Extinction intensity during Ordovician and Cenozoic glaciations explained by cooling and paleogeography

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A striking feature of the marine fossil record is the variable intensity of extinction during superficially similar climate transitions. Here we combine climate models and species trait simulations to explore the degree to which differing paleogeographic boundary conditions and differing magnitudes of cooling and glaciation can explain the relative intensity of marine extinction during greenhouse-icehouse transitions in the Late Ordovician and the Cenozoic. Simulations modelled the response of virtual species to cooling climate using a spatially explicit cellular automaton algorithm. We find that paleogeography alone may be a minor contributing factor, as identical changes in meridional sea surface temperature gradients caused greater extinction in Late Ordovician simulations than in Cenozoic simulations. Differences in extinction from paleogeography are significant but by themselves insufficient to explain observed differences in extinction intensity. However, when simulations included inferred changes in continental flooding and interval-specific models of sea surface temperature, predicted differences in relative extinction intensity were more consistent with observations from the fossil record. Our results support the hypothesis that intense extinction in the Late Ordovician is partially attributable to exceptionally rapid and severe cooling compared to Cenozoic events.

The fossil record documents substantial variation in extinction rates over the past 540 million years, punctuated by major extinction events[1,2]. The degree to which major extinction events have common trigger mechanisms remains the subject of intense debate, but considerable evidence suggests that superficially similar trigger mechanisms can have very different impacts depending on their magnitude and variation in the local and global boundary conditions under which they occur. For example, although several extinction events are thought to have been caused by emplacement of large igneous provinces (LIPs)[3], the extreme severity of the Permian-Triassic Mass Extinction (252 Ma) may be attributable to the particular characteristics of the sedimentary rocks into which Siberian Traps volcanics were intruded[4]. The Late Ordovician Mass Extinction (LOME, ~ 445 Ma) has long posed a conundrum because it is the only major mass extinction thought to have been driven by climate cooling (although causes of the Late Devonian Mass Extinction remain uncertain and may include glaciation[5]). Late Ordovician extinctions cluster in two distinct pulses, with the first and largest appearing to coincide with cooling, expansion of south polar ice sheets, and sea level fall near the Katian-Hirnantian boundary, and the second appearing to coincide with warming and deglaciation in the mid-late Hirnantian[6-8]. Although more recent episodes of cooling and glaciation have been associated with elevated extinction of marine invertebrates[9-13], none of these cooling events caused the magnitude of extinction characteristic of the LOME. This disparity has led to suggestions that cooling alone cannot account for the LOME, and that other factors such as eutrophication, anoxia, heavy metal toxicity, or eruption of a large igneous province may be the primary cause of the event[14-23].

Here we explore the degree to which differing boundary conditions may help to explain the very different extinction intensities associated with greenhouse-icehouse transitions in the Late Ordovician and in the Cenozoic. We focus in particular on a relatively unexplored factor—the role of paleogeography and continental configuration. Previous work suggests that many marine ectotherms have thermal niches that are relatively stable on evolutionary timescales and rarely evolve at coarse scales in response to climate change, especially if change is relatively rapid[24-26]. Instead, the more common response of marine ectotherms to temperature change is habitat tracking[27-31]—shifts in the geographic range of species to follow preferred abiotic/biotic conditions. The relative ability of entire faunas to track habitat can therefore provide a measure of faunal resilience to extinction[32]. We hypothesize that the geographic arrangement of continental crust may be important because it has the potential to facilitate or inhibit habitat-tracking during periods of climate change[33].

To illustrate this, consider a geologically rapid temperature change of comparable magnitude occurring in a world with (i) a single continent that spans from the north to the south pole, and (ii) a single circumequatorial continent (Fig. S1). In the former world, shallow marine species restricted to shelf and slope depths (which constitute the majority of the marine fossil record) would be able to disperse along the north-south oriented coastlines to track habitats within their thermal tolerance range. Shallow marine species in the latter world would have no such option, and, if the new climate state included temperatures outside of their thermal tolerance range, would be driven to extinction. A similar phenomenon would be expected in a world with many island systems, especially if the island chains are dispersed longitudinally more than latitudinally. Thus, the arrangement of continental crust could play an important role in modulating the expected severity of extinction for a given climate perturbation. The arrangement of continents during the Late Ordovician differed strikingly from that during the Cenozoic (Fig. 1). Whereas the Cenozoic world is characterized by long, dominantly north-south oriented coastlines, the Late Ordovician world had only a single, north-south oriented supercontinent (Gondwana) and numerous island paleocontinents and terranes[34].

A second potentially important difference in boundary conditions is that, whereas epicontinental seaways were of relatively limited extent during the Cenozoic, the Late Ordovician world was characterized by extensive continental flooding. Epicontinental seaways were, in many cases, characterized by temperature ranges and environmental conditions quite distinct from those of open oceans, limiting the ability of epicontinental endemics to colonize adjacent ocean-facing shelves[35]. Thus, the potential effects of glacioeustatic sea level changes on the area and availability of suitable shallow marine habitat may have been greater in the Late Ordovician than during the Cenozoic. Finally, available proxy data suggest that the Late Ordovician glaciation may have been more severe than those of the Cenozoic, both in terms of the volume of continental ice sheets (and associated eustatic changes) and the degree of cooling of surface waters[36-42].

We evaluate the influence of all three of these factors (paleogeography, glacioeustasy, and temperature) on expected extinctions of shallow marine taxa during three major cooling events in Earth history: Late Ordovician (~445 Ma), Eocene–Oligocene (~34 Ma), and Pliocene–

Pleistocene (~4 Ma). Our goal is not to precisely model the pattern of extinctions, but rather to evaluate whether the exceptionally high extinction during the first pulse of the LOME can be explained by any one or a combination of these factors, or instead requires additional explanation. We first isolate the expected effects of paleogeography, holding all other factors constant. We then utilise a series of climate model simulations to examine how glacio-eustatically-forced sea level change and estimated temperature change can explain differences in extinction magnitude observed amongst the three events.

Results

Effect of Varying Paleogeography

Proportional extinction was statistically higher when using a Late Ordovician paleogeographic configuration than when using late Eocene or late Pliocene paleogeographies by up to 0.12 (Table S5). The difference occurs for virtually all simulated dispersal, niche, and continental shelf combinations (Fig. 3 & Fig. S5). The only group of species that did not exhibit higher extinction in the Late Ordovician was those with broad thermal niches and poor dispersal ability, but differences in proportional extinction in this case across the three paleogeographies were minimal (< 0.02; Table S5). As expected, overall extinction was highest when assuming narrow shelves and when considering simulated species with narrow niches and poor dispersal abilities. Differences across paleogeographic scenarios were largely consistent regardless of whether a narrow or broad marine shelf was assumed (Fig. S5; Table S5). Proportional extinction was highest on islands and in equatorial regions (Fig. 1 & Fig. S6) and generally lowest along north-south coastlines (Fig. 4).

Effect of Varying Paleogeography and Sea Level

When estimated changes in sea level were included in simulations, proportional extinction was substantially higher in the Late Ordovician scenario than the Eocene and Pliocene scenarios for all niche breadth and dispersal combinations regardless of continental shelf extent by up to 0.24 (Fig. S7; Table S5). Simulations run with broad marine margins returned slightly lower extinction compared to those run under narrow marine margins (Fig. 3 & S7). Proportional extinction was highest on islands and in equatorial regions (Fig. 1; Fig. S6). Patterns were broadly similar for simulations that allowed species more than one opportunity to disperse to new cells following sea level fall, although extinction magnitudes were generally lower across all scenarios (Fig. S8).

Effect of Varying Temperature Change

When using interval-specific and paleogeographically-explicit surface temperature change estimates from AOGCMs, extinction magnitudes were substantially higher for the Late Ordovician scenarios than for the Eocene and Pliocene scenarios, in most cases by about a factor of 10 (Fig. 1; Figs. 3 & S9–12; Table S5). These relative patterns held regardless of dispersal ability, marine margins, or the AOGCMs used to characterise the greenhouse-icehouse transitions. Proportional extinction was dampened slightly for simulations run with broad marine margins compared to those run with narrow marine margins, but relative differences across models and types of species were similar.

The high extinction magnitude predicted for the Late Ordovician is largely a function of the large average temperature drop estimated by AOGCMs for this interval (Fig. S13). This cooling substantially exceeds the cooling estimated for Cenozoic greenhouse-icehouse transitions. Although constraints on the magnitude of cooling during the Late Ordovician are few, modelled difference in tropical cooling between the Late Ordovician and Cenozoic transitions are generally consistent with available proxy data[36,40,42-44] (Fig. S14). When comparing the Cenozoic cooling events, Robertsons Plc. models for the Eocene–Oligocene (AOGCM transition codes 4 to 7, see Table S3) and Pliocene–Pleistocene (transition codes 10 to 12, Table S3) resulted in higher rates of extinction, consistent with the higher cooling predicted by these AOGCMs (Fig. S13). Although temperature declined less, on average, for the Eocene–Oligocene Getech model compared to the Eocene–Oligocene FOAM model (Fig. S13), proportional extinction was generally lower for the latter. The Eocene–Oligocene FOAM model returned lower extinction, even given greater climate change, because glacioeustasic sea level did not change for this AOGCM (although coastlines were artificially changed for simulations focused on glacioeustacy, see methods S.1.3).

The effect of shallow marine area definition

Patterns were broadly consistent when simulations were run in an area defined by every cell within 0 to 200 m water depth (Fig. S4), accounting for the extent of continental flooding. Extinction magnitude was higher for the Late Ordovician in virtually all simulated combinations when considering (i) the effect of paleogeography alone (Fig. S15), (ii) paleogeography and sea level change (Fig. S16), and (iii) using interval-specific and paleogeographically-explicit surface temperature change estimates from AOGCMs (Fig. S17).

Discussion

Our simulations suggest that paleocontinental configuration alone could explain a small part of the observed variation in extinction intensity between the Late Ordovician and Cenozoic greenhouse-icehouse transitions: identical changes in sea surface temperature caused higher extinction with a Late Ordovician continental configuration than with Cenozoic continental configurations. This difference reflects both the relative paucity of long north-south oriented coastlines spanning large latitudinal ranges and the relative abundance of small islands and terrains in the Late Ordovician compared to the Cenozoic (Fig. S18). As the climate cooled, the proportion of species able to disperse along continental margins without crossing large areas of open ocean may have been higher in the Cenozoic than in the Late Ordovician. Our simulations do not account for the many dispersed island arcs and terranes with poorly constrained locations in the Late Ordovician that are not included in simplified paleogeographic reconstructions. Many of these terranes experienced very high apparent extinction rates in the Late Ordovician, although it is not always easy to disentangle the effects of the mass extinction and continental amalgamation[17,45].

Although interesting, the predicted differences in extinction intensity as a consequence of paleogeography alone are too small to account for the exceptional severity of the LOME compared to Cenozoic cooling events. Modelling changes in sea level substantially amplified the expected difference in extinction intensity between the Late Ordovician and Cenozoic. Simulations that also varied the magnitude and pattern of sea surface cooling predicted Late Ordovician extinction magnitudes far exceeding those associated with Cenozoic events (Fig. 1).

It is difficult to compare the geographic pattern of extinctions from our simulations with empirical patterns for a variety of reasons: our simulations make the unrealistic assumption that species with different ecological attributes are uniformly distributed on continental margins and do not account for possible latitudinal diversity gradients. The biogeographic distributions of species with different ecological attributes in the past are largely unknown, and the geographic distributions of extinct taxa may be obscured and distorted by spatiotemporal variation in sedimentary rock deposition, preservation, exposure, and sampling. However, proportional extinction of marine invertebrate genera across paleolatitudes during the first (end-Katian) pulse of the LOME shows some similarity to predicted patterns, notably relative peaks in the tropics and at high southern latitudes (Fig. S6).

Although thermal niche breadth cannot be measured easily for extinct species, it is notable in this context that thermal tolerance range and latitudinal range are highly correlated in modern marine ectotherms[46], and the first pulse of the Late Ordovician Mass Extinction was characterized by exceptionally high extinction of brachiopod genera with relatively narrow (<35°) absolute paleolatitudinal ranges[47]. Genera with ranges largely or entirely limited to epicontinental seaways also experienced elevated extinction risk[47,48]. When considered in light of these patterns, the results of our simulations bolster the argument that the combined effects of paleogeographic configuration, exceptional cooling, and draining of epicontinental seaways might help to explain the severity of the first pulse of the Late Ordovician Mass Extinction relative to Cenozoic greenhouse-icehouse transitions.

Our analysis focused only on paleogeography, sea level drop, and temperature change, but other factors almost certainly worked in concert to elevate extinction intensity during the Late Ordovician, as evidenced by the fact that extinction rates substantially exceeded those of the Cenozoic even in regions that our simulations suggest should have experienced comparatively low extinction (Fig. S6). For example, preferential extinction of deeper-water brachiopods[47,49] and other benthic taxa suggests widespread anoxic and euxinic conditions may have played an important role in the extinctions[14,16,17,20]. Due to the dependence of both organismal metabolic rates and oxygen availability on ambient temperature, changes in water temperature and oxygenation may have interactive effects on the distribution of suitable habitat for many species[50,51].

Climate changes are linked intimately to changes in ocean and atmospheric circulation, which themselves are influenced by continental configuration. Thus, disentangling the relative contributions of these variables in empirical systems is difficult, which is why we implemented a simulation framework. We reiterate that our goal was not to create the most realistic simulations, but rather to generate models that isolate the effects of various factors. We used multiple AOGCMs to characterize uncertainty generated by model AOGCM choice, obtaining congruent patterns across model combinations. Whether surface temperatures predicted by AOGCMs are, in fact, representative of the simulated intervals is an open question pending more and better proxy constraints, but predicted changes in tropical sea surface temperatures are generally consistent with available data (Fig. S14).

Another potential source of error is paleogeography. Simulations were performed at relatively coarse spatial resolution (1°x1°), and therefore removed small islands and smoothed complex geographic features, some of which could have functioned as important biogeographic barriers. We do not, however, anticipate this smoothing affected proportional extinction in a systematic fashion across events, and higher-resolution reconstructions would not reflect true (low) confidence in paleogeography during these time periods. Although Cenozoic paleogeography is comparatively well constrained, there are many uncertainties remaining regarding the positions of paleocontinents and terranes during the Late Ordovician[34,45,52]. However, the relative positions of major continental landmasses, especially those with well-sampled fossil records, are similar across most recent reconstructions, and we do not anticipate that using alternative paleogeographic models would have a major impact on our findings.

Our simulation framework assumes that species thermal niches are highly conservative and do not evolve in response to climate change. Although overly simplistic, we regard this as a reasonable assumption based on previous research that has shown species’ tolerances are stable over millions of years[24]. Niche evolution, if included, would likely dampen extinction rates in simulations, but we do not expect it would systematically affect extinction magnitudes for any one climate transition over another, unless niches were more or less labile through time. The static niches employed in our simulation framework resulted in a zone of very high tropical extinction for warm-adapted species with narrow thermal niches. These simulated species are doomed to extinction when climate cools as no suitable habitats remained available to them. Our simulations suggest that the proportion of species unable to disperse to suitable habitat may have been higher during Late Ordovician cooling than during Cenozoic cooling events, both because of the relative lack of continuous north-south coastlines and presence of numerous small islands and terranes, and because a greater proportion of shallow marine habitat area was located in the tropics (Fig. S4). Whether tropical regions have, in fact, consistently experienced exceptionally high extinction rates during greenhouse-icehouse transitions is unclear[10,12,13,48,53].

All of our simulations assumed the same rate of transition from greenhouse to icehouse states—simulated species were forced to track suitable habitat as climate changed from warm to cold in only a set number of 'time steps'. In reality, these climatic transitions occurred over timescales of 10^3-10^6 years, which may have allowed species to more effectively track suitable habitat. Simulating more gradual climate transitions would, in general, reduce proportional extinction by permitting species to more effectively track preferred temperatures via small dispersal steps, but whether this reduction would apply equally to all simulated transitions is unclear. At present it is difficult to constrain the rate of cooling during the Late Ordovician greenhouse-icehouse transition, and hence meaningful comparison of rates across all three events is not possible. For this reason, it is also difficult to account for the potential effects of changes in paleogeographic configuration (e.g. accretion of peri-Laurentian terranes in the Late Ordovician[45], uplift of the Isthmus of Panama in the Plio-Pleistocene[54]) that may have occurred over the same timeframe as greenhouse-icehouse climate transitions.

Despite these caveats, our simulation framework provides clear evidence that the expected effects of greenhouse-icehouse transitions differ depending on paleogeographic configuration, sea level change, and magnitude of temperature change. We suggest that this framework represents a promising way forward to provide further constraints on the relative contribution of boundary conditions to extinction and speciation rates, particularly as more sophisticated models and better proxy/paleogeographic data become available.

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Author Contributions

EES and SF designed the study, collected the data, and wrote the manuscript. AF, AP, ATK-A, DJL, J-BL, NS, PV, and YD contributed climate modeling data. EES and HQ performed analyses. All authors read and commented on the manuscript.

Financial and non-financial competing interests

The authors declare no competing financial interests.

Figure captions

Figure 1. Per-cell proportional extinction for each greenhouse-icehouse transition. Simulated patterns are shown isolating the effect of (a) paleogeography, (b) paleogeography and sea level change, and (c) paleogeography, sea level and temperature change (c). Results show the average extinction across all dispersal and niche scenarios for the broad continental shelf. Temperature change was represented by the FOAM climate model for the Late Ordovician and Eocene–

Oligocene, and by the Robertson HadCM3BL climate model for the Plio–Pleistocene (see Table S3 for details). Note that the FOAM AOGCMs do not incorporate changes in sea level; thus, simulations incorporating estimates of temperature change would likely produce even greater extinction if sea level and temperature effects were modelled jointly in these AOGCMs.

Figure 2. Schematic of dispersal and extinction in the simulation. Cells represent a hypothetical portion of gridded shallow marine shelf in which simulations were run. Blue and green cells indicate unsuitable and suitable conditions for species, respectively. (a) Brachiopod image denotes the location of a seed cell where a simulation initiated. (b) Once the simulation began, the incipient species searched for suitable habitat and dispersed to other suitable cells under a warm, stable climate. (c) The climate then cooled, altering the cells suitable for the species. In scenario 1, the virtual species was capable of jumping over multiple, unsuitable cells to colonize newly suitable regions: this species survived the climatic change. In scenario 2, the virtual species could not traverse as many unsuitable cells (i.e., had poor dispersal ability) and therefore went extinct.

Figure 3. Proportional extinction (expressed as percentages for ease of reading) resulting from simulations testing the effect of (i) paleogeography only (first column), (ii) paleogeography and estimated changes in sea level (second column), and (iii) paleogeography, sea level, and temperature change from AOGCMs (third column). Simulations were run in shallow marine area directly adjacent to land, and only the narrow marine margin is represented here. AOGCM results are depicted for AOGCM model combination [1-2] for the Late Ordovician, [5-8] for the Eocene–Oligocene, and [10-12] for the Plio–Pleistocene (see Table S3). The Late Ordovician and the FOAM Eocene AOGCMs do not incorporate changes in sea level; thus, simulations incorporating estimates of temperature change would likely produce even greater extinction if sea level and temperature effects were modelled jointly in these AOGCMs. For other scenarios, see Figs. S5, S7-S12, and S15-S17. Eoc = Eocene; Ord = Ordovician; Plio = Pliocene.

Figure 4. Proportional extinction on north-south coastlines compared to east-west coastlines and ‘islands.’ Results are shown for simulations considering paleogeography alone, for different niche and dispersal combinations. ‘Islands’ were defined as small isolated shallow marine shelf areas with contiguous cells. Error bars are 95% binomial confidence intervals. For predicted extinction patterns, color and symbols indicate niche breadths (narrow and broad) and dispersal abilities (poor and good) of simulated species. As expected, extinction is higher on islands and east-west coastlines compared to north-south coastlines. However, many species occupied both north-south and east-west coastlines, and therefore proportional extinction differences are minimal. See methods section S.1.3.4 and Fig. S18 for additional details.

Methods

Simulation overview

A full description of our methods is provided in the Supplementary Materials. We used a gridded simulation framework[1-3] to examine potential effects of paleogeography, glacio-eustatically-forced sea level fall, and temperature change on extinction magnitude across three greenhouse to icehouse transitions: Late Ordovician, Eocene–Oligocene and Plio–Pleistocene. The gridded world in these simulations consisted of shallow marine margins around continents (both broad and narrow; Fig. 1 & Fig. S2). Virtual species occupied cells in this gridded world if the average surface temperature of the cell fell within the species' niche (i.e., was suitable), and searched for suitable cells based on assigned dispersal ability (methods S1.2.2). We simulated four types of virtual species characterized by different conditions of thermal niche breadth (narrow or broad) and dispersal ability (poor and good). Sea surface temperatures are derived from either simplified hypothetical meridional gradients (methods S1.2.1) or interval-specific ocean-atmosphere general circulation models (AOGCMs; see S3 in SI). Each simulation begins in warm 'greenhouse' conditions, during which virtual species are seeded and allowed time to disperse and colonize suitable habitat. Following this burn-in period, cold 'icehouse' conditions are imposed, changing the extent and distribution of suitable cells for each species (Fig. 2; methods S1.2.3). Species unable to disperse to suitable habitat under the colder conditions become extinct, whereas species with suitable habitat within their dispersal range survive (Fig. 2).

Paleogeography

To isolate the influence of paleogeography on extinction potential we used a single set of simplified 'greenhouse' and 'icehouse' surface temperature gradients (methods S1.2.1, Fig. S3) and varied only paleogeography across the three greenhouse-icehouse transitions (Late Ordovician, Eocene–Oligocene and Plio–Pleistocene). Paleogeography, specifically the configuration of shallow marine margins (Fig. 1; Fig. S2), was estimated from reconstructions by [4] for the Late Ordovician, Scotese[5] for the late Eocene (Ypresian), and Robertson Plc. for the Pliocene[6]. Virtual species were generated (i.e., simulations initiated) at every possible shallow marine cell bordering land in each paleogeographic reconstruction, for a total of 2233, 2258, and 2892 virtual species in the Ordovician, Eocene, and Pliocene, respectively. We tabulated the number of virtual species that became extinct when the climate cooled and compared proportional extinction for each paleogeographic configuration (methods S1.3.4). This process was repeated for each possible combination of ecological and shelf parameters (niche breadth x dispersal ability x marine shelf extent).

Eustatic Sea level

The second set of simulations focused on the effect of changing sea level on habitat reachability and hence extinction magnitude across the three greenhouse-icehouse transitions. When climate transitioned to ‘icehouse’ conditions, we changed the position of shallow marine margins to simulate the effect of glacioeustatic drawdown (methods S1.3). We employed the same hypothetical meridional temperature gradients used in the first set of simulations, such that paleogeography and sea level change, but not climate change, varied across the three climate transitions. Shallow marine margins from the first set of simulations were used to model greenhouse conditions, and marine margins during icehouse conditions were estimated by either assuming a globally uniform sea level drop (for the Ordovician and Eocene or based on specific paleogeographic reconstructoins (Pleistocene)[6] (see methods S.1.3). Aside from shifting the position of shallow marine habitat (i.e., sea level change), simulations differed from the previous round only in that the probability of a species dispersing to the new coastline following sea level drop was specified as a function of both its dispersal ability and the distance from the prior coastline (Table S1). For simplicity and because we have few constraints on rates of sea level drop, we invoked ‘jump’ dispersal to new coastlines, rather than attempt to estimate rates of sea level change. That is, species were allowed only one opportunity to jump to the changed marine shelf position. These simulations used the same virtual species and ecological and shelf parameters as the first set of simulations, and extinction magnitudes across simulations were compared using the same framework.

Temperature

The third set of simulations evaluated the potential role of differences in degree of cooling on extinction magnitude across the three greenhouse-icehouse transitions (methods S1.4). These simulations employed surface temperature layers from interval-specific AOGCMs instead of the hypothetical meridional gradients used in previous simulations, and therefore model the combined effects of variation in paleogeography, magnitude of eustatic changes, and magnitude and distribution of sea-surface cooling. Note, however, that the FOAM AOGCMs for the Ordovician and Eocene did not incorporate change in eustatic sea level. Temperature changes for the Late Ordovician were represented by one AOGCM combination, for the Eocene–Oligocene by three AOGCM combinations, and for the Pliocene–Pleistocene by two AOGCM combinations, based on stage-level model availability (models and parameters described in supplementary materials S3, Tables S2 & S3). These simulations used the same virtual species and combinations of ecological and shelf parameters as the first two sets of simulations, and extinction magnitudes across simulations were compared using the same framework.

Sensitivity to definition of shallow marine areas

To evaluate the potential effect of eustatically-driven changes in area of shallow marine habitat on extinction magnitude across the three climate transitions, we ran additional simulations in which every cell within 0 to 200 m water depth was considered as potentially inhabitable if thermal conditions were within the virtual species' niche (see methods S1.5 and Fig. S4). Shallow marine cells were defined based on coarsely-resolved bathymetric layers and virtual species seeded in each of cell (see Table S4 for numbers). Species could disperse to cells within the extent of this shallow marine area based on their dispersal ability. The same simulation framework described above was then used to test for the effect of (i) paleogeography, (ii) paleogeography and sea level drop, and (iii) paleogeography, sea level drop, and temperature change on extinction magnitude across the three greenhouse to icehouse transitions. Unlike the above simulations, both the position *and* the extent of suitable habitat changed with sea level drop in these simulations.

Data Availability Statement

Data from simulations are provided as Supplementary Data.

Code Availability

Simulation code is provided as Supplementary Software.

References Only in Methods

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