

1 Selectivity of mass extinctions: patterns, processes, and future directions

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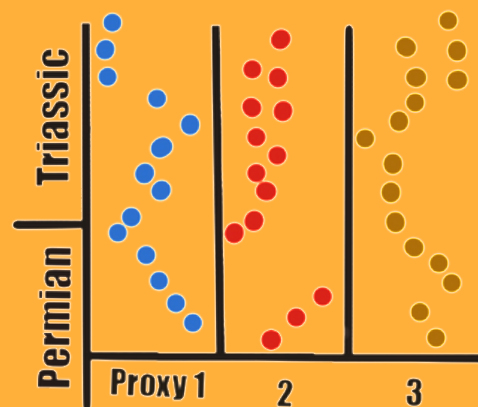
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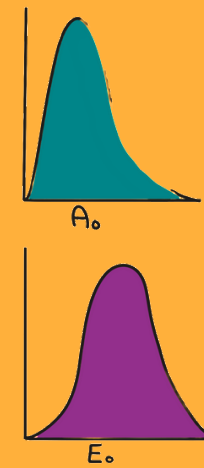
Geological evidence can reveal the physical and chemical changes that trigger mass extinctions, but differences in **biological traits** between victims and survivors provide key insights into actual **kill mechanisms**.

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.

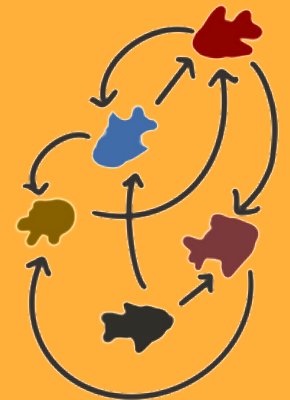
PROXY CONSTRAINTS



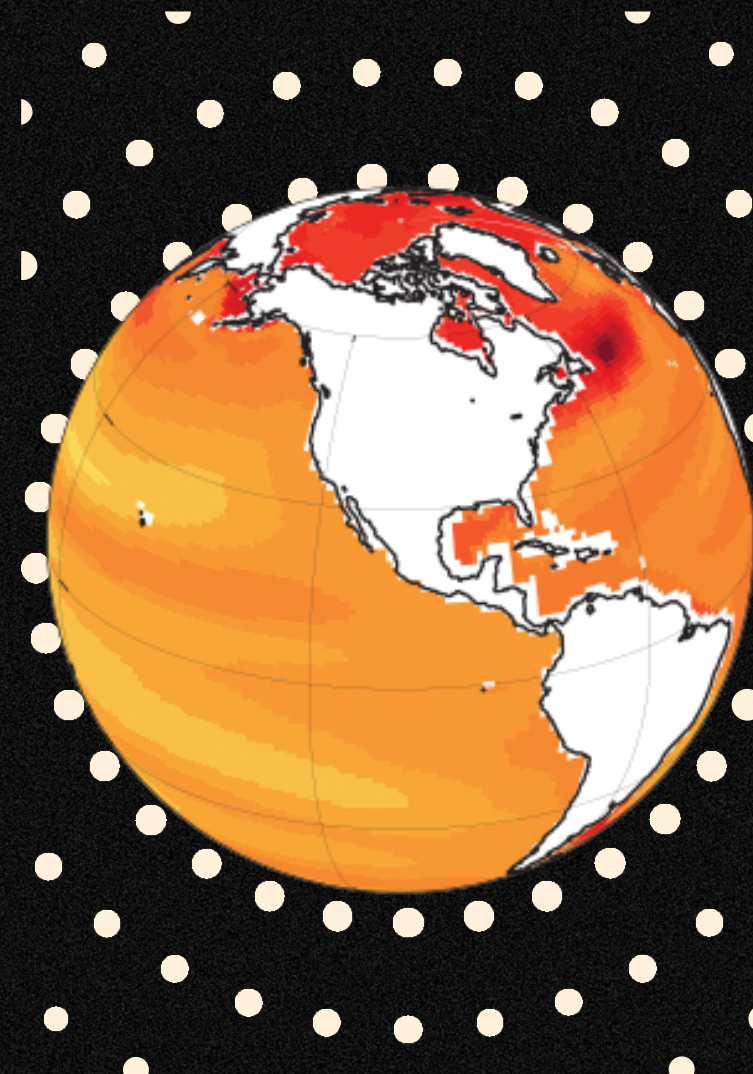
ECOPHYSIOTYPES



ECOLOGICAL CONSTRAINTS



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



IMPACT STATEMENT

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

ABSTRACT

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

KEYWORDS

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

SOCIAL MEDIA SUMMARY

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

1. INTRODUCTION

Earth is currently undergoing a biodiversity crisis on a scale unprecedented in the history of the human species (Barnosky *et al.* 2011; Dirzo *et al.* 2014; McCauley *et al.* 2015), but crises of similar or greater magnitude have occurred at least five times across the 600-million-year history of animal life (Fig. 1A) (Barnosky *et al.* 2011; Raup & Sepkoski 1982). All major mass extinction events are associated with evidence of rapid environmental change. In some cases, such as the end-Permian (252 million years ago [Mya]) and end-Triassic (201 Mya) mass extinctions, there is evidence for rapid and pronounced climate warming (Blackburn *et al.* 2013; Bond & Sun 2021; Burgess *et al.* 2014; Kiessling & Simpson 2011; Payne & Clapham 2012). By contrast, the Late Ordovician (443 Mya) and Late Devonian (372 Mya) extinctions occurred in association with climate cooling (Finnegan *et al.* 2011; Joachimski & Buggisch 2002). The end-Cretaceous extinction (66 Mya) was associated with an asteroid impact event whose aftermath resembled the consequences of a hypothetical global thermonuclear war (Pollack *et al.* 1983; Turco *et al.* 1983). Due to the magnitude and global scale of the current “Sixth” extinction, these events from Earth’s past provide historical reference points for predicting the long-term magnitude, ecological impact, and recovery timescale from the current crisis or other, potential, human-mediated catastrophes.

While mass extinctions have been identified in the fossil record based largely on the magnitude of diversity loss across many higher taxa (Newell 1963, 1967; Raup & Sepkoski 1982), causal inference has relied more on geological and geochemical evidence of potential triggers (Alvarez *et al.* 1980; Finnegan *et al.* 2011; Svensen *et al.* 2009) and patterns of extinction selectivity interpreted to reflect proximal kill mechanisms (Finnegan *et al.* 2012; Jablonski 1986; Jablonski & Raup 1995; Knoll *et al.* 1996, 2007; Penn *et al.* 2018; Sheehan & Hansen 1986; Smith & Jeffery 1998; Valentine & Jablonski 1986). Selectivity patterns have been assessed with respect to a wide range of traits (Fig. 1B-E), including geographic range (Dunhill & Wills 2015; Jablonski 1986; Kiessling & Aberhan 2007; Payne & Finnegan 2007), body size (Allen *et al.* 2019; Friedman 2009; Jablonski & Raup 1995; Longrich *et al.* 2012; Monarrez *et al.* 2021; Payne & Heim 2020), abundance (Lockwood 2003; Payne *et al.* 2011), larval ecology (Valentine & Jablonski 1986), diet (Wilson 2013), functional ecology (Bambach *et al.* 2002; Hughes *et al.* 2021; Payne *et al.* 2016b), environmental breadth (Jablonski & Raup 1995), respiratory and circulatory anatomy (Clapham 2017; Knoll *et al.* 1996, 2007), and shell mineralogy (Clapham & Payne 2011; Kiessling & Simpson 2011).

Extinction selectivity provides our most direct evidence of proximal kill mechanisms (Raup 1986), but to date most testing of observed extinction patterns against hypothesized kill mechanisms has been semi-quantitative, focused on establishing consistency between predicted and observed directions of selectivity under various hypothesized kill mechanisms. Recently, advances in paleontological databases, geochemical proxies, physiological experiments, and Earth system and ecosystem models have enabled the comparison of observed and predicted extinction patterns within quantitative, self-consistent frameworks (Fig. 2) (Penn *et al.* 2018). Although quantitative model-data comparison between observed and predicted extinction patterns is still in its early days, the door for direct comparison of past and future biotic response to climate change is now open, increasing the value of the fossil record in the mitigation of the current biotic crisis.

2. PATTERN

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

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

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

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

Some mass extinction events exhibit selectivity patterns that can be mapped onto respiratory and circulatory anatomy, potentially reflecting underlying differences in susceptibility to metabolic stress from hypercapnia, anoxia, climate warming, or their interactive effects. For example, the end-Permian mass extinction preferentially affected heavily calcified marine animal genera with limited respiratory and circulatory systems (Fig. 1B), suggesting a role for hypercapnia and/or direct and indirect fitness effects of acidification on shell dissolution (Calosi *et al.* 2017) in driving the extinction (Knoll *et al.* 1996). At the same time, the lack of sophisticated oxygen supply mechanisms would also make these taxa more sensitive to temperature-dependent hypoxia (Deutsch *et al.* 2020; Endress *et al.* 2022) and metabolic differences among groups likely influence taxonomic selectivity patterns from changes in CO₂, temperature, and O₂. Similar patterns as seen in the end-Permian apply to other extinction events, including the end-Triassic mass extinction (Clapham 2017; Kiessling & Simpson 2011), consistent with shared kill mechanisms. By contrast, the end-Cretaceous mass extinction exhibits the opposite pattern, with taxa thought to be more sensitivity to ocean acidification surviving preferentially (Kiessling & Simpson 2011), potentially reflecting differences in extinction patterns triggered primarily by volcanism *versus* impact events. The extent to which these patterns stand out from background extinction remains incompletely studied. A study controlling for differences between benthic *versus* planktonic and nektonic taxa indicates that many background intervals show the same selectivity, often of similar magnitude (Payne *et al.* 2016a). As discussed below, results of physiological experiments on living relatives of species in the fossil record are enabling quantitative prediction of biological response to past environmental changes inferred from geological and geochemical proxies. This is currently an area of rapid progress.

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

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

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

3. PROCESS

3.1 Introduction

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

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

3.2 Example: Metabolic Index

One promising avenue for examining physiological kill mechanisms for ancient extinction events is the Metabolic Index, which was initially developed to test whether the biogeographic distributions of species are physiologically limited by O₂ supply and demand in the modern ocean (Deutsch *et al.* 2015). This ecophysiological model quantifies habitat viability for a species, in terms of its ability to carry out aerobic respiration, by taking a ratio of environmental oxygen supply to biological oxygen demand as a function of temperature and taxon-specific metabolic and O₂ supply traits (Eq. 1). The metabolic energy demands of water-breathing marine animals increase with water temperature and body size (Gillooly *et al.* 2001), raising corresponding biological O₂ requirements. Temperature and body size also impact the rates of organismal O₂ supply through diffusion, ventilation, and internal circulation (Deutsch *et al.* 2022; Endress *et al.* 2022), while

warmer water holds less ambient O₂. The ratio of temperature and body size (B)-dependent rates of potential O₂ supply and organismal metabolic demand, termed the Metabolic Index (Φ), quantifies the metabolic viability of a habitat for a given species:

$\Phi = A_0 B^\varepsilon pO_2 \exp \left(-\frac{E_0}{k_B T} - \frac{1}{T_{0\&}} \right)$	Eq. 1
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where A_0 (atm⁻¹) is the ratio of O₂ supply to resting demand rate coefficients, or hypoxia tolerance at a reference temperature and body size (B), with allometric scaling exponent ε and Arrhenius temperature sensitivity, E_0 (eV), and pO_2 and T are the oxygen partial pressure and temperature of ambient water, respectively (Fig. 3) (Deutsch *et al.* 2015, 2020). These physiological traits and their distributions across taxa can be estimated from critical oxygen thresholds in respirometry experiments conducted for diverse marine biota over the past half century (Chu & Gale 2017; Rogers *et al.* 2016). Critical oxygen thresholds define the Metabolic Index to be 1 (i.e., $\Phi = 1$), allowing the traits to be estimated for organisms in a resting state under laboratory conditions. In the environment, O₂ requirements are elevated by more strenuous activities important for population persistence, such as growth, reproduction, feeding, defense, or motion. These additional energy demands require the O₂ supply to be raised by a factor, Φ_{crit} , corresponding to sustained metabolic scope (Peterson *et al.* 1990). Stable aerobic habitat barriers thus arise in ocean regions where the Metabolic Index falls below Φ_{crit} , while the geographic positions of these barriers depend on the species' traits (Deutsch *et al.* 2020). The habitability of any given parcel of water can therefore be determined from the temperature and oxygen partial pressure given the species values of A_0 , E_0 , and Φ_{crit} . Earth system models can be populated with hypothetical species by drawing combinations of values from the trait distributions (Fig. 3). The promise of this framework for paleontological application is that trait distributions can be used to predict the patterns of biodiversity, providing a means for testing the model against the fossil record. Indeed, the observed tropical dip in marine species richness observed for diverse animal groups in the modern ocean (Chaudhary *et al.*, 2021) can be explained by aerobic habitat limitation implied by modern species Metabolic Index traits (Penn & Deutsch, 2022). Environmental temperature and oxygen concentration can be quantified using geochemical proxies for ancient events to calibrate Earth System models and body size can be measured from fossil specimens. In principle, ecological interactions can be further incorporated to model, allowing extinction cascades to be accounted for alongside direct, climate-driven habitat loss (Fig. 4).

During periods of climate warming, rising water temperatures can drive the metabolic O₂ demand above a supply declining from ocean deoxygenation, leading to the loss of available aerobic habitat, and eventually species extinctions at local and global scales (Penn *et al.* 2018; Reddin *et al.* 2020). At regional scales, such as in the California Current System, aerobic habitat changes have been linked to multi-decadal fluctuations of anchovy populations, including near-extirpation of larvae from portions of their range (Howard *et al.* 2020). At global scales, aerobic habitat loss under the climate change simulated for the end-Permian mass extinction predicted a geographic selectivity of extinction consistent with the fossil record (Fig. 5A): Extinction risk was greater for species inhabiting higher latitudes. This geographic selectivity arises because species previously occupying the tropics would already have been adapted to warm, low-O₂ conditions that became

more widespread, whereas polar habitat niches disappeared more completely (Penn *et al.* 2018). In contrast to the geographic selectivity predicted for warming, periods of global cooling, such as during the Late Ordovician, are expected to generate extinctions focused on the low latitudes (Saupe *et al.* 2020), consistent with the patterns observed for that mass extinction (Finnegan *et al.* 2012) and may also occur through aerobic habitat loss if accompanied by deoxygenation (Finnegan *et al.* 2016) or due to declining hypoxia tolerance in cold water in species with thermal optima (Boag *et al.* 2018; Endress *et al.* 2022). Aerobic habitat loss is also predicted to select against large-bodied species, with a strong variability within size classes that depends on a species' temperature sensitivity (Deutsch *et al.* 2022). Extinctions driven by aerobic habitat loss may also explain the amplified background extinction rates observed for the early Phanerozoic, because of dramatically lower atmospheric O₂ levels and thus species living closer to their ecophysiological limits (Stockey *et al.* 2021). Trait adaption to different past climate states (Bennett *et al.*, 2021) has the potential to buffer or amplify predicted extinction risks. The role of differences in ecophysiological traits across taxonomic groups in explaining observed patterns of extinction selectivity across higher taxa (Knoll *et al.* 1996, 2007) remains an open area of research.

Primary extinctions driven by the loss of aerobic habitat have the potential to be amplified by secondary extinctions arising from food web effects (Fig. 4) or co-occurring environmental stressors that exacerbate direct aerobic habitat loss (Fig. 5J-O). Aerobically tolerant species could still be lost if they are ecologically tied to vulnerable ones, for example through the food web (Fig. 4) or other critical interactions. Ocean acidification (Fig. 5M,N,O) has the potential to further deplete aerobic habitat through direct CO₂ effects on critical oxygen thresholds, but the magnitude and direction of this effect is uncertain and variable across limited available experimental studies (Fig. 3E) (Lefevre *et al.* 2015; Rosa *et al.* 2013). On its own, the magnitude of primary extinction from climate warming and associated physiological stresses depends on the amount of habitat loss beyond which a species can no longer sustain a viable population (i.e., the extinction threshold) (Penn *et al.* 2018; Penn & Deutsch 2022; Urban 2015), even if population decline takes a long time to occur. Extinction thresholds may vary across species, but the average value at the global ecosystem level has been estimated from comparison of end-Permian model simulations to the fossil record, and assuming a similar loss of habitat that drove extinctions in the past would apply in the modern ocean (Penn & Deutsch 2022). Calibration of this parameter from the fossil record has recently been used to project future extinction risk from climate changes resembling those of the end-Permian, which are arising today due to accelerating anthropogenic greenhouse gas emissions (Fig. 5).

3.3 Example: Food Webs

Terrestrial paleo-community dynamics are usually modeled according to trophic ecology and body size to investigate the role of food-web topology in the propagation of disruptions caused by environmental change. Models of extinction cascades suggest that responses can be complex, resulting from both bottom-up and top-down effects (Kaneryd *et al.* 2012), with debate about 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 CO₂ 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 21st 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 21st century and beyond (Fig.
361 5H) (Breitburg *et al.* 2018).

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

Studies from the fossil record show that the ecophysiological constraints on marine taxa due to global warming and ocean deoxygenation will exert a key role in determining their risk to extinction under current and future emissions scenarios. The fossil record can even be used to calibrate the Earth system models used to predict future extinctions and changes in geographic range, just as paleoclimate records are used to calibrate models providing climate projections (Zhu *et al.* 2022). Under a high emissions scenario (Fig. 5C) the marine biological richness could be reduced to 65% of its current state due to global warming and oxygen loss from oceans by 2300 (Penn & Deutsch 2022). The combined climate-ecophysiological models indicate that the local loss of species is expected to be the highest in tropical to temperate regions where taxa are expected to undergo a significant loss of aerobic habitat at their warm/low-O₂ range boundaries. In contrast, in terms of global habitat loss and extinction risk, the equatorial taxa are expected to fare better overall in low oxygen and warmer oceans compared to polar species due to their higher tolerance limits to warm climates and opportunities to expand their available habitats as the poles become more like the present-day tropics. This scenario has precedent in the fossil record with the end-Permian mass extinction where a similar latitudinal extinction pattern unfolded (Fig. 5A, B) (Penn *et al.* 2018; Reddin *et al.* 2019). Further work to integrate the effects of changes in pH, pCO₂, salinity, and other key environmental variables into physiological performance models has the potential to make these models more general and accurate in reconstructing the causes of past extinction and predicting the consequences of future global change.

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

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AUTHOR CONTRIBUTION STATEMENT

All authors contributed to the conceptualization, original draft preparation, review, and editing of the manuscript.

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CONFLICT OF INTEREST STATEMENT

Conflicts of Interest: None.

DATA AVAILABILITY STATEMENT

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

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FIGURE CAPTIONS

Figure 1. Extinction patterns in the fossil record. A) Graph of marine animal diversity across the past 600 million years, illustrating the diversity declines associated with the five major mass extinction events (modified from Raup and Sepkoski, 1982). B) Extinction selectivity during the end-Permian mass extinction, illustrating the preferential extinction of heavily calcified marine animal classes with less complex respiratory and circulatory systems (modified from Knoll et al. 2007 and Knoll and Fischer 2011). C) Extinction selectivity with respect to geographic range, illustrating the preferential survival of broadly distributed genera during background intervals and the greatly reduced selectivity during mass extinction events (modified from Payne and Finnegan 2007). D) Principal components analysis of logistic regression coefficients of ecological traits and body size selectivity of the Big Five mass extinction events and the modern oceans, demonstrating the unique selectivity of the modern extinction threat (modified from Payne et al. 2016). E) Extinction selectivity with respect to body size for major classes of marine animals, illustrating the general bias of background extinction against smaller-bodied genera *versus* the variable direction of selectivity for classes that exhibit distinct patterns during mass extinction (modified from Monarrez et al. 2021).

Figure 2. Workflow illustrating the use of geological and geochemical data to constrain Earth system models (ESMs), physiological experiments to constrain parameters used to populate models with species of different ecophysiotypes, and fossil occurrence data to conduct model-data comparison. Ecosystem structure remains to be incorporated into such models and can be used to predict extinction cascades. Calibration of models against selectivity patterns in ancient extinction events will improve their use in forecasting biotic response to current and future environmental change. Panels on right showing CO₂ emissions curves and future biodiversity projections are from Penn and Deutsch (2022).

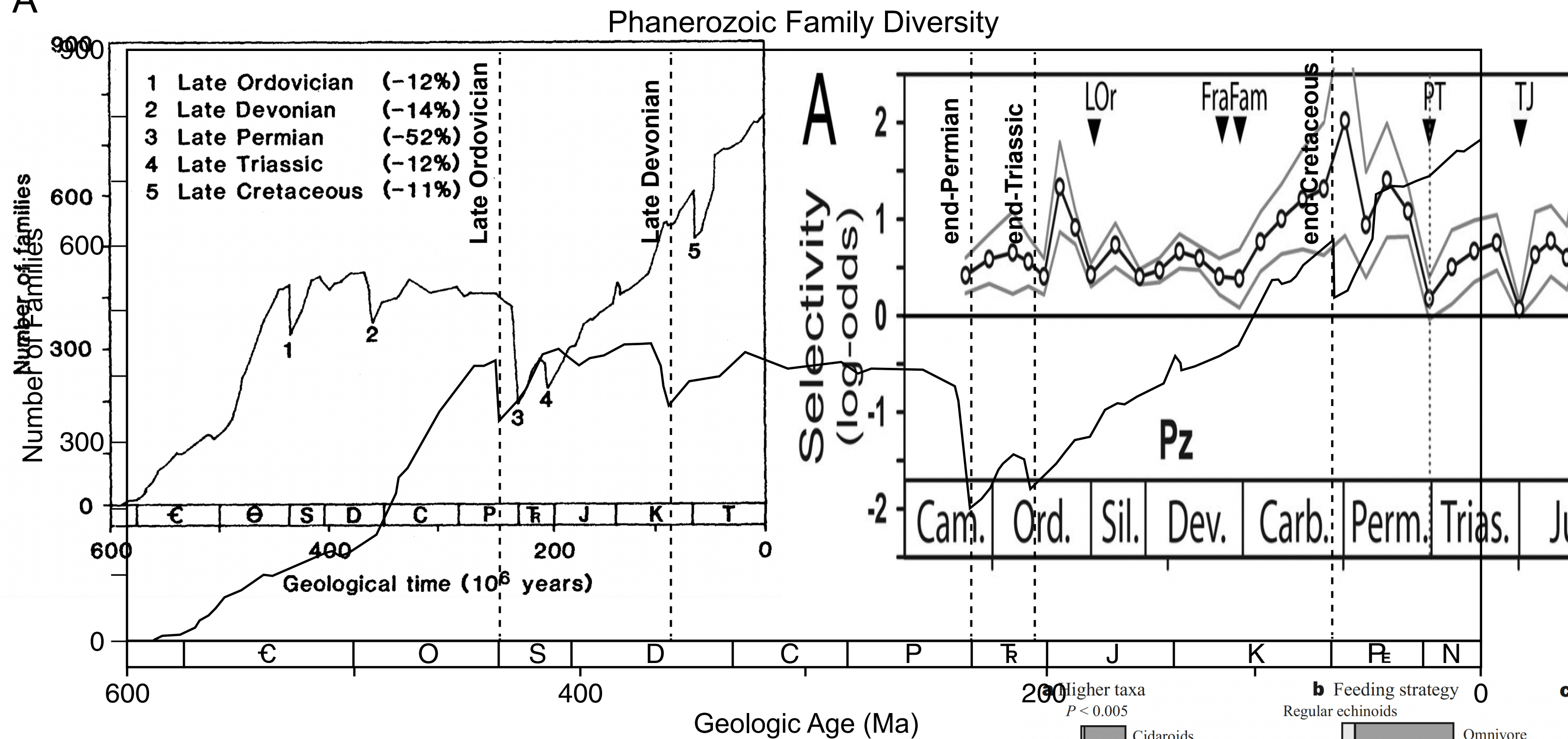
Figure 3. Graphs illustrating the key species traits of the Metabolic Index (ϕ) along with how ϕ relates to temperature and oxygen partial pressure. A-C) Frequency distributions of the Metabolic Index parameters for marine animals. D,E) Graphs of variation in ϕ as a function of temperature and oxygen for species with negative (D) and positive (E) temperature sensitivities (E_o) of hypoxia tolerance (A_o), which is the inverse of the critical oxygen threshold (red circle) at a reference temperature (T_{ref}), as derived from respirometry experiments. For species in a resting state, the aerobic habitat limit occurs when $\phi = 1$, but in the environment a species' activity level or Sustained Metabolic Scope (SMS) elevates the habitat limit to ϕ_{crit} . For species with negative E_o , aerobic habitat availability increases with temperature, whereas for those with positive E_o (i.e., most species; panel B), aerobic habitat declines with warming. Changes in PO₂ has the potential to lower aerobic habitat availability, and thus the amount of warming a species can withstand, as exemplified for two scenarios of with different fractions of present atmospheric levels of O₂ (PAL; yellow dots and arrows). A change in CO₂ also has the potential to alter hypoxia tolerance, but the magnitude and direction of this effect is unknown across marine biota and is illustrated here from experimental data for a single species under Δ pH = +0.5 (Rosa et al., 2013). Arrows in A-C denote species traits in D and E.

Figure 4. Hypothetical progression of a mass extinction highlighting sources of trait-

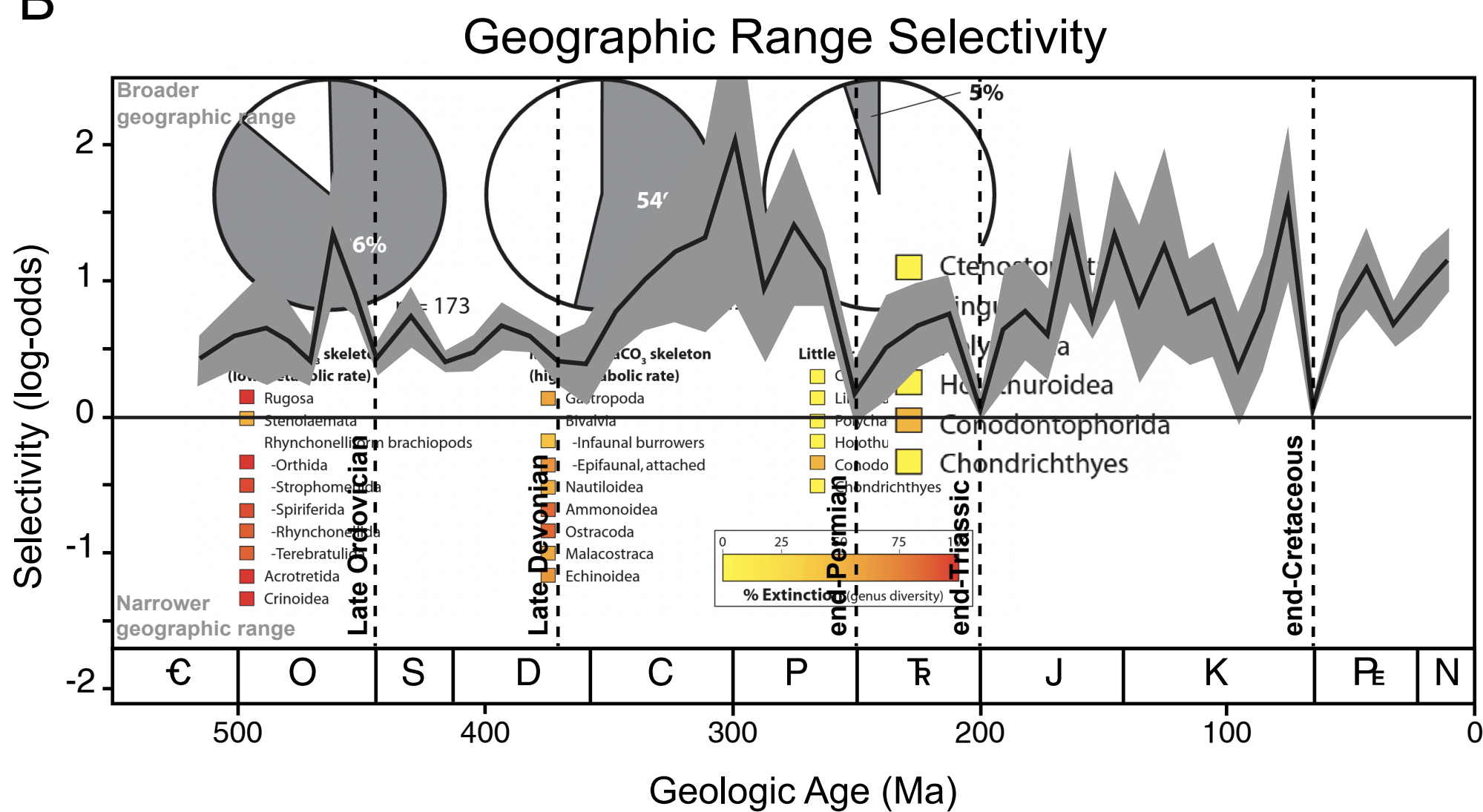
based and geographic selectivity and potential ecological amplification. A) An initial distribution of species (or “ecophysiotypes”) defined by traits under selection by large-scale environmental conditions will likely result in systematic correlations between traits and geographic range. The range metric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

Figure 5. Geographic patterns of extinction and ocean changes in Earth system model simulations of the end-Permian climate transition (left column) and under anthropogenic greenhouse gas forcing (C) to 2300 C.E. (middle column). Line plot comparisons of end-Permian and potential future environmental changes *versus* latitude are shown in panels on the right (F,I,L,O). Model extinctions (A,B) are driven by ocean warming (D,E) and O_2 loss (G,H), as quantified through the Metabolic Index, and in (A) reproduce the latitudinal pattern from the fossil record of the end-Permian (red points). These primary extinctions have the potential to be amplified by other environmental stressors like changes in net primary productivity (NPP) (J,K) or pH (M,N) or through secondary extinctions via the food web. Shaded region in (A) shows uncertainty in end-Permian extinction magnitudes across a range of potential extinction threshold parameters. Solid line in (B) shows future extinction risk averaged across Earth system models, using an extinction threshold calibrated from the end-Permian (same as the solid line in A) (see Penn et al., 2022 for calibration details), while the shading in (B) shows the inter-model range. Future changes are projected under a high greenhouse gas emissions scenario, leading to a net radiative forcing of 8.5 W m^{-2} in 2100 C.E. (C) and are relative to the pre-industrial era (1850-1900). Model fields are averaged over the upper 500 m, and for the future projections, they are averaged across Earth system models ($n = 5$). Model details are provided in Penn et al. (2018, 2022). Panels 5A and 5B,C are modified from Penn et al., (2018) and (2022), respectively.

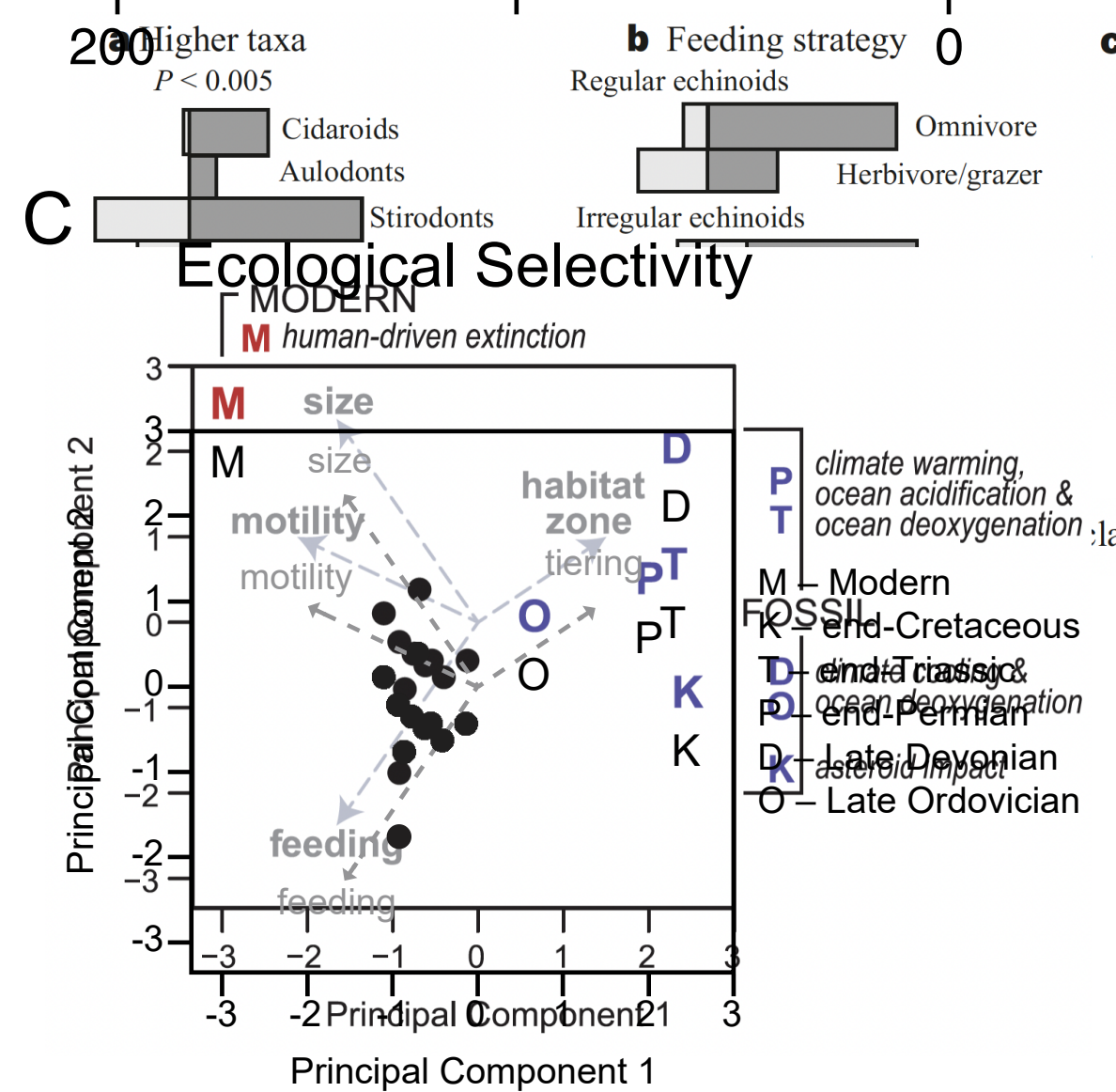
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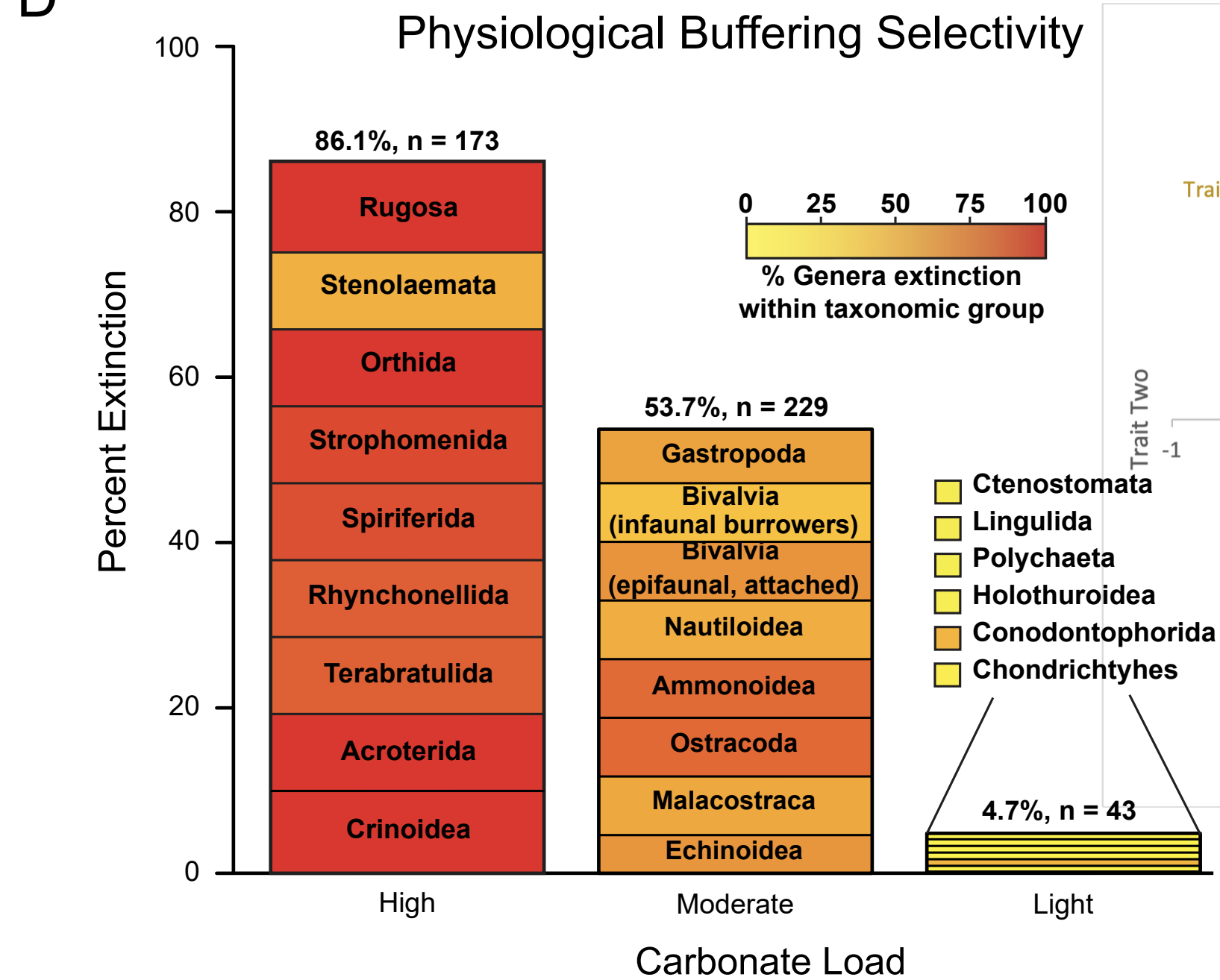
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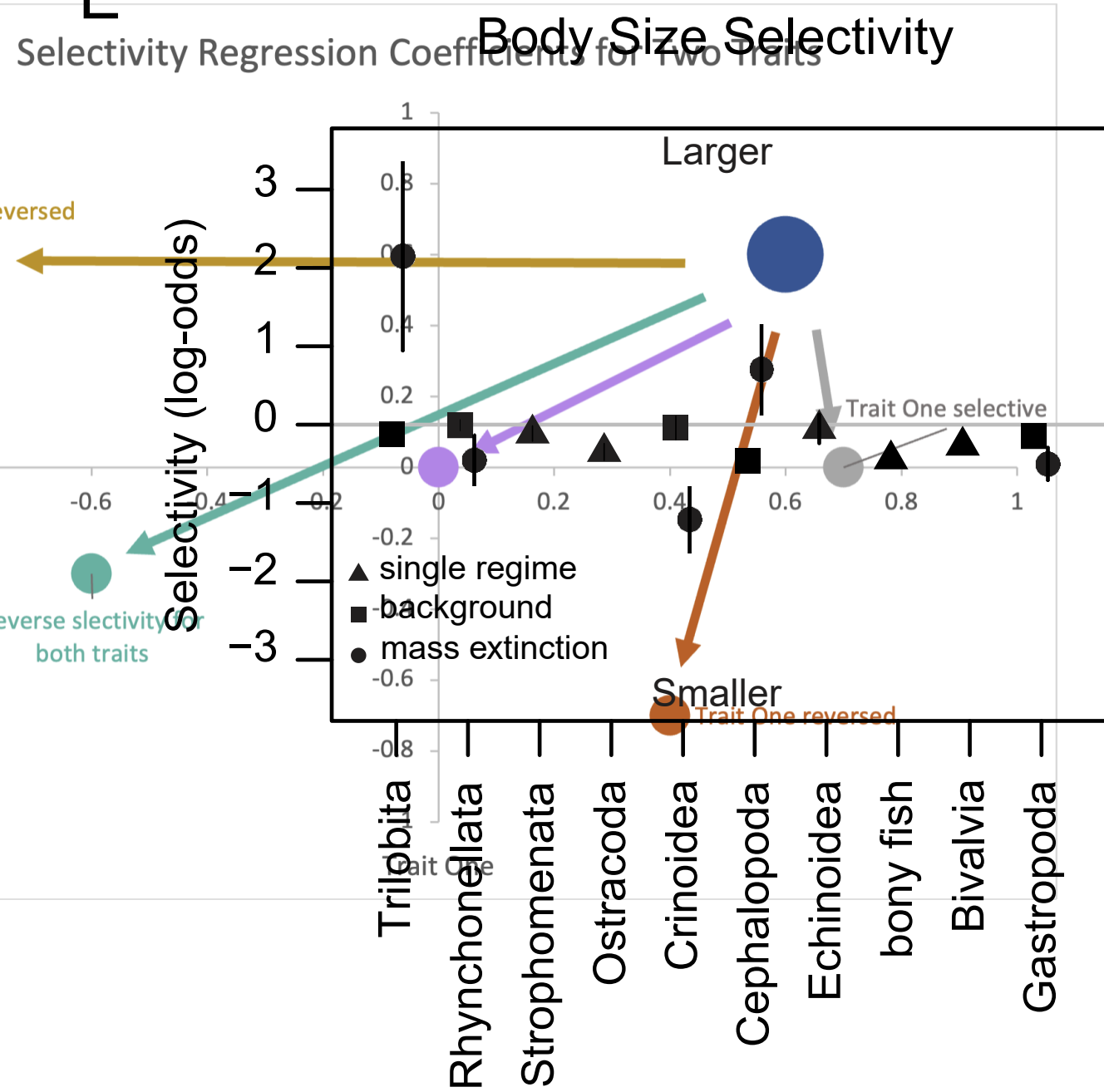
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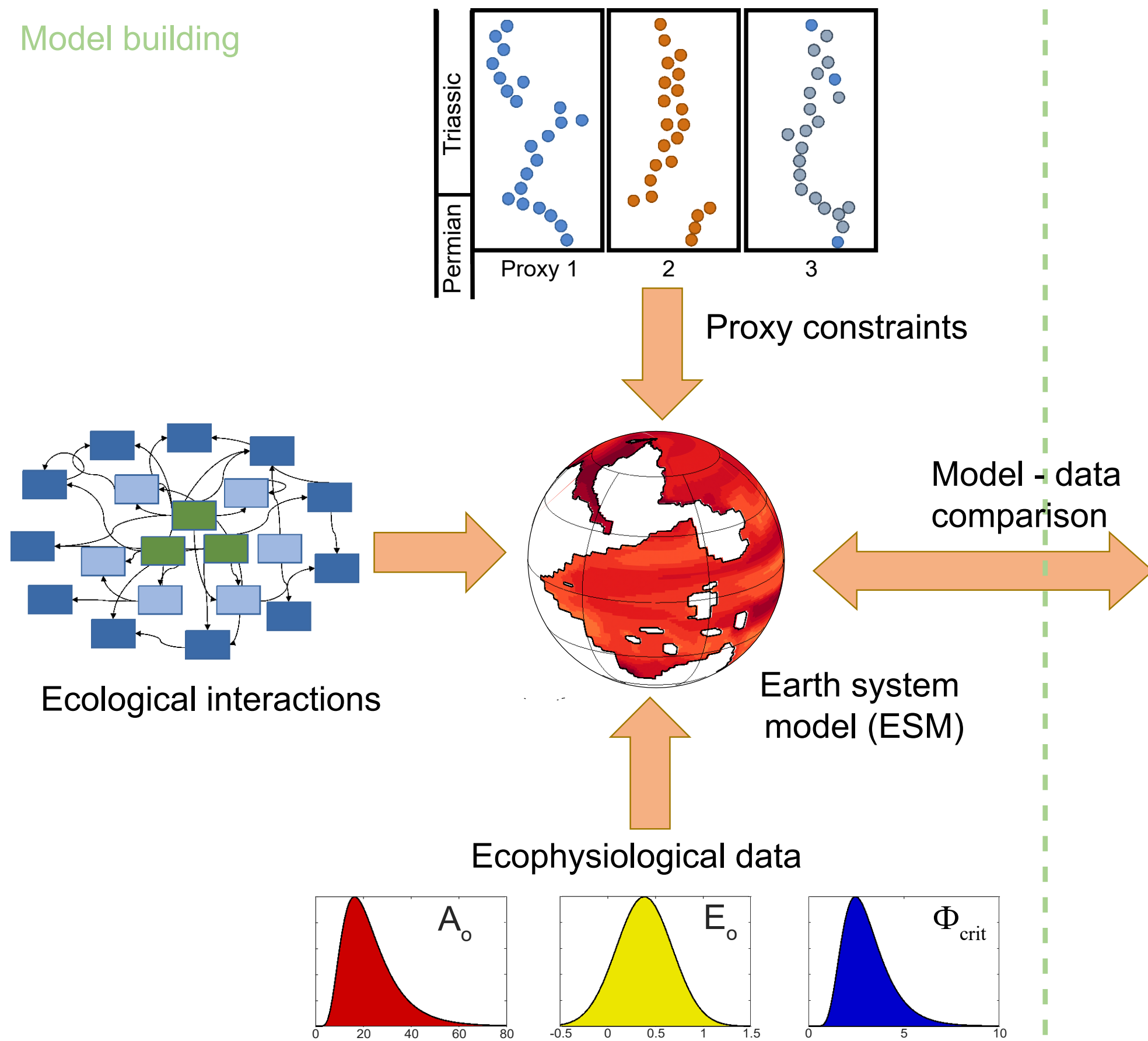
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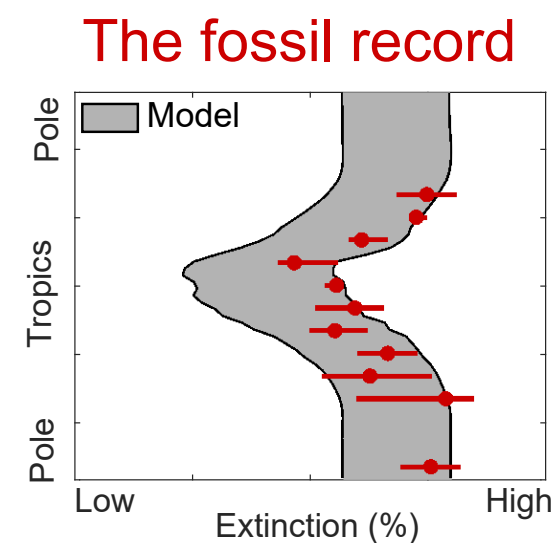
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Model building

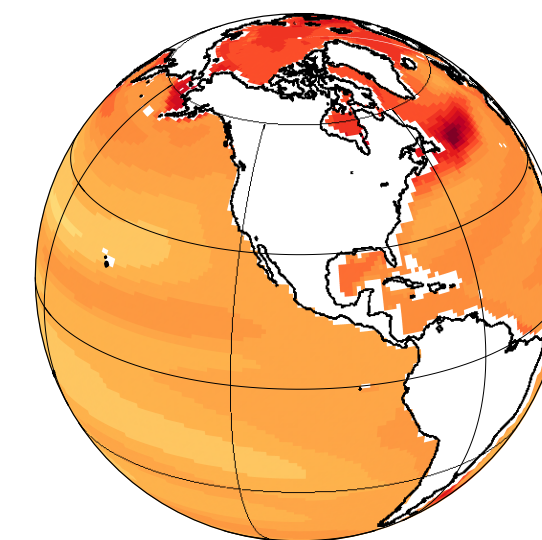
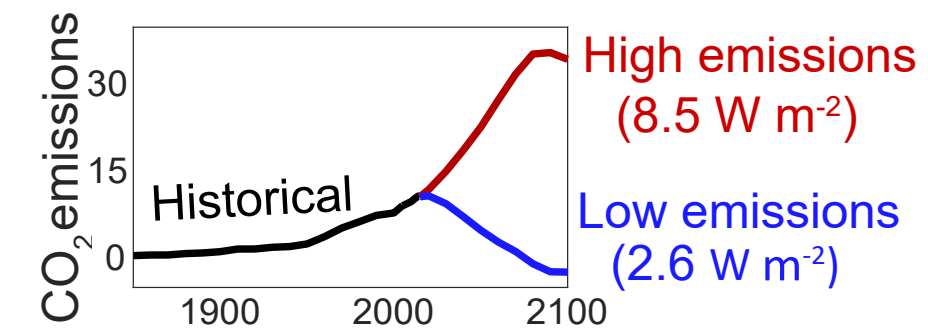


Hypothesis testing

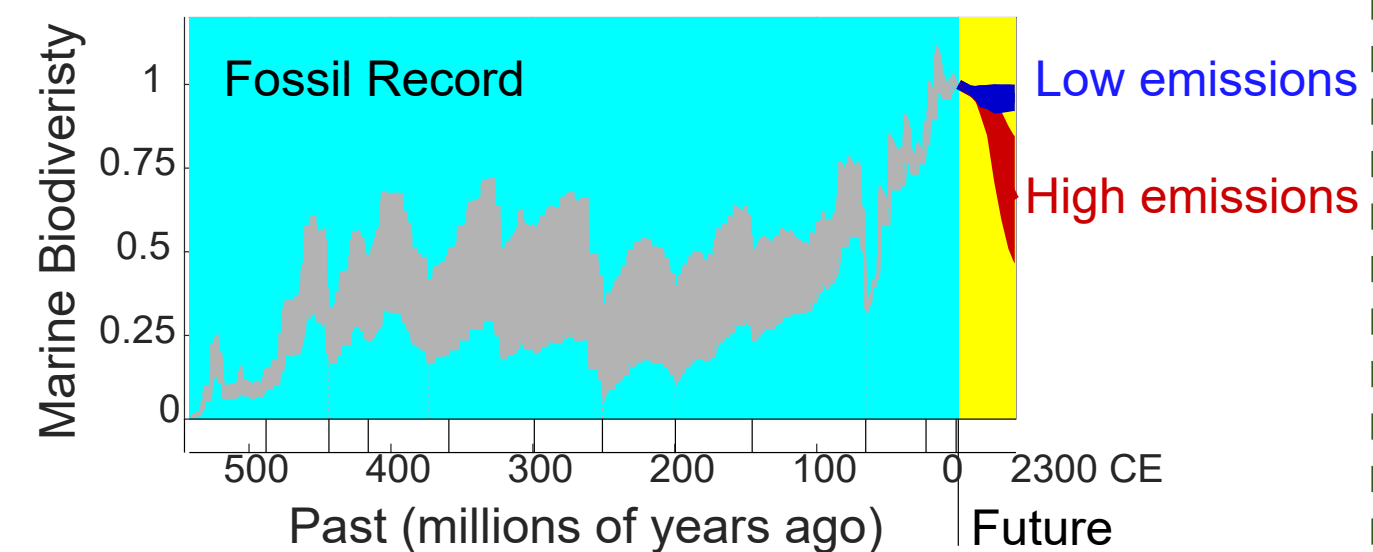


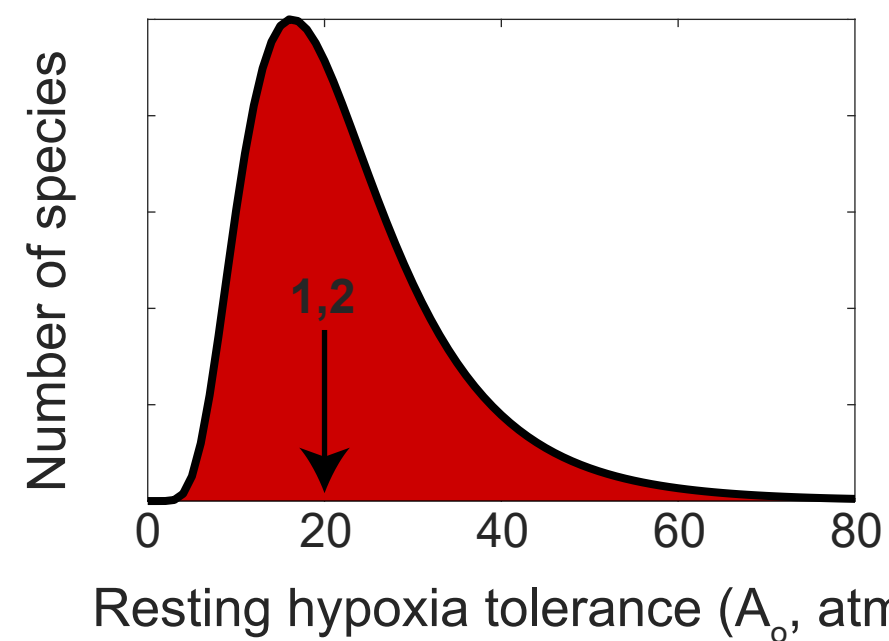
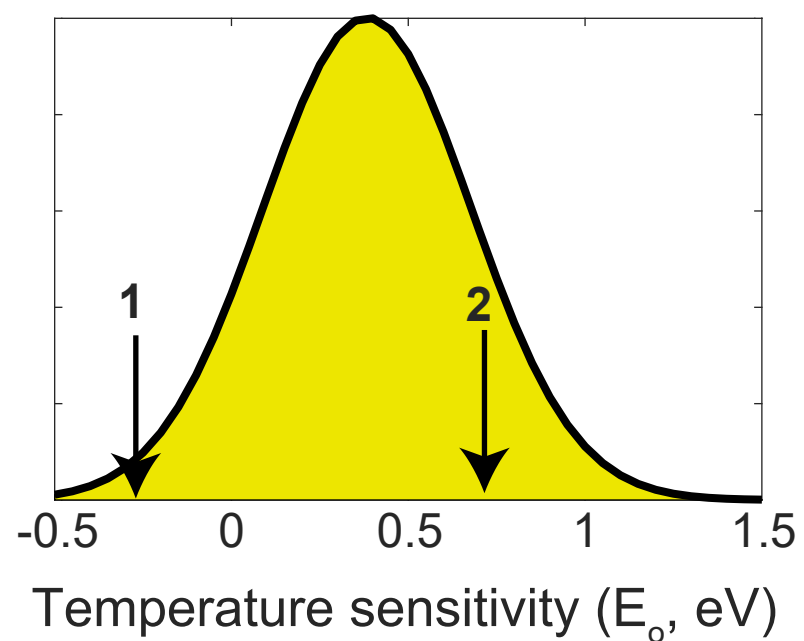
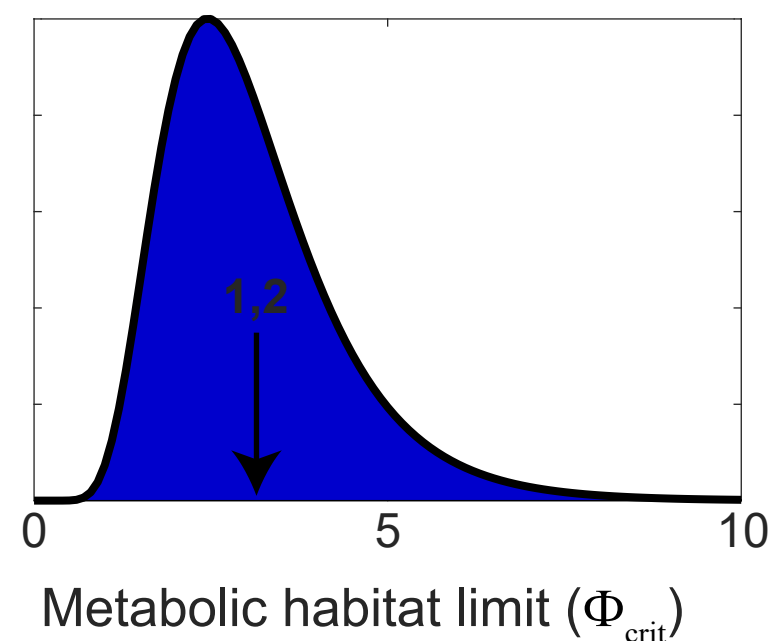
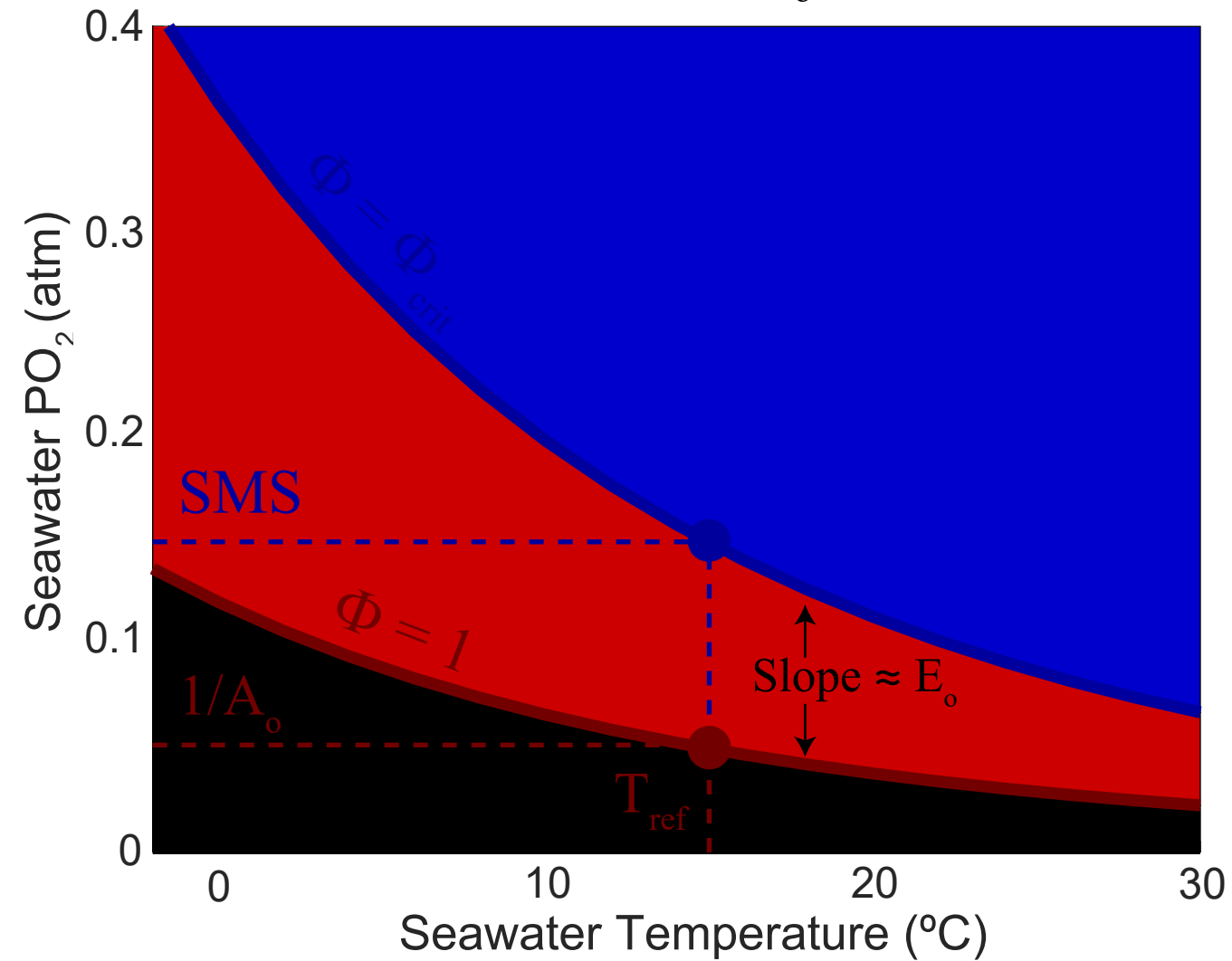
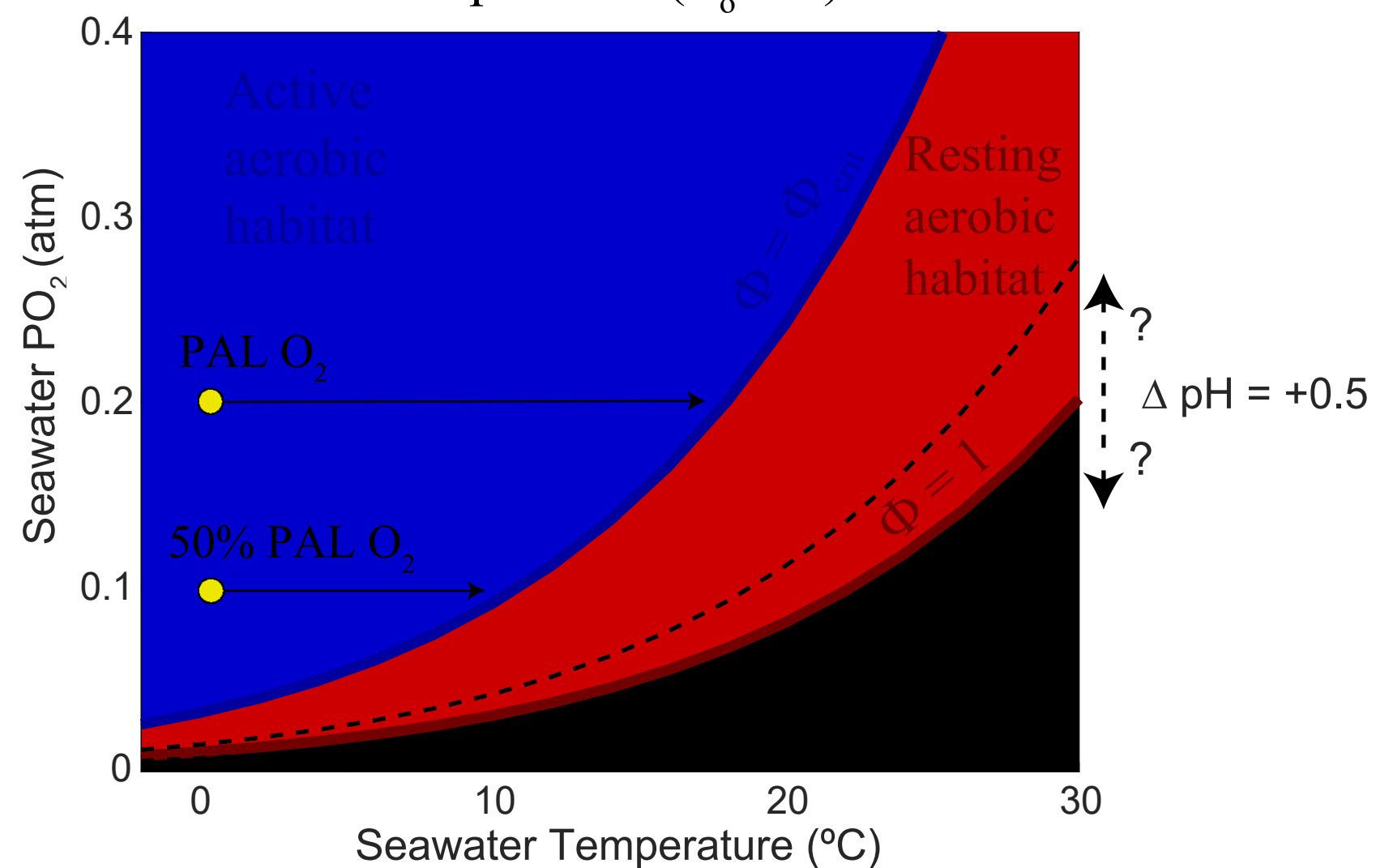
Forecasting

Anthropogenic Forcing

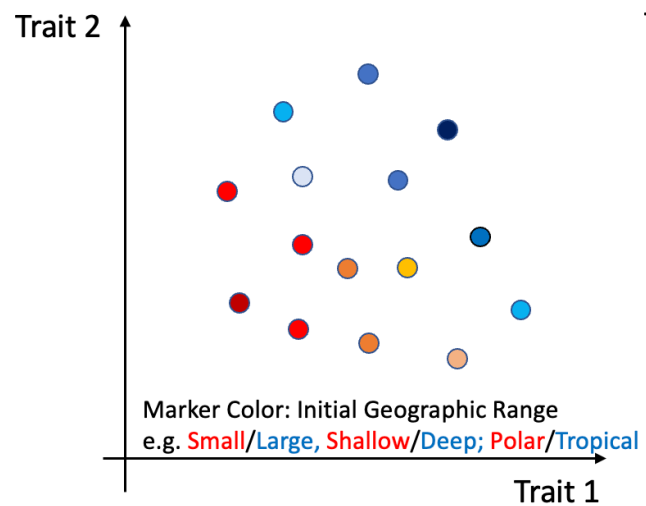


Projected future extinctions using calibrated ESM

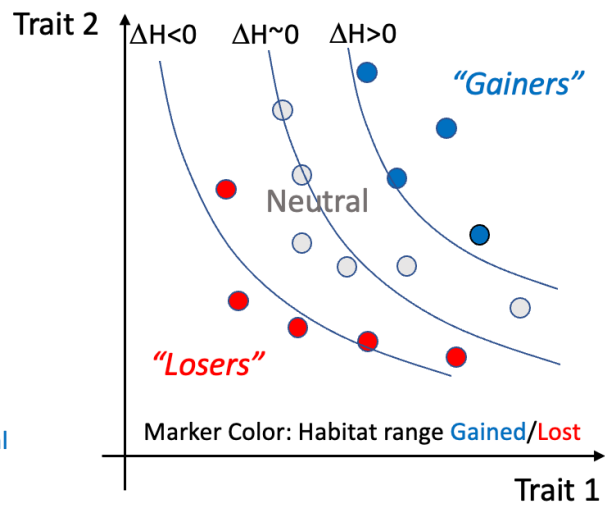


A**B****C****D**Species 1 ($E_o < 0$)Species 2 ($E_o > 0$)**E**

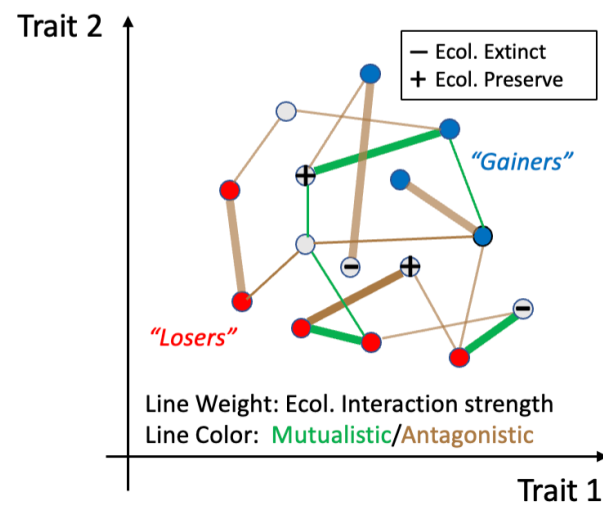
A) Initial Climate/Ecosystem



B) Physiological Habitat Risk



C) Ecological Network Risk



D) Final Climate/Ecosystem

