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Deep-time climate legacies affect origination rates of marine genera

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Abstract

Biodiversity dynamics are shaped by a complex interplay between current conditions and historic legacy. The interaction of short and long-term climate change may mask the true relationship of evolutionary responses to climate change if not specifically accounted for. These paleoclimate interactions have been demonstrated for extinction risk and biodiversity change but their importance for origination dynamics remains untested. Here we show that origination probability in marine fossil genera is strongly affected by paleoclimate interactions. Overall, origination probability increases by 27.8% (95% Confidence Interval [27.4%, 28.3%]) when a short-term cooling adds to a long-term cooling trend. This large effect is consistent through time and all studied groups. The mechanisms of the detected effect might be manifold but are likely connected to increased allopatric speciation with eustatic sea level drop caused by sustained global cooling. We tested this potential mechanism through which paleoclimate interactions can act on origination rates by additionally examining a proxy for habitat fragmentation. This proxy, continental fragmentation, has a similar effect on origination rates as paleoclimate interactions, supporting the importance of allopatric speciation through habitat fragmentation in the deep-time fossil record. The identified complex nature of paleoclimate interactions might explain contradictory conclusions on the relationship between temperature and origination in the previous literature. Our results highlight the need to account for complex interactions in evolutionary studies both between and among biotic and abiotic factors.

Significance Statement

The effect of climate change on biodiversity is dependent on previous climatic trends. For example climate warming is more deleterious when added to a long-term warming trend. We tested how the interaction of short and long-term climate change affects origination rates through time. Using data from the marine fossil record, we show that origination rates in the last 485 million years tend to increase when climate cooling is superimposed on longer-term cooling trends. These findings might clarify the ongoing debate on the relationship between climate and origination and underline the complexity of evolutionary dynamics and the presence of intricate interactions in Earth's system.

Main Text

Introduction

Biodiversity responses to modern climate change are dependent on past climate (1–3). Climate legacies were important drivers of both extinction and diversification dynamics in the Quaternary (3–6). However, the effect of these legacies on deep-time origination dynamics is largely unknown.

The interaction of climate change with previous climate might affect origination dynamics through a variety of ecological mechanism. If short-term change adds to a long-term temperature trend in the same direction (e.g. a short-term cooling following a prolonged cooling trend), species are less likely to have adaptations to the climatic situation due to niche conservatism (7–9). This lack of adaptation to climatic conditions might result in bottleneck and subsequent founder effects, as well as ecological releases (10–12). Such ecological effects influence rates of evolution and speciation (13, 14). Additionally, climate history can hypothetically drive origination rates of marine genera through global sea level changes, affecting the amount of habitat fragmentation in the continental shelf area. Habitat fragmentation and loss is correlated with the intensity of ecological interactions (15–17) and speciation rates (18, 19).

Building on these ecological concepts through which past climate might affect origination dynamics, we expect that the interaction between climate change and previous temperature trends is a strong determinant of origination rates in the deep-time fossil record. We hypothesize that origination processes are more strongly influenced by temperature change if the change adds to a previous temperature trend in the same direction (synergistic paleoclimate interaction) rather than if the focal change withdraws previous trends (antagonistic paleoclimate interaction). Among synergistic paleoclimate interactions, we expect to detect a weakened origination signal after cooling-cooling due to the “common cause” of sampling biases and biological signal that is driven by low sea levels (20).

Here we analyze how global trajectories of past climate can affect origination probabilities of twelve marine fossil phyla in the last 485 million years (Annelida, Arthropoda, Brachiopoda, Bryozoa, Chordata, Cnidaria, Echinodermata, Foraminifera, Hemichordata, Hyolitha, Mollusca, Porifera). We use paleoclimate interactions as explanatory variables, which are defined as the interaction of short-term temperature change with long-term temperature trends. We first apply regression models using paleo-temperature estimates and sample-standardized genus-level fossil data using a dynamic modeling framework. Dynamic implies that we let the long-term trend vary for each paleoclimate interaction, and subsequently select the best performing model. We then test whether cumulative paleoclimate interactions increase the origination probability of fossil taxa. Our results show, on average, a substantial increase in origination rates when a short-term cooling adds to a long-term cooling trend. To estimate whether this increase is caused by a reduction in available habitat space subsequently to cooling-cooling paleoclimate interaction, we also analyze the effect of a proxy for shelf-area habitat space on origination rates using the same modeling framework.

Results

Origination probability

Cooling-cooling paleoclimate interactions concurred with an increased origination probability (Fig. 1, Table S1). We compared the origination probability for marine groups per paleoclimate interaction, based on the output of our regression models. The overall origination probability was lower after cooling-warming, warming-cooling, and warming-warming paleoclimate interactions compared to the average origination probability of 13.3% per geological stage. To the contrary, cooling-cooling paleoclimate interactions coincides with an increased mean origination probability of 15.1%, whereas the origination probability in all other cases was 11.4%.

Effect size

The effect of cooling-cooling paleoclimate interactions on origination probability is large (Fig. 2, Table S2). The absolute difference between the mean origination probability of cooling-cooling compared to all other paleoclimate interactions was 3.7 (95% Confidence Interval (CI) [3.7, 3.8]). This difference represents a 27.8% percentage increase compared to all other interactions (95% CI [27.4%, 28.3%]). We used the Cohen’s d statistic to compute the effect size as a standardized measure. Cohen’s d for cooling-cooling was greater than 1, indicating a large effect size. All results for the absolute difference, the percentage change, and the effect size are based on generalized mixed effect models and stay consistent when analyzed in a Bayesian regression framework (Fig.2).

Group differences

We additionally tested whether cooling-cooling paleoclimate interactions raised the origination probability of all studied marine groups and if the signal remains robust through time (Fig. 3, Table S3). This was the case for all major phyla with sufficient data and throughout all 80 geologic stages, as all log-odds values including 95% CI’s were above zero. Among all groups, Arthropoda, Brachiopoda, and Bryozoa showed an above average response to cooling-cooling paleoclimate interactions. Through time, the Paleozoic Era showed the highest origination probabilities which then decrease through time, with the lowest values present in the Cenozoic Era. This decrease over time is mainly driven by changing abundances of taxa (Fig. S13). Note that we excluded the Cambrian from the analysis due to insufficient data (see Methods section). Genera from onshore settings showed a greater response to cooling-cooling paleoclimate interactions of 8.5% (95% credible interval [7.1%, 9.8%]) compared to genera from offshore settings (Fig. S1). Our large effect size of cooling-cooling interactions on origination probability remained consistent throughout all studied groups and throughout the whole Phanerozoic.

Continental fragmentation

Approximating potential causal paths through which paleoclimate interactions can act on origination rates, we further tested the effect of continental fragmentation on origination within our modeling framework. We found that a short-term increase in continental fragmentation following on a long-term increase coincides with a substantial spike in origination rates (Fig. 4). The origination probability after such a continental fragmentation interaction was 22% (95% CI [21.1%, 23%]) greater than the average origination rate.

Discussion

The interplay of short-term climate cooling adding to a long-term average global cooling coincided with a profound increase of origination probability. We found this effect to be consistent through time and across all studied groups. Previous studies on the relationship between temperature and origination came to ambiguous conclusions, ranging from a negative relationship (21), no relationship (22, 23), to a positive one (24). Our results show that the relationship between origination rates and temperature is dependent on baseline conditions, which were not previously considered. The large effect size and the conditional dependency of paleoclimate interactions may have obscured any apparent relationship between temperature and origination in previous analysis. Explicitly accounting for dynamic interactions will hence provide a more robust foundation to assess the relationship between Phanerozoic marine diversity and climate. This has been recently demonstrated for modern terrestrial and marine assemblages, where biodiversity responses to recent climate change were conditional on the baseline climate (1).

Our results are remarkable as we expected to detect a weakened origination signal after cooling-cooling paleoclimate interactions due to the “common cause” hypothesis (20). Sampling biases caused by low sea levels partly arise from the removal of originating taxa from the fossil record or a shift of their detection to a later origination datum, leading to an artificially reduced origination probability. These extrinsic biases of fossil data cannot be addressed by sampling standardization (25). The large effect size of cooling-cooling paleoclimate interactions might hence even be an underestimation of the true magnitude. However, we only tested the effect of temperature on origination rates and did not include other environmental parameters (e.g., sea-level, nutrient input) which could be more direct drivers of origination rates than temperature (26). Nevertheless, current research shows that temperature remains a significant predictor of origination rates after accounting for additional environmental parameters (24). Further, temperature can act as a top-down effect, driving the change in other environmental parameters such as sea-level and shelf area weathering. Directly correlating temperature to origination rates, instead of fitting additional mediatory variables, might hence give a more precise estimate of the relationship between climate and origination dynamics.

Other abiotic factors affecting origination probability are not related to temperature. Continental fragmentation can increase the number of geographic barriers restricting animal movement and thus enhancing allopatric speciation rates (27–29). Our results show that the effect of fragmentation on origination rates is particularly large when an increase in continental fragmentation adds to a previous long-term increase. A drop in eustatic sea level is an additional driver for habitat fragmentation. Cooling-cooling paleoclimate interaction resulting in a drop in eustatic sea level due to glaciation leads to reduced continental shelf area and emerging barriers in this main habitat of the majority of the studied fossil groups. Changes in habitat fragmentation are correlated to the rate of ecological interactions (15–17) and speciation rates (18, 19). Both variables used in our analysis, paleoclimate and continental fragmentation, thus share a common causal mechanism to drive origination probabilities. Our results may therefore support the importance of allopatric speciation through vicariance in the deep-time fossil record (30–32).

Habitat fragmentation may not only drive origination rates but also influence the effect of paleoclimate interactions on extinction. Cooling-cooling paleoclimate interactions have also been shown to drive temperature related extinctions in the fossil record, with warming-warming interactions showing the same signal albeit with lower effect size (2). Vicariance might explain why the effect size for warming-warming interactions on extinction risk is reduced compared to cooling-cooling, even though the supposed underlying mechanism of niche conservatism does not differentiate between the two types of synergistic paleoclimate interactions (7–9). During warming-warming paleoclimate interaction, marine taxa could potentially escape adverse environment through range shifts. During cooling-cooling, however, geographic barriers resulting from sea level drop might impede migration, resulting in the observed increased extinction risk (2) and origination probability (this study) compared to warming-warming and all antagonistic paleoclimate interactions. Our findings agree with this proposed mechanism, as we found that paleoclimate interactions have a stronger impact on the origination rate of shallow water taxa, where a drop in sea level does result in more habitat fragmentation than for offshore taxa (see Supplementary Information).

Our study supports that evolutionary processes interact with climate by complex effects showing conditional dependencies. Explicitly integrating these interactions within a dynamic modeling framework leads to an improved discernment of origination patterns in the fossil record. Previous studies on the relationship of temperature and biodiversity in Earth's history came to ambiguous conclusions, a non-conformance likely to be fixed in the future by accounting for paleoclimate interactions (Fig. S2 and S3). However, the mechanisms underlying the grand association between evolution and the observed effect are still unclear. The interpretation offered here, a combination of niche conservatism and ecological effects arising from sea level change resulting in vicariance and allopatric speciation, could be at least partially tested by comparing responses of terrestrial and marine fossil groups to paleoclimate interactions. If sea level change plays a key role, terrestrial groups should show a distinctively different response to cooling-cooling compared to marine groups. Given the large effect of paleoclimate interactions on both extinction and origination, as well as the consistency of this effect through time and studied groups, determining the underlying causes of paleoclimate interactions will improve our mechanistic comprehension of evolutionary dynamics in Earth's history (33).

Materials and Methods

Fossil data

All analyses were conducted at the genus level. We accessed data from the Paleobiology Database (PaleoDB, paleobiodb.org) on 21 April 2021, including all occurrences from the Ediacaran to the Holocene. We filtered the data to only comprise marine animal taxa and heterotrophic protists, i.e. the same taxonomic groups listed in Sepkoski's (33) compendium, following common processing recommendations (34). Previous studies on the relationship between temperature and biodiversity were mainly based on Sepkoski's compendium, rendering this data optimal for comparison purposes of our model structures. We binned the data to one of 80 geological stages (35), ranging from the Ordovician to the Pleistocene. Ordovician stages were resolved using biozone and formation entries due to potential stratigraphic errors (34). Further data cleaning included removal of uncertain taxonomical ranks, duplicates in bins, single-collection, and single-reference taxa as well as missing higher-level taxonomy. Taxa confined to a single stage (singletons) were excluded as they tend to produce undesirable distortions of the fossil record (36). Collections from unlithified sediments were omitted to reduce sampling bias (18). We then applied shareholder quorum subsampling (SQS) for sampling standardization (37), using the divDyn R package (35). SQS is based on frequency distribution coverage of taxa, drawing collections until estimated coverage reaches a fixed target (i.e., until a shareholder quorum is attained). For this, we used a shareholder quorum of 0.8. SQS was applied excluding dominant taxa from all calculations involving frequencies and with a separate treatment of the largest collection in each time slice. We then used the first appearance datum of a genus as its time of origination. The origination signal for each genus was then expressed with a 1 for the time of origination, and a 0 for each time interval the genus was found in the fossil record after the time of origination. The final data set contained twelve major marine fossil phyla with sufficient data to include in the subsequent analysis (Fig. S4, Table S4).

Climate proxy data

To reconstruct temperature change over time, we used the tropical whole surface water (mixed layers < 300 m deep) oxygen isotope data set from a compilation of marine carbonate isotopes (38). This temperature proxy is based on $\delta^{18}O$ values of well-preserved calcareous shells. To get from raw $\delta^{18}O$ values to temperature estimates, we applied the recommended data processing steps of Veizer & Prokoph (38). We first adjusted for the long-term trend in oxygen isotopic composition of seawater and averaged records from tropical and subtropical records. We then assigned the temperature data to geological stages to provide global mean temperature for each of the 80 stages used in our analysis. We additionally tested whether our choice in $\delta^{18}O$ source and processing method biased our inference by repeating our whole analysis with $\delta^{18}O$ isotope values from a different compilation and a different conversion of isotope values to temperature (see Supplementary Information).

Generalized linear mixed effect models

All analyses were carried out in R (39). We used the lme4 package (40) to perform the regression analysis, and the tidyverse package compendium (41) for data processing and visualization. We quantified the effect of temperature change interacting with past temperature trends on origination probability using generalized linear mixed effect models with a binomial family error (GLMMs) (42). We used the origination signal from the fossil data as a response variable and a single interaction term including the long-term temperature trend and the short-term temperature change as a predictor variable:

GLM (Origination ~ Trend : Change + (1 **|** Genus), Family = Binomial).

Using the genus-level as a random effect, we accounted for the multiple occurrence of the same genus within the time-series fossil data. Additionally including stages as a second random effect did not increase model performance (Table S8, Fig. S5).

The short-term temperature change was calculated as the change in temperature for each geologic stage compared to the previous stage. Long-term temperature trends were calculated using ordinary least squares following the processing steps of Mathes et al. (2). For each stage included in the analysis, we calculated ten stages starting one stage prior to the focal stage, each covering a successively growing time of temperature history. We then used a dynamic model framework to select the best performing long-term trend (Table S5). This implies calculating 10 GLMMs for each trend while keeping the short-term change fixed. From these 10 GLMMs, we then selected the best performing model using Akaike's Information Criterion (AIC) . Instead of calculating one model for all short-term changes, we distinguished short-term warming from short-term cooling. This enabled us to quantify the differences in origination probability per paleoclimate interaction (cooling-cooling, warming-cooling, cooling-warming, warming-warming, where the first word denotes the long-term temperature trend, and the second word the short-term temperature change). We used AIC for comparison of model performance. For likelihood approximation, we applied adaptive Gauss-Hermite quadrature (43), which reduces bias and is more robust than other approximation methods (42). We used 25 quadrature points per scalar integral, which is the maximum number of nodes in the quadrature formula of the lme4 package.

Origination probability

We separated the predicted origination response of each type of paleoclimate interaction from our GLMMs using the predict() function on the actual fossil data. Any resulting distributions for the origination probability hence reflect climate conditions experienced by the focal fossil group. We calculated the average origination probability as the mean of both model intercepts (i.e., of the model for short-term warming and for short-term cooling).

Effect size

We applied non-parametric bootstrapping (44) (Fig. S6) and Bayesian estimation (45) to the predicted origination response of our GLMMs to calculate the difference in means between origination probability after cooling-cooling compared to all other paleoclimate interactions. While doing so, we accounted for the non-parametric nature of the data (Fig. S7). Bootstrapping was conducted via the infer package (47) based on 2000 repetitions. For Bayesian estimation, we used a Markov Chain Monte Carlo method with four chains, 1000 iterations, and 500 warm-up iterations via the brms package (48). We used a weakly informed prior for the group mean based on realistic values for origination rates. We further constrained this prior to values between 0 and 100, representing the absolute minimum and maximum values for origination rates expressed in percentage points. The prior for the response variable was sampled from the Student's t-distribution, rendering the model more robust against outliers. We further modeled the sigma coefficient for each paleoclimate interaction individually, allowing group-wise comparisons. The prior for these group variances was sampled from the cauchy-distribution. All model estimates successfully converged using these priors and model parameters. The overall increase of origination probability after cooling-cooling paleoclimate interactions was calculated by dividing the estimated difference of means by the baseline probability of origination. Further, we calculated Cohen's d effect size based on the raw output of our GLMMs as well as posterior distributions after Bayesian estimation using the formula:

$$\frac{\left(\mu_1 - \mu_2\right)}{\sqrt{\left(\sigma_1^2 + \sigma_2^2\right)/2}}$$

We then calculated 95% Wald confidence intervals for the applied non-parametric bootstrapping results and 89% highest posterior density intervals for the Bayesian estimation (49). Cohen's d is reported to present the magnitude of the reported effects in a standardized, scale-independent metric and is aimed to facilitate the incorporation of our results in a meta-analytical framework.

Group differences

Based on the results from our GLMMs, we calculated the log-odds ratio for each major fossil group and for each Phanerozoic Era spanning all studied stages. A second approach was to group geologic stages together to get to a finer temporal resolution than the Phanerozoic Eras (Table S3). Grouping of the stages was necessary to obtain a sufficient number of observations to calculate the log-odds ratio and was based on the number of stages included, resulting in evenly spaced intervals. The oldest interval ranged from the Tremadocian to Lochkovian, the second from the Pragian to Artinskian, the third from the Kungurian to Pliensbachian, the fourth from the Toarcian to Turonian, and the youngest period from the Coniacian to Pleistocene. We did not calculate group differences for phyla where data were insufficient to get a log-odds ratio estimate. To compare changes between shallow and deep-water taxa, we used the environmental information included in the fossil occurrence data set. We separately predicted the origination response for onshore and offshore taxa using our GLMMs. We then calculated the difference in means between origination probability after cooling-cooling compared to all other paleoclimate interactions for each group using Bayesian estimation. The comparison between onshore and offshore taxa was then conducted using samples from the posterior of the Bayesian estimation model (Fig. S1).

Continental fragmentation

To estimate whether habitat space and vicariance might be the mechanisms through which paleoclimate interactions act on origination probability, we included continental fragmentation as an explanatory variable in our model framework. We used a continental fragmentation index (29) (Fig. S8) accessed via the accompanying GitHub repository (https://github.com/UW-Macrostrat/PNAS_201702297). Data processing was similar to processing of temperature data, including the calculation of short-term changes and long-term trends in continental fragmentation. We then compared the origination probability for marine genera for each possible interaction of short-term and long-term continental fragmentation (increase-increase, increase-decrease, decrease-increase, decrease-decrease) using the same analysis as for paleoclimate.

Robustness testing

We further conducted additional tests on both raw data and our models to test for explicit biases in our analytical framework. These robustness tests and their results are described in detail in the accompanying supporting information file and include: A model comparison between traditional model estimates and paleoclimate interactions, cross-correlation tests for temperature data and the continental fragmentation index, tests for the inclusion of an additional random effect in the GLMMs, tests for the dependence of inference on $\delta^{18}O$ isotope data for paleo-temperature estimation, and posterior predictive checks as well as convergence diagnostics for the Bayesian estimation.

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Figure legends

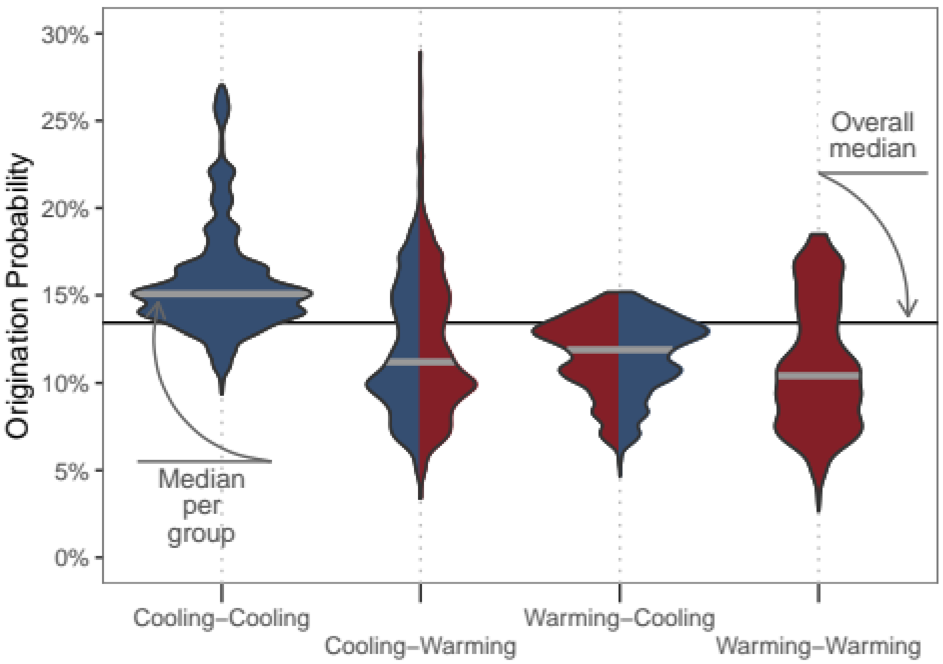

Figure 1. Origination probability. Total response distributions to paleoclimate interactions as predicted by generalized linear mixed effect models. Thick gray lines show the median origination probability per paleoclimate interaction, and the black line depicts the median probability for all interactions combined.

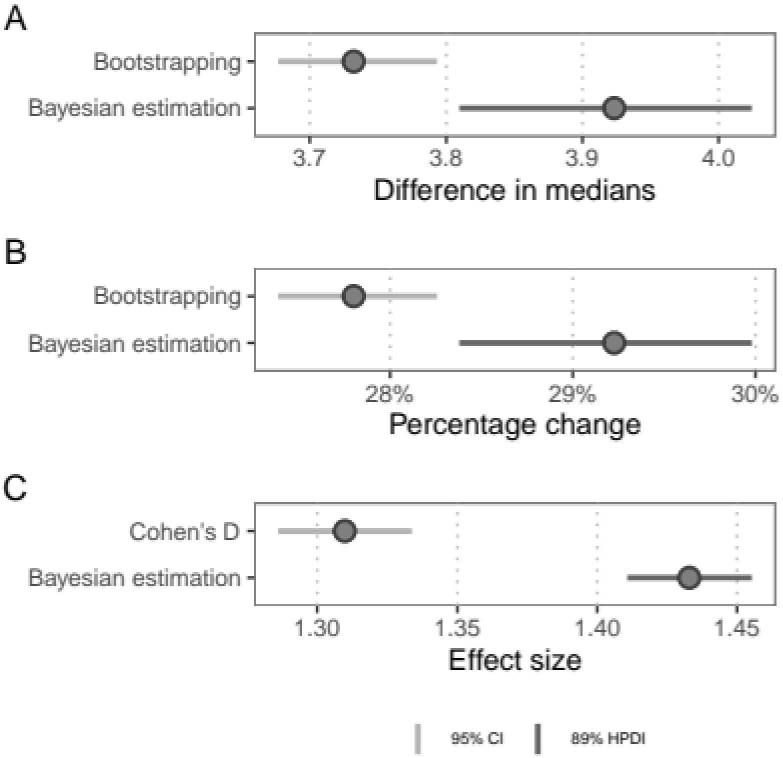

Figure 2. Effect size. A) Difference in medians between origination probability after cooling-cooling compared to all other paleoclimate interactions. B) Overall increase of origination probability after cooling-cooling paleoclimate interactions compared to baseline probability. C) Cohen's d effect size of the observed change in probability after cooling-cooling paleoclimate interactions. Points show median estimates. Light gray lines delineate 95% confidence intervals (CI) based on non-parametric bootstrapping. Dark gray lines depict 89% highest posterior density intervals (HPDI) based on Bayesian regression.

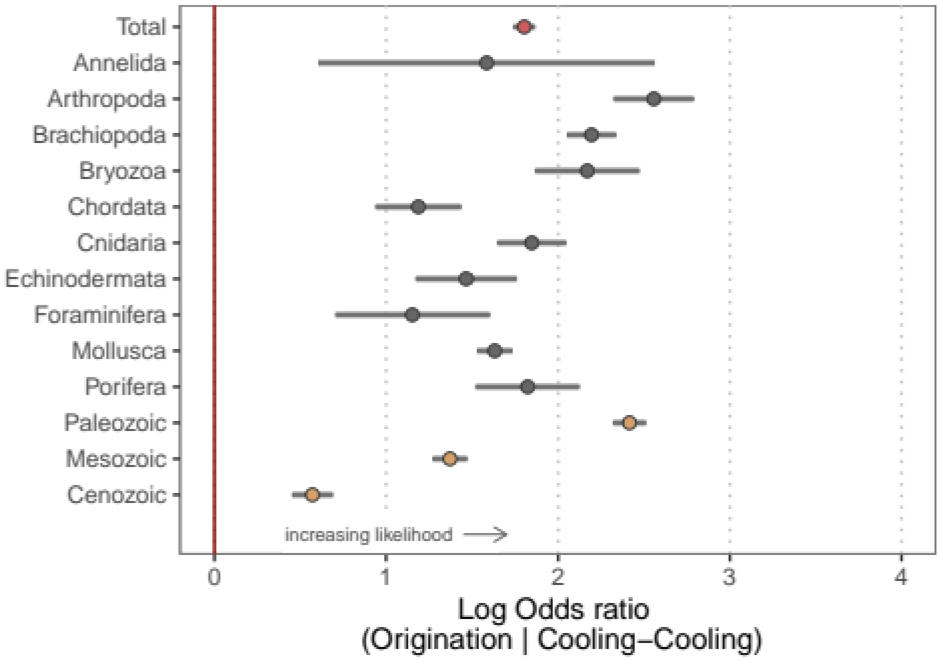

Figure 3. Group differences. Origination likelihood for all major phyla and across time after cooling-cooling compared to all other paleoclimate interactions. The red point shows the overall response, gray points per phyla, and brown points response per Era. Gray lines show 95% confidence intervals. The phyla Hemichordata and Nematoda as well as the Cambrian were removed from the analysis due to insufficient data. The red line delineates a log odds ratio of zero. Values above this line indicate a higher probability to originate after cooling-cooling compared to all other paleoclimate interactions.

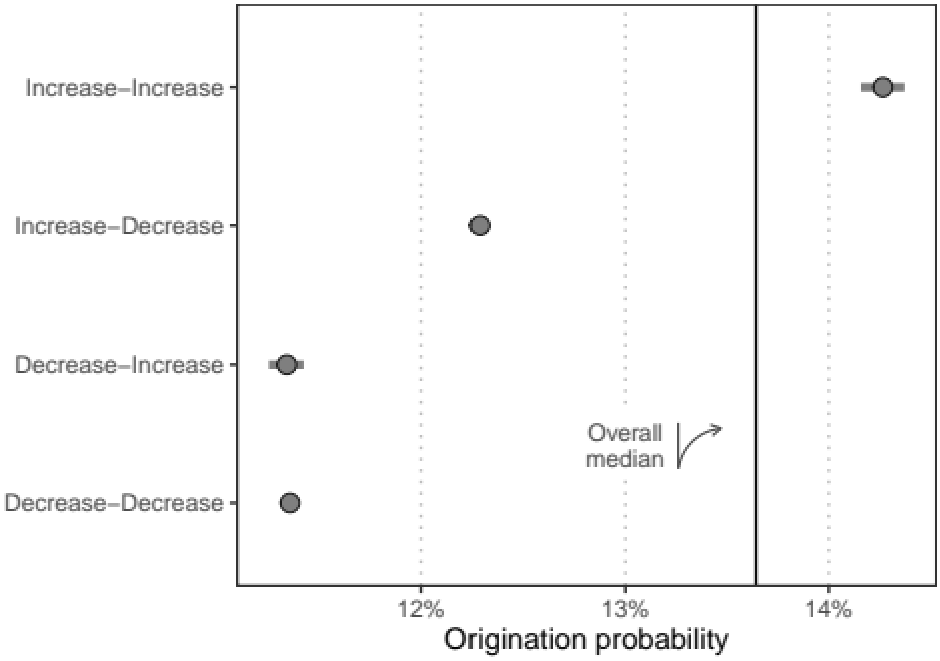

Figure 4. Continental fragmentation. Median origination response per continental fragmentation interaction as predicted by generalized linear mixed effect models based on a continental fragmentation index. The black line depicts the median origination probability for all marine genera, and gray lines delineate 95% confidence intervals.