunities to expand their available habitats as the poles become  
389 more like the present-day tropics. This scenario has precedent in the fossil record with the end-  
390 Permian mass extinction where a similar latitudinal extinction pattern unfolded (Fig. 5A, B) (Penn  
391 *et al.* 2018; Reddin *et al.* 2019). Further work to integrate the effects of changes in pH, pCO<sub>2</sub>,  
392 salinity, and other key environmental variables into physiological performance models has the  
393 potential to make these models more general and accurate in reconstructing the causes of past  
394 extinction and predicting the consequences of future global change.  
395

396 The ecological functions disrupted by global warming and marine defaunation are also bound to  
397 have cascading effects which could lead to extinction of vulnerable taxa. Modeling such effects is  
398 challenging due to the complexity of the interactions involved. The fossil record is our only source  
399 of data on the effects of major environmental disturbance at global scale. Fortunately, calibration  
400 of environmental change to physiologically expected extinction is becoming possible due to  
401 parallel advances in geochemistry, Earth system modeling, and physiological experimentation.  
402 The next decade will require integration of food webs and other types of ecosystem models to  
403 extract the full value of the lessons from Earth's past in forecasting and guiding its future.  
404

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408

#### 409 AUTHOR CONTRIBUTION STATEMENT

410 All authors contributed to the conceptualization, original draft preparation, review, and editing of  
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412

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416

#### 417 CONFLICT OF INTEREST STATEMENT

418 Conflicts of Interest: None.

419

#### 420 DATA AVAILABILITY STATEMENT

421 No data were collected or analyzed as part of this review paper.

422

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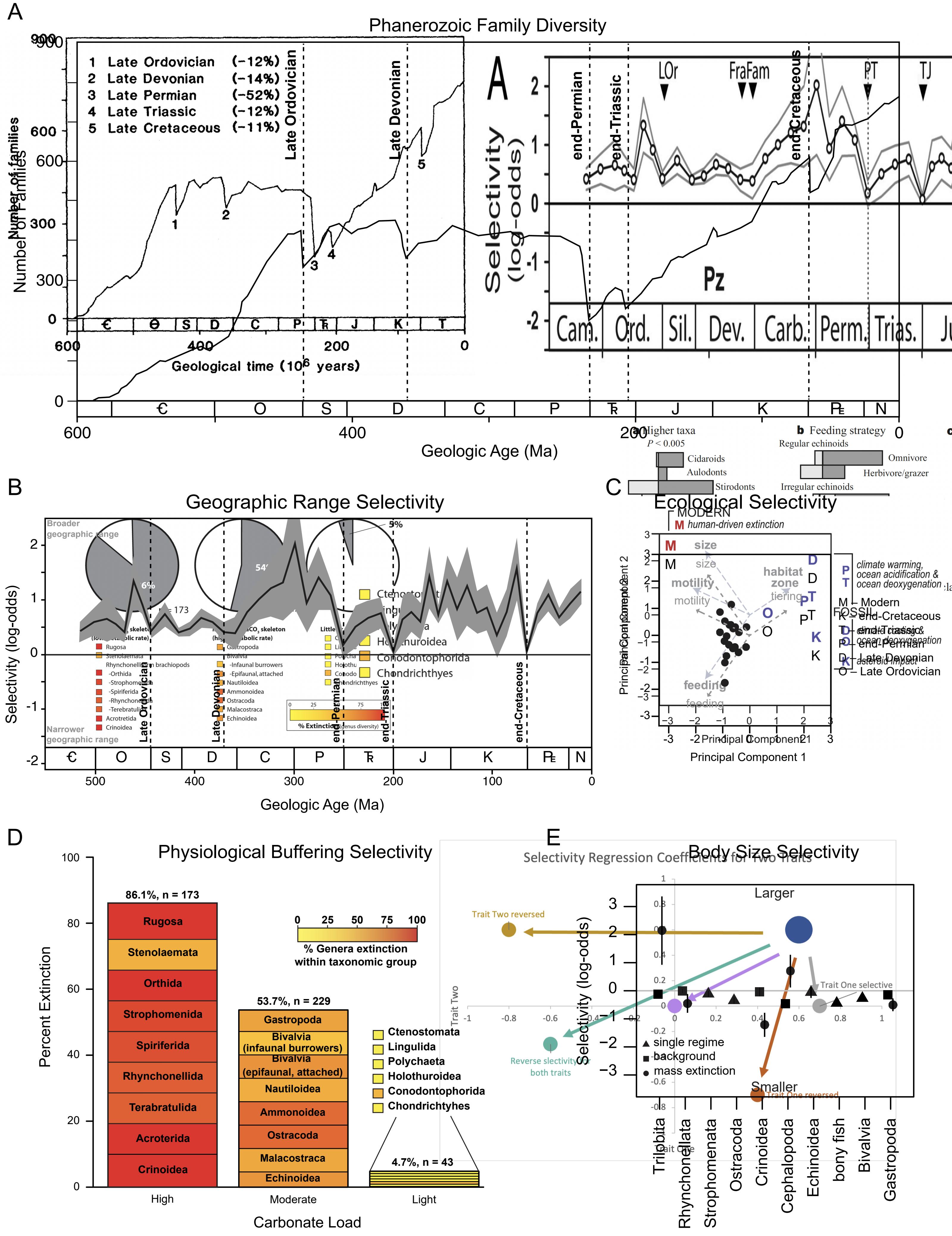
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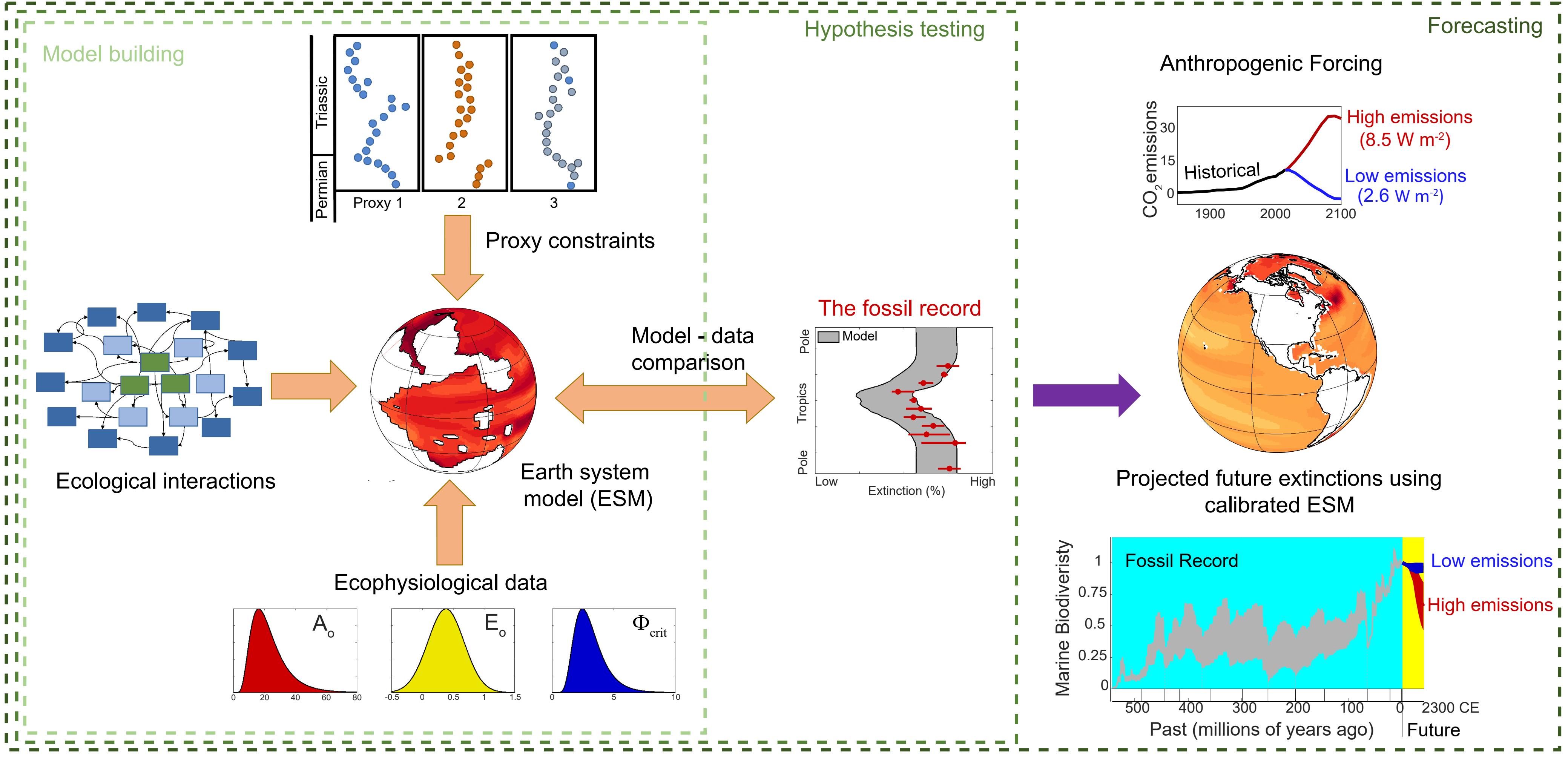
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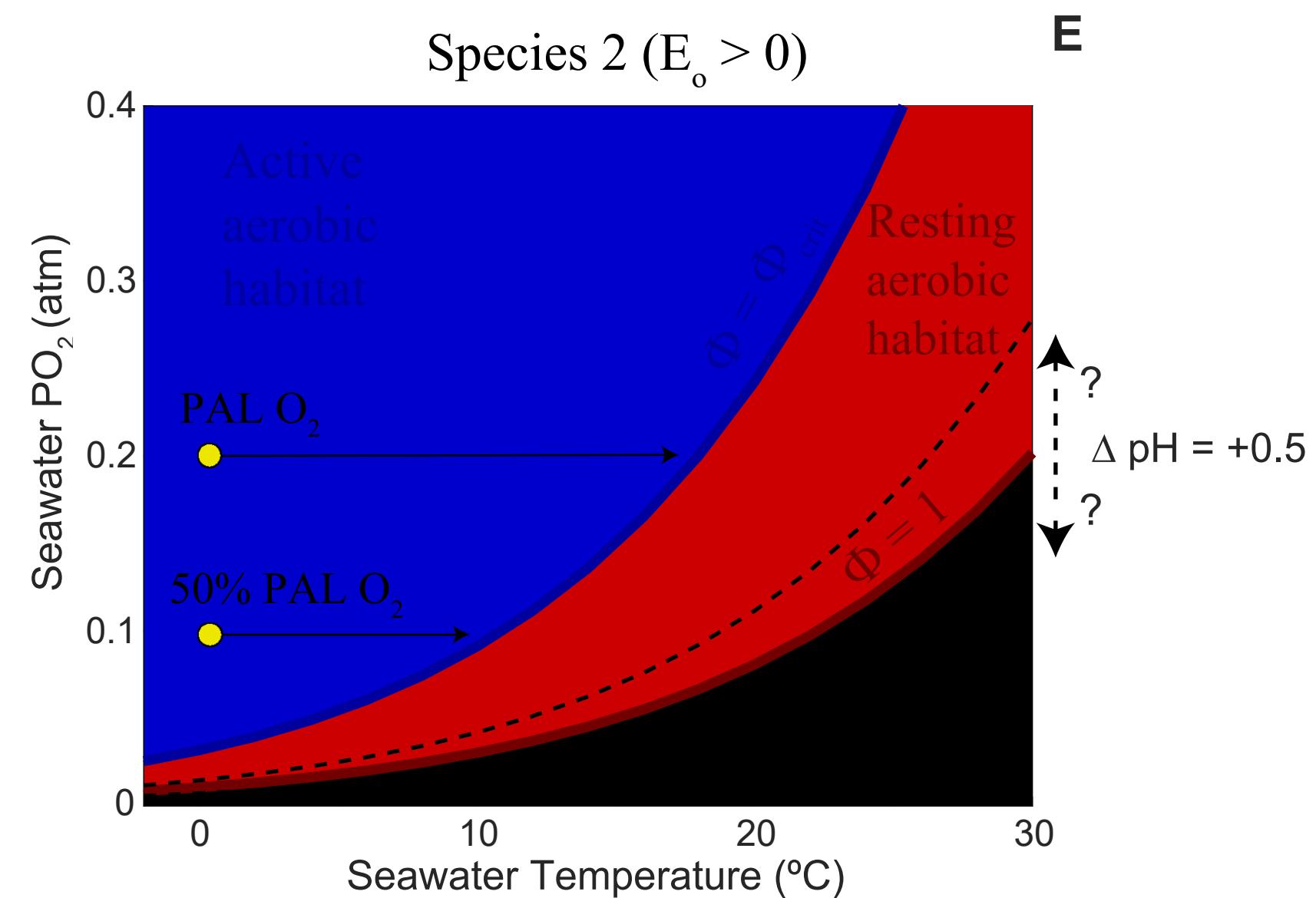
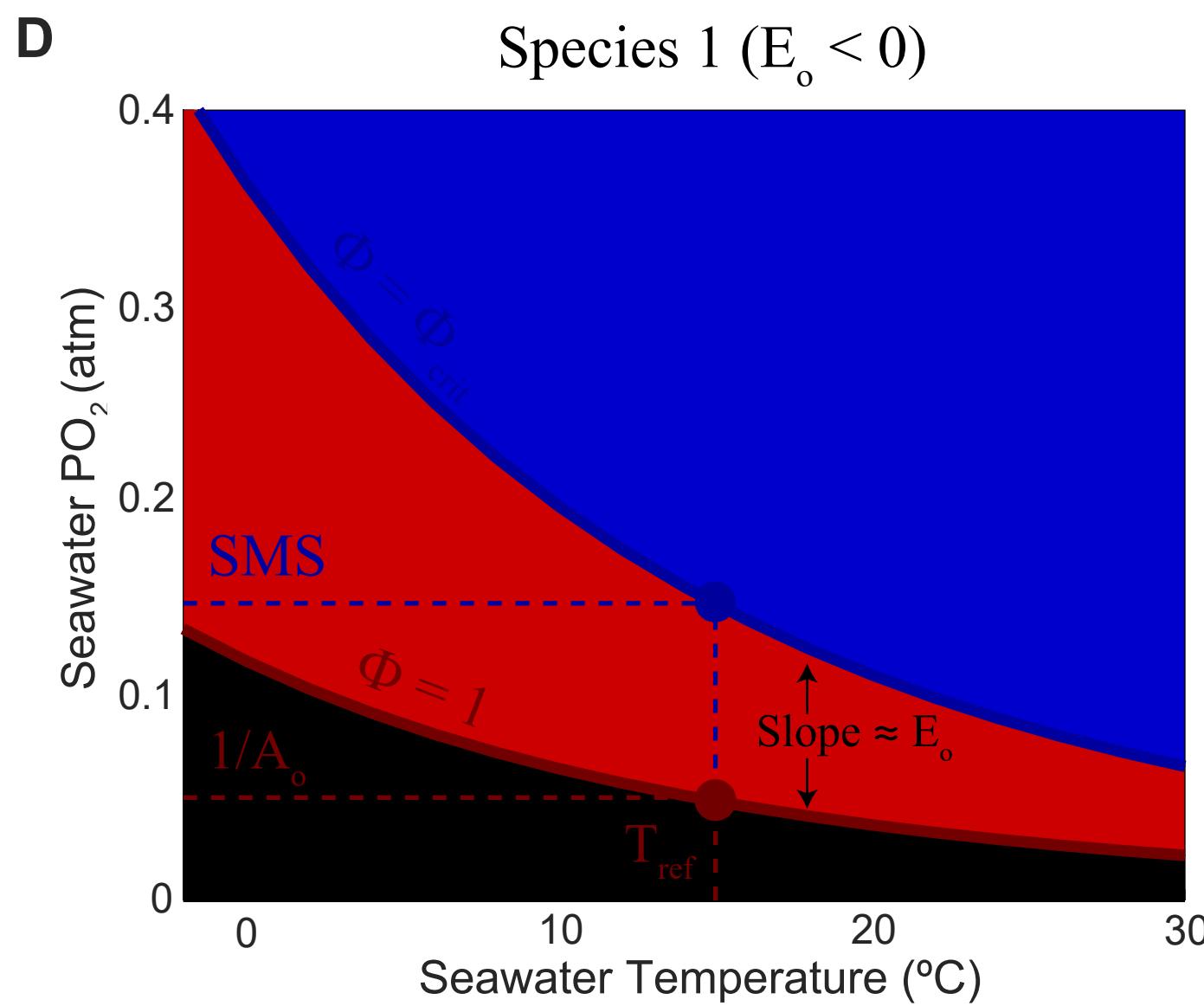
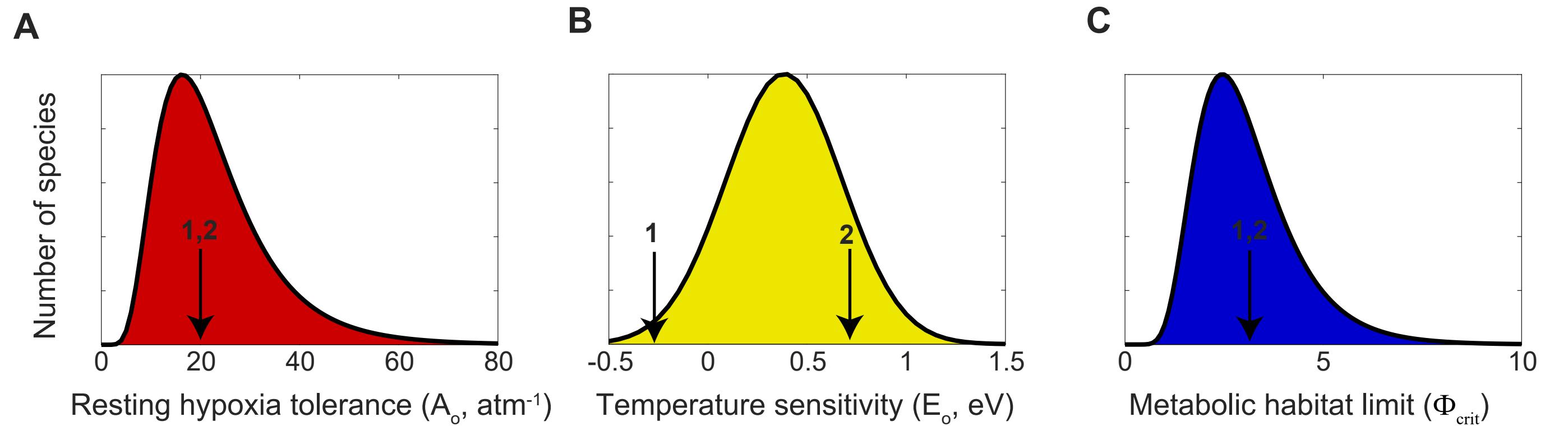
672 FIGURE CAPTIONS  
673674 **Figure 1. Extinction patterns in the fossil record.** A) Graph of marine animal diversity across  
675 the past 600 million years, illustrating the diversity declines associated with the five major  
676 mass extinction events (modified from Raup and Sepkoski, 1982). B) Extinction selectivity  
677 during the end-Permian mass extinction, illustrating the preferential extinction of heavily  
678 calcified marine animal classes with less complex respiratory and circulatory systems  
679 (modified from Knoll et al. 2007 and Knoll and Fischer 2011). C) Extinction selectivity with  
680 respect to geographic range, illustrating the preferential survival of broadly distributed genera  
681 during background intervals and the greatly reduced selectivity during mass extinction  
682 events (modified from Payne and Finnegan 2007). D) Principal components analysis of  
683 logistic regression coefficients of ecological traits and body size selectivity of the Big Five  
684 mass extinction events and the modern oceans, demonstrating the unique selectivity of the  
685 modern extinction threat (modified from Payne et al. 2016). E) Extinction selectivity with  
686 respect to body size for major classes of marine animals, illustrating the general bias of  
687 background extinction against smaller-bodied genera *versus* the variable direction of  
688 selectivity for classes that exhibit distinct patterns during mass extinction (modified from  
689 Monarrez et al. 2021).  
690  
691692 **Figure 2.** Workflow illustrating the use of geological and geochemical data to constrain Earth  
693 system models (ESMs), physiological experiments to constrain parameters used to  
694 populate models with species of different ecophysiotypes, and fossil occurrence data to  
695 conduct model-data comparison. Ecosystem structure remains to be incorporated into  
696 such models and can be used to predict extinction cascades. Calibration of models against  
697 selectivity patterns in ancient extinction events will improve their use in forecasting biotic  
698 response to current and future environmental change. Panels on right showing CO<sub>2</sub>  
699 emissions curves and future biodiversity projections are from Penn and Deutsch (2022).  
700  
701702 **Figure 3. Graphs illustrating the key species traits of the Metabolic Index ( $\phi$ ) along with**  
703 **how  $\phi$  relates to temperature and oxygen partial pressure.** A-C) Frequency  
704 distributions of the Metabolic Index parameters for marine animals. D,E) Graphs of  
705 variation in  $\phi$  as a function of temperature and oxygen for species with negative (D) and  
706 positive (E) temperature sensitivities ( $E_o$ ) of hypoxia tolerance ( $A_o$ ), which is the inverse of  
707 the critical oxygen threshold (red circle) at a reference temperature ( $T_{ref}$ ), as derived from  
708 respirometry experiments. For species in a resting state, the aerobic habitat limit occurs  
709 when  $\phi = 1$ , but in the environment a species' activity level or Sustained Metabolic Scope  
710 (SMS) elevates the habitat limit to  $\phi_{crit}$ . For species with negative  $E_o$ , aerobic habitat  
711 availability increases with temperature, whereas for those with positive  $E_o$  (i.e., most  
712 species; panel B), aerobic habitat declines with warming. Changes in PO<sub>2</sub> has the potential  
713 to lower aerobic habitat availability, and thus the amount of warming a species can  
714 withstand, as exemplified for two scenarios of with different fractions of present  
715 atmospheric levels of O<sub>2</sub> (PAL; yellow dots and arrows). A change in CO<sub>2</sub> also has the  
716 potential to alter hypoxia tolerance, but the magnitude and direction of this effect is  
717 unknown across marine biota and is illustrated here from experimental data for a single  
718 species under  $\Delta$  pH = +0.5 (Rosa et al., 2013). Arrows in A-C denote species traits in D  
719 and E.  
720  
721722 **Figure 4. Hypothetical progression of a mass extinction highlighting sources of trait-**

723 **based and geographic selectivity and potential ecological amplification.** A) An initial  
724 distribution of species (or “ecophysiotypes”) defined by traits under selection by large-scale  
725 environmental conditions will likely result in systematic correlations between traits and  
726 geographic range. The range metric here can be considered overall range size (area,  
727 volume), or centroid (e.g., low latitude *versus* high latitude, shallow *versus* deep). B) The  
728 initial biota are subjected to climate perturbation that poses a direct stress through a  
729 reduction in fitness whose magnitude depends on species traits and on local climate  
730 trends. The resulting change in available habitat ( $\Delta H$ ; contours) presents an  
731 ecophysiological extinction risk that is geographically selective because it is trait selective  
732 (but may also be caused by climate patterns themselves). In this hypothetical case habitat  
733 loss ( $\Delta H < 0$ ) selects against species with high values of two traits (habitat “Losers”) and  
734 may even benefit species with low values of those traits (habitat “Gainers”;  $\Delta H > 0$ ). C)  
735 Physiological extinction poses further ecological risks (or advantages) depending on the  
736 mutualistic or adversarial interactions with ecophysiotypes (nodes in graph) that are under  
737 trait-selective risk. Ecological risk is complex and for any particular species will depend on  
738 the physiological risk faced by the other species with which it interacts, which may be  
739 positive (green lines) or negative (brown lines), and strong (thick lines) or weak (thin  
740 lines). The results of these associations, which may be multiple and indirect, could alter  
741 extinction risk by either preserving ecological fitness (“+” symbol) or reducing it (“-”  
742 symbol). Changes in extinction risk are likely to be most pronounced for those in the  
743 neutral zone whose antagonists go extinct or who are buoyed by prey/mutualists that are  
744 under positive selection. D) Post-extinction ecosystem, equal to the initial one (panel A)  
745 minus the ecotypes that have gone extinct from either primary (panel B) or secondary  
746 (panel C) effects.  
747

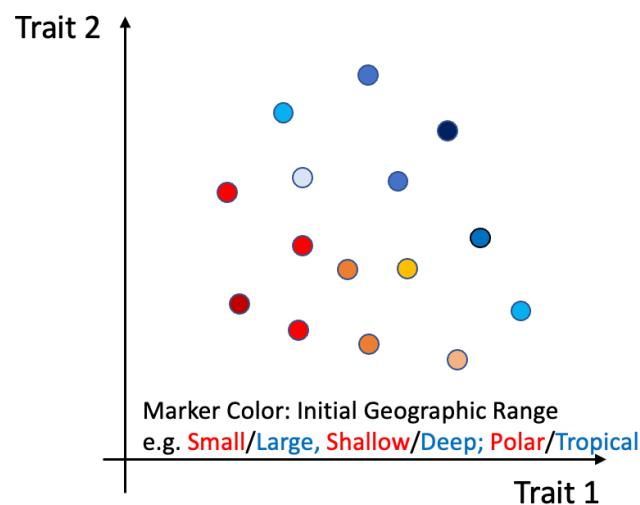
748 **Figure 5. Geographic patterns of extinction and ocean changes in Earth system model**  
749 **simulations of the end-Permian climate transition (left column) and under**  
750 **anthropogenic greenhouse gas forcing (C) to 2300 C.E. (middle column).** Line plot  
751 comparisons of end-Permian and potential future environmental changes *versus* latitude  
752 are shown in panels on the right (F,I,L,O). Model extinctions (A,B) are driven by ocean  
753 warming (D,E) and O<sub>2</sub> loss (G,H), as quantified through the Metabolic Index, and in (A)  
754 reproduce the latitudinal pattern from the fossil record of the end-Permian (red points).  
755 These primary extinctions have the potential to be amplified by other environmental  
756 stressors like changes in net primary productivity (NPP) (J,K) or pH (M,N) or through  
757 secondary extinctions via the food web. Shaded region in (A) shows uncertainty in end-  
758 Permian extinction magnitudes across a range of potential extinction threshold parameters.  
759 Solid line in (B) shows future extinction risk averaged across Earth system models, using  
760 an extinction threshold calibrated from the end-Permian (same as the solid line in A) (see  
761 Penn et al., 2022 for calibration details), while the shading in (B) shows the inter-model  
762 range. Future changes are projected under a high greenhouse gas emissions scenario,  
763 leading to a net radiative forcing of 8.5 W m<sup>-2</sup> in 2100 C.E. (C) and are relative to the pre-  
764 industrial era (1850-1900). Model fields are averaged over the upper 500 m, and for the  
765 future projections, they are averaged across Earth system models (n = 5). Model details  
766 are provided in Penn et al. (2018, 2022). Panels 5A and 5B,C are modified from Penn et  
767 al., (2018) and (2022), respectively.



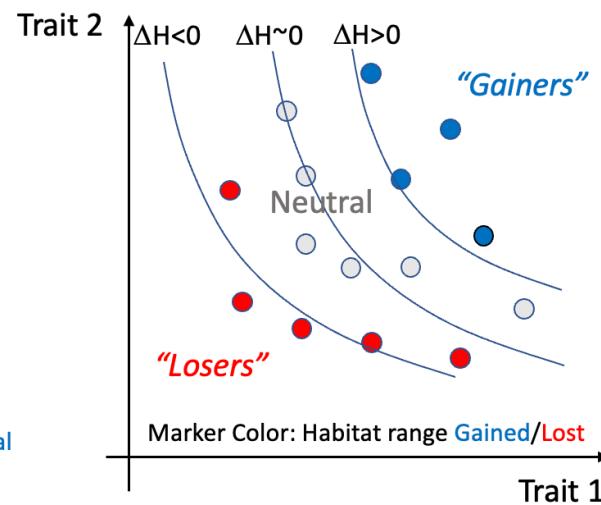




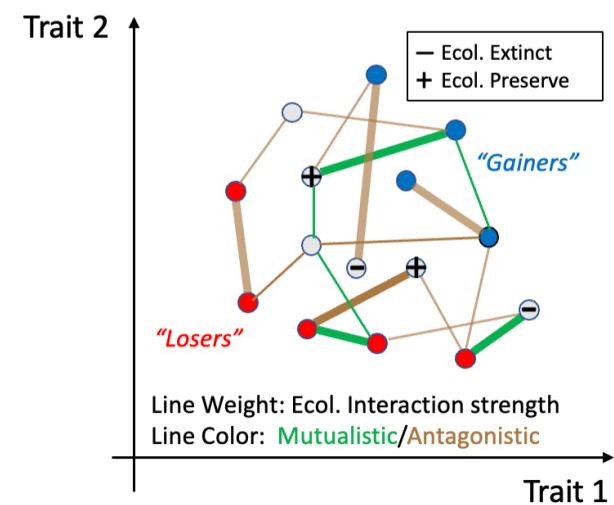
**A) Initial Climate/Ecosystem**



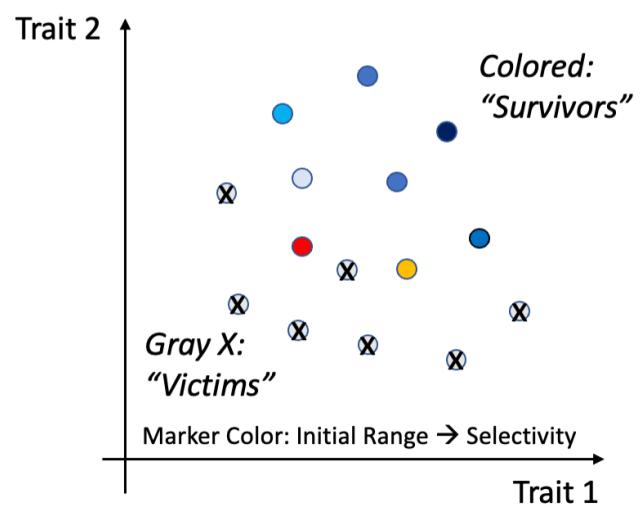
**B) Physiological Habitat Risk**

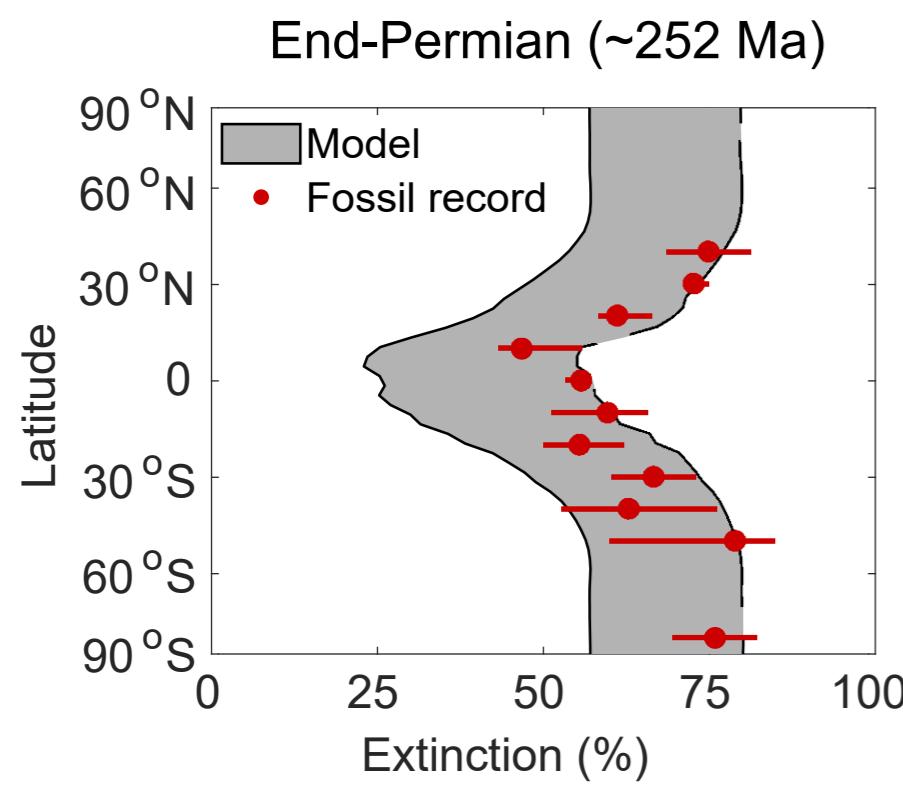
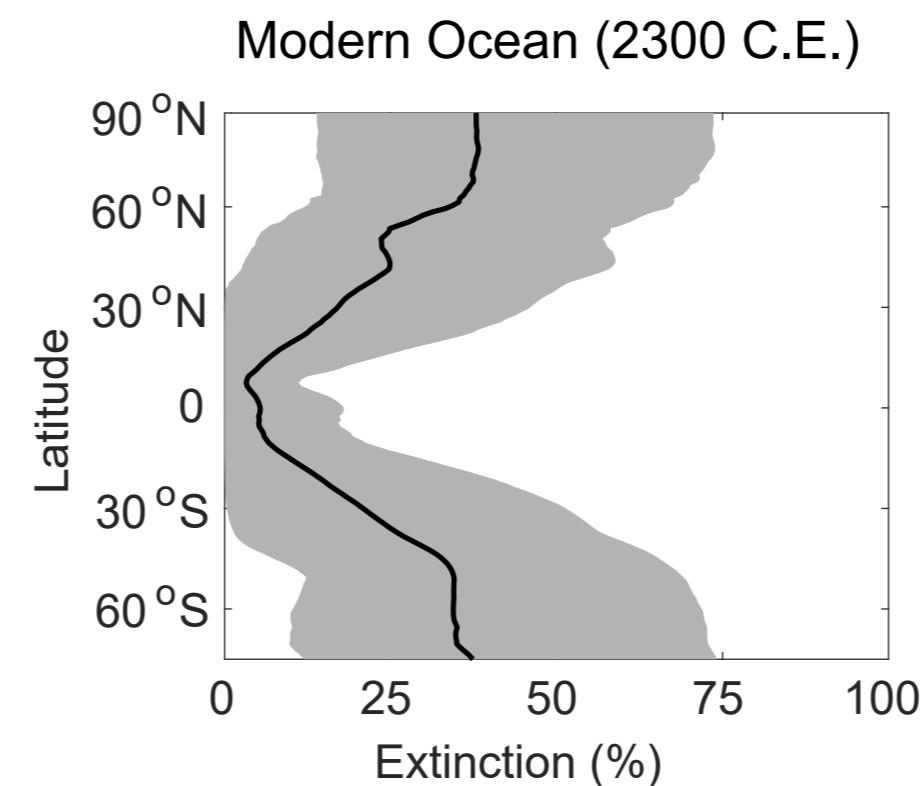
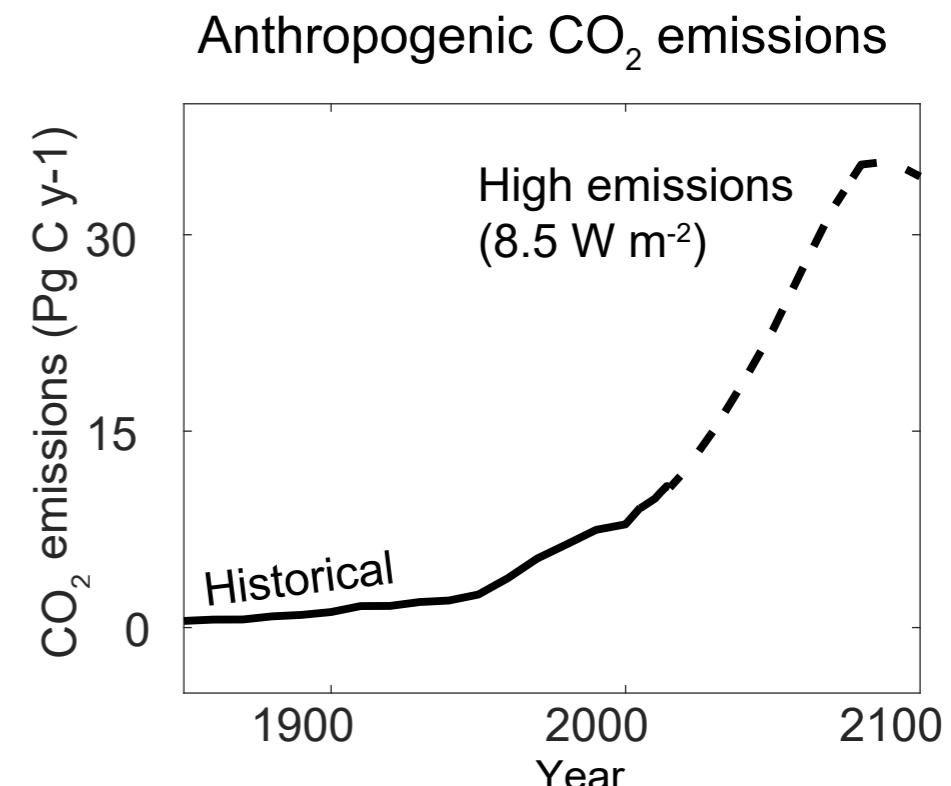
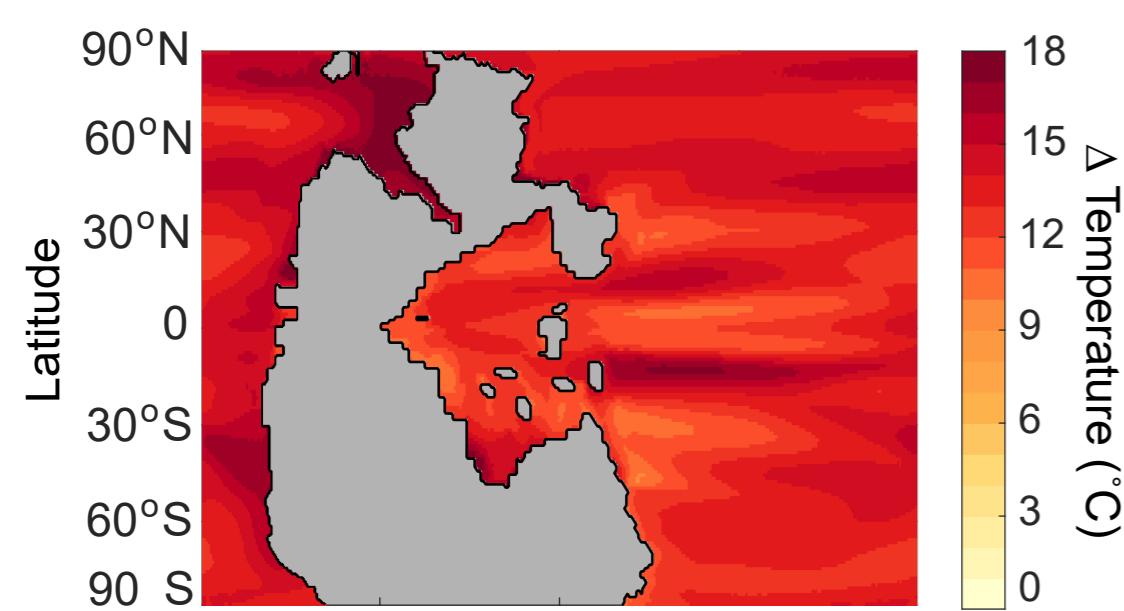
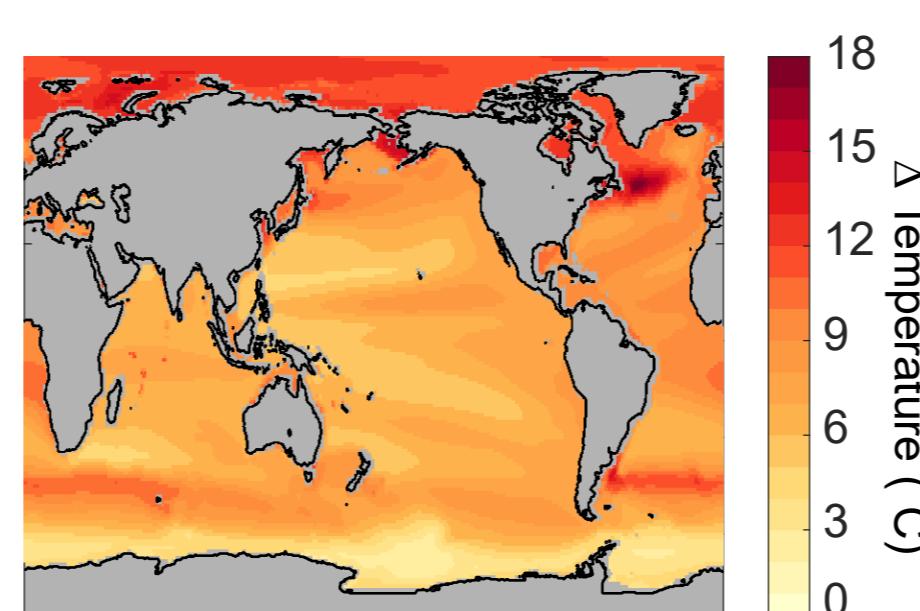
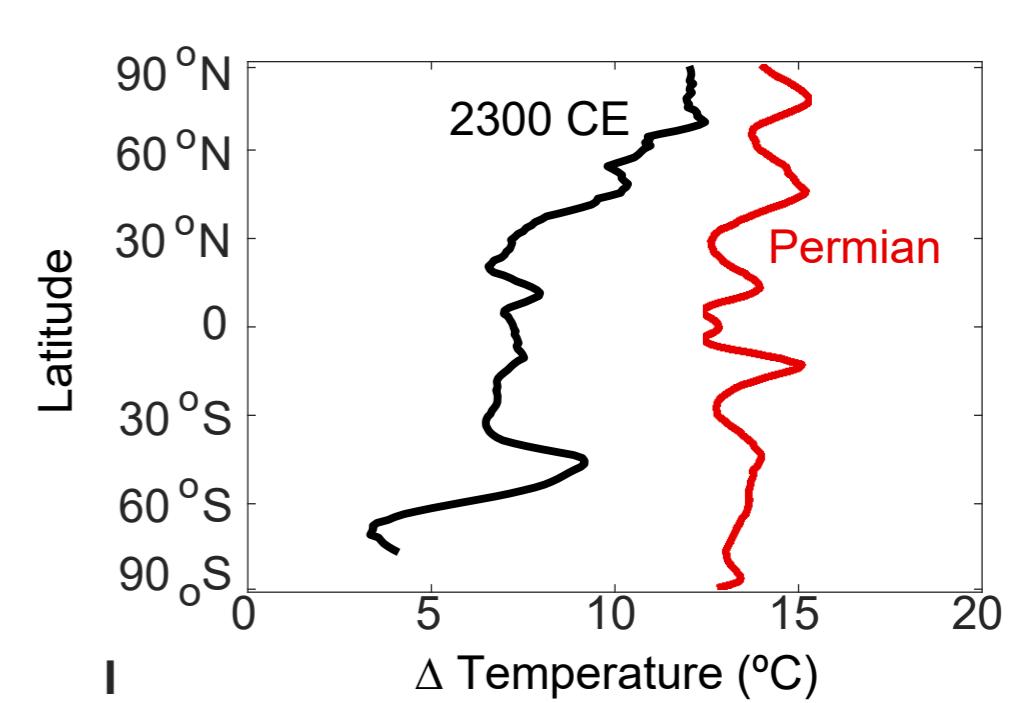
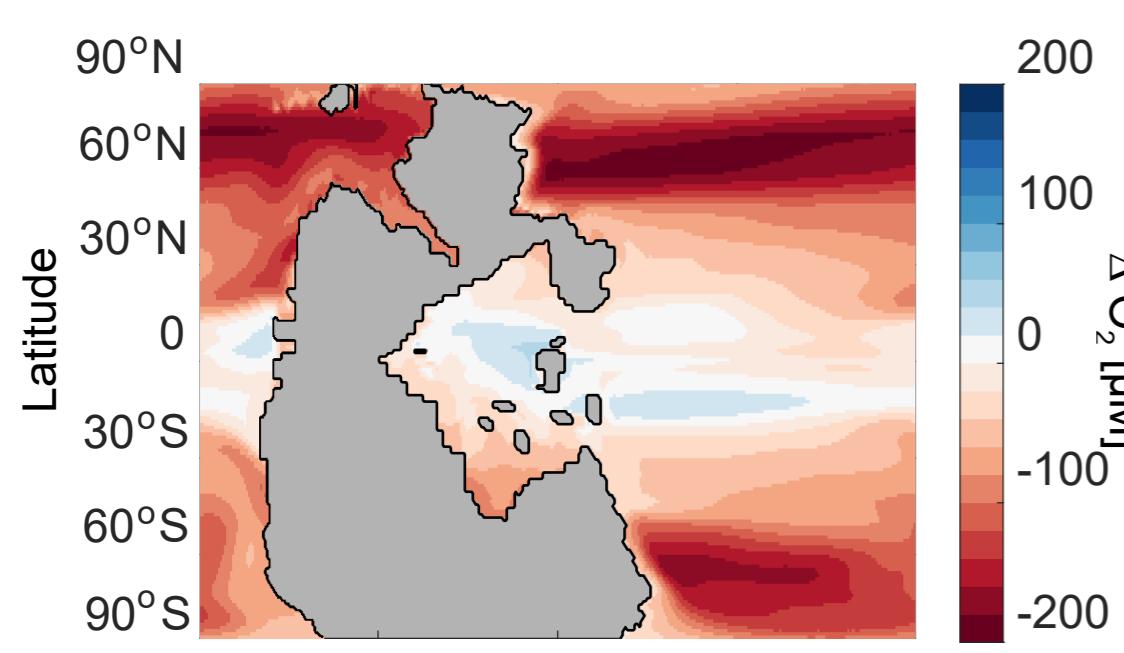
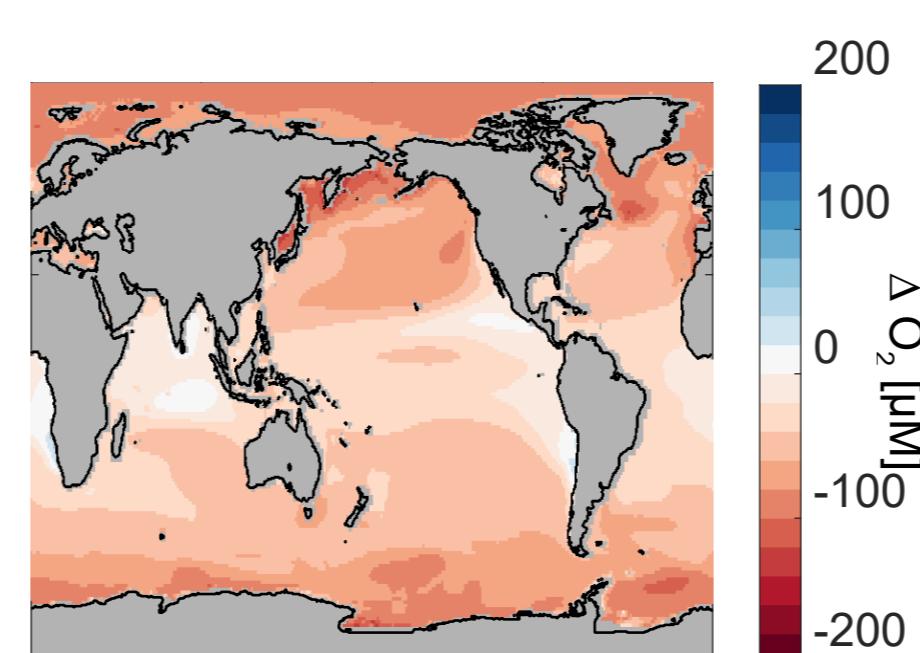
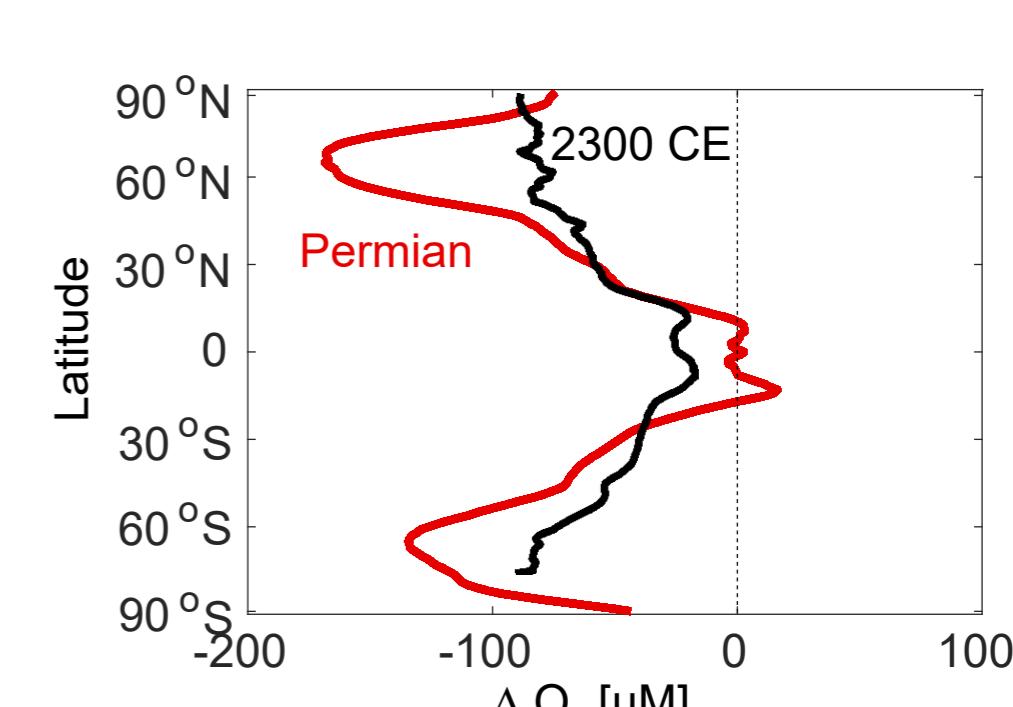
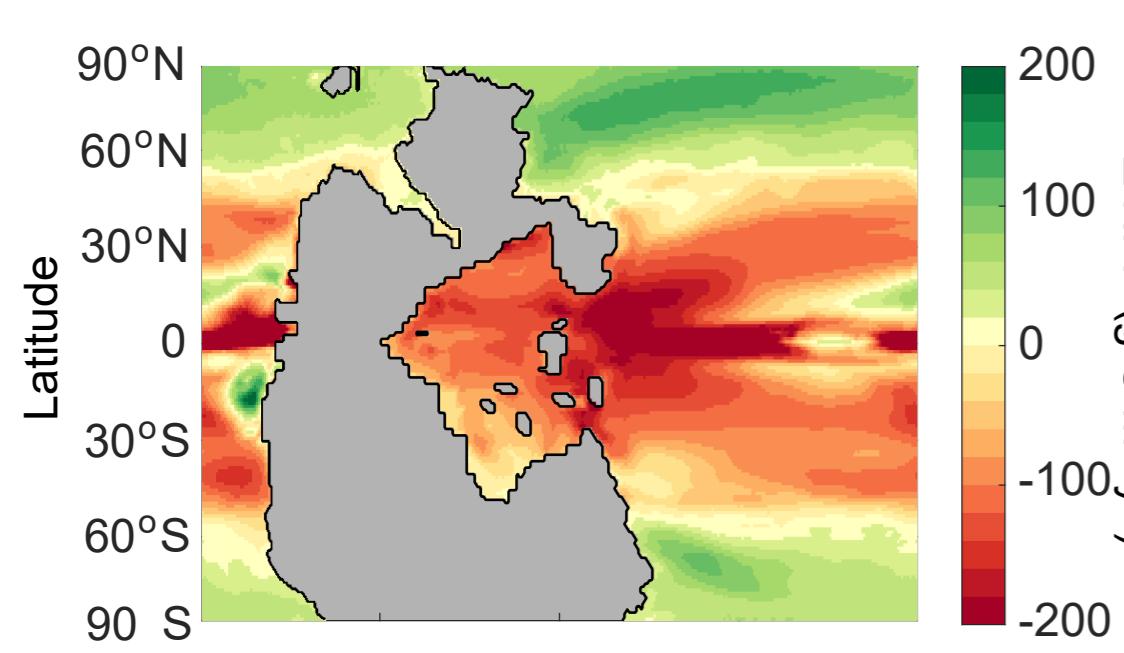
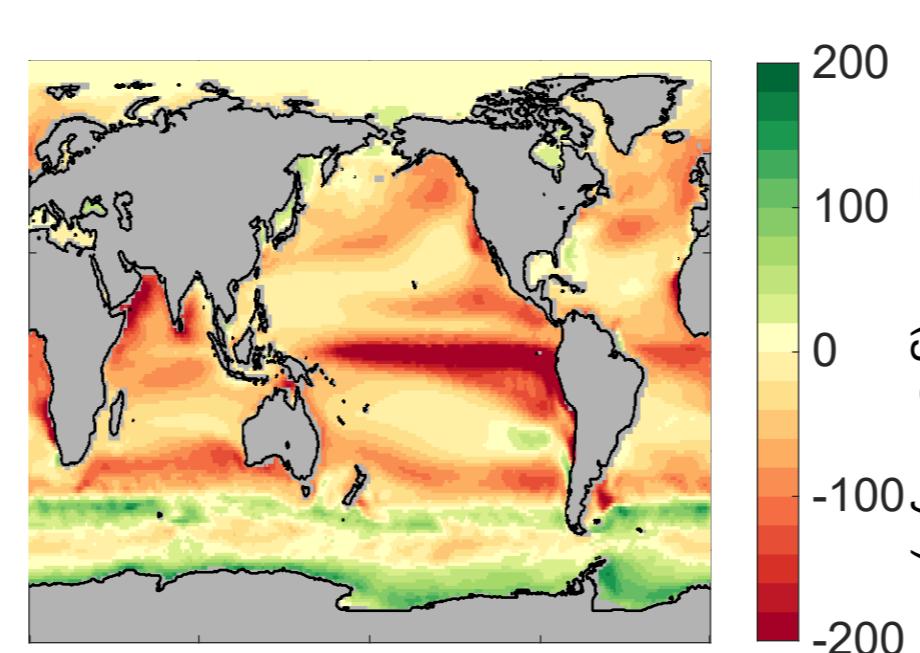
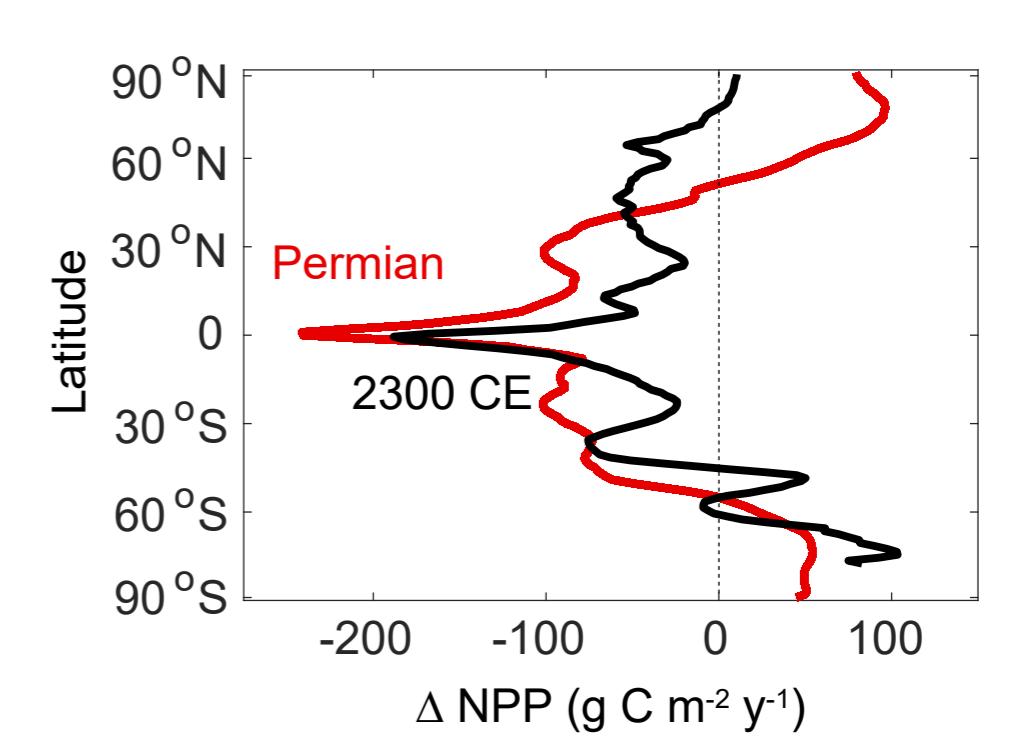
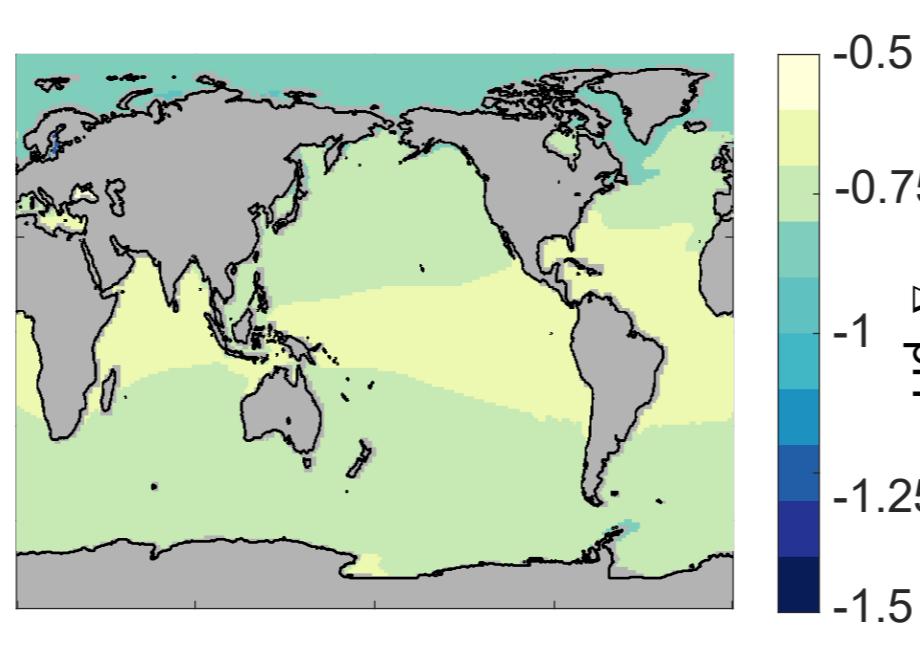


**C) Ecological Network Risk**



**D) Final Climate/Ecosystem**



**A****B****C****D****E****F****G****H****I****J****K****L****M****N****O**