

How predictable is extinction? Forecasting species survival at million-year timescales

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Abstract

A tenet of conservation palaeobiology is that knowledge of past extinction patterns can help us to better predict future extinctions. Although the future is unobservable, we can test the strength of this proposition by asking how well models conditioned on past observations would have predicted subsequent extinction events at different points in the geological past. To answer this question we analyze the well-sampled fossil record of Cenozoic planktonic microfossil taxa (foramanifera, radiolarians, diatoms, and calcareous nanoplankton.) We examine how extinction probability varies over time as a function of species age, time of observation, current geographic range, change in geographic range, climate state, and change in climate state. Although the best-performing model includes time-varying effects and historical covariates (change in range and change in climate) the improvement in predictive power over models with constant effects and no historical covariates is very minor. Our models have a 70-80% probability of correctly forecast the rank order of extinction risk for a random out-of-sample pair, implying that determinants of extinction have varied only modestly through time. An important caveat is that human impacts may substantially disrupt range-risk dynamics so that the future will be less predictable than it has been in the past.

Keywords: conservation, palaeobiology, extinction, forecasting

1 Introduction

The intensifying biodiversity crisis confronts conservation biologists with the difficult task of trying to predict which species are most threatened with extinction in the near future. Predicting which species will go extinct is difficult because reliable population and geographic range time series are typically known for only the past few decades in even the best-studied groups, and because few modern extinctions have been adequately documented. This has led to the suggestions that some risk assessments might be improved by incorporating palaeontological data [1, 2]. The fossil record preserves information about the full histories, include ultimate extinction, of thousands of lineages, and this information can help to augment the shorter-term higher-resolution data used to make risk assessments of extant taxa.

Past palaeobiological studies of extinction have frequently focused on identifying and measuring the effect of various potential predictors on extinction risk [3–9] or on how to identify or measure these effects [10–15]. This focus means that while we have a good understanding of which factors are strong and general determinants of extinction risk, we have less knowledge of how accurate or strong our predictions about the differences in extinction risk are.

Here we ask how precise risk predictions based on fossil data might be. Because future extinctions are unobservable we cannot directly evaluate the ultimate performance of such predictions. However, we can address the question by taking a given point in the geological past, developing a predictive model based on extinction patterns prior to that point, and assessing the predictive performance of this model on unobserved (e.g. “future”, from the point of view of the model) extinction/survival events.

Extinction intensity (average rate) and selectivity (difference in risk between taxa) vary through time and the relative risk of extinction exhibited by different taxonomic groups and how that risk varies over time is an important dynamic which shapes the rate and structure of extinction [6, 8, 16, 17]. This variation also raises a question: given that extinction intensity and selectivity change over time, how accurate are our assessments based on past events likely to be when applied to the future? Putting aside the important question of how human activities will alter the determinants of future extinction risk, we can address this uncertainty by specifically including and modeling the temporal variation in extinction risk across a range of extinction intensities and selectivities.

Numerous studies have established that geographic range is one of the most important determinants of extinction risk in the fossil record, and that a species geographic range can be highly variable over geologic time [6, 18–24]. The degree to which the past can help to predict the future fates of species depends in part on the degree to which species geographic range trajectories are deterministic versus Markovian [20, 21, 25, 26]. In the former case, knowledge of the specific past trajectory of a species – whether its range has expanded or contracted over a given time span – might help to improve assessments of its current risk. In the latter case, only the current range of the species conveys useful information about its current risk, although we can still use prior extinction patterns to augment predictions by evaluating the relative extinction risk of species that had similar ranges in the past. Discriminating among these alternative models is thus very important for determining how best to incorporate fossil data in present risk assessments.

For this exercise we chose to analyze one of the best-sampled and studied fossil records – the Cenozoic record of skeletonized marine planktonic microorganisms (Foraminifera, Radiolaria, Diatoms, and Coccolithophores). These data are readily available through the Neptune database, an online repository of species occurrences obtained through the Deep Sea Drilling Program and the Ocean Drilling Project [27, 28]. This database provides abundant samples in space and time, a high degree of temporal resolution for the entirety of the Cenozoic, and has an internally consistent taxonomic identification strategy – as close to ideal data for this analysis as possible. The Neptune database records multiple phyla-scale taxonomic groups for over 60 million years, with incredible temporal resolution supported by the various age-models of the deep-sea cores from which the occurrences are recorded. Analyzing patterns of extinction and global occurrence at fine temporal scales means we can better elucidate

72 how well we can predict species extinction at human-relevant scales.

2 Materials and Methods

2.1 Data Specifications

75 We analyzed microfossil occurrence information from the Neptune Database <http://www.nsb-mfn-berlin.de/nannotax> [27, 28]. This occurrence-based dataset includes calcareous
nannoplankton, diatoms, foraminifera, and radiolarians. Occurrences were filtered to include
78 only those species with first occurrence was no more than 63 Mya. This filtering criterion
excludes taxa that survived the K/Pg extinction or arose during its ecologically unusual
recovery interval, and ensures that our occurrence histories fully overlap with the temperature
81 time-series used as a potential extinction risk predictor (see below).

All fossil occurrences were assigned to 1 My bins based on the estimated age of the fossil
occurrence as listed in the Neptune Database. After binning, each taxon’s geographic range was
84 calculated for each of the 1 My bins in which it occurred. Geographic range was calculated as
the maximum great circle distance on an ellipsoid (i.e. the Earth) between any two occurrences
of that species; this distance was measured in kilometers.

87 Average global temperature of each 1 My bin was calculated from estimates based on
Magnesium/Calcium isotope ratios Cramer et al. [29]. We use Mg/Ca rather than oxygen
isotopes to avoid confounding effect of varying ice-volume – this property is of particular
90 importance for this analysis as polar ice-caps develop midway through the Cenozoic. Our
data source, Cramer et al. [29], estimated temperature for every 0.1 My from 0 to 63 Mya.
The temperature estimate for each 1 My interval was calculated as the mean of all estimates
93 within that interval.

See Section S1.1 for a further explanation on how observations were temporally binned, and
how our covariates were standardized and transformed prior to analysis.

96 2.2 Model Specifications

We used a discrete-time survival modelling framework to estimate how well we can predict
extinction risk at one million year time scales. At its core, our model is a multilevel logistic
99 regression with taxon age in millions of years as a varying intercept [30]. We considered four
different models involving different permutations of covariate effects (fixed or time-varying)
and historical covariates: covariate effects constant over time and no historical covariates
102 included (Model C), covariate effects allowed to vary over time but no historical covariates
included (Model V), covariate effects constant over time and historical covariates included
(Model CP), and covariate effects allowed to vary over time and historical covariates are
105 included (Model VP). The C and P models attempt to predict based only on present state,

whereas the CP and VP models allow for the possibility of non-Markovian behaviour by including change in state from the previous time increment.

108 We always included species age at time of observation (i.e. observed prior duration) as a
non-nested varying intercept term. This factor may or may not contribute to differences in
species extinction risk over time [4, 31–35], but its inclusion in our model is critical to its
111 nature as a survival model [30].

See Table 1 for further explanation of how the four models we considered differ from each
other. A complete description of the statistical model used in this analysis is available in
114 Section S1.2. Additionally, the full description of how these models were implemented and
coded, including choice of priors, is available Section S1.3.

Table 1: Models and their definitions

Code	Description	Covariates	R Formula Syntax ^a
C	Constant effects, no historical cov.	Geographic range, temperature	event ^b \sim range ^c + temp ^d + (1 age ^e /phylum ^f)
V	Varying effects, no historical cov.	Geographic range, temperature	event \sim range + temp + (1 + range + temp phylum) + (1 age/phylum)
CP	Constant effects, historical cov.	Geographic range, change in geographic range, temperature, previous temperature	event \sim range + range_diff ^g + temp + temp_lag ^h + (1 age/phylum)
VP	Varying effects, historical cov.	Geographic range, change in geographic range, temperature, previous temperature	event \sim range + range_diff + temp + temp_lag + (1 + range + range_diff + temp + temp_lag phylum) + (1 age/phylum)

^a See Equation S2 for full statistical model definition.

^b Species observation where 1 if time of last observation, otherwise 0.

^c Species geographic range in log km². Mean centered, scaled to sd = 1.

^d Global temperature in degrees C. Mean centered, scaled to sd = 1.

^e Species are at observation in millions of years.

^f Taxonomic group of species (i.e. Foraminifera, Diatoms, Radiolarians, Calcareous nannoplankton).

^g Change in geographic range since last observation.

^h Temperature at previous observation.

2.3 In-sample and out-of-sample forecasting

We are interested in our models' performance in two contexts: in-sample performance, and out-of-sample predictive performance (i.e. forecasting).

In-sample forecasting means we are estimating how well our model predicts extinction probability for observations that that model was fit to. This is a posterior predictive check in that we are comparing the posterior predictive distribution to our observed data. In-sample forecasting measures, however, are not necessarily good estimates of the model's ability to predict data from the future [36].

We are particularly interested in understanding how well our model forecasts extinction probability of data from the future that the model was not fit to (out-of-sample data). To quantify our ability to forecast species' extinction risk, we estimated average out-of-sample forecasting performance using 5-fold time-series cross-validation. For time-series data, the folds (data partitions) are approximately equal segments of time. Each fold represents a sequence of time points. With 63 time points, each of the five folds represents approximately 13 million-year time increments. It is important to bear in mind, however, that each time increment includes many (100s-1000s) individual observations.

k -fold cross-validation for time series follows a specific sequence of procedures [37, 38]. First, the model is fit to the first fold (time segment), and the posterior estimates of that fit are then used to forecast the extinction probability of the second fold (i.e. the future). Then the model is fit to the combined first and second folds, and the posterior estimates of that fit are used to forecast the extinction probability of the third fold. Continuing, the model is then fit to the first three folds combined and is then used to forecast extinction probabilities for the fourth fold. Finally, the model is fit to the first four folds combined and then is used to forecast the fifth fold. The results from these forecasts are then combined to yield our estimate of expected out-of-sample performance.

The relative adequacy of the four model variants was compared using the area under the receiver operating characteristic curve or AUC [39, 40]. This measure is commonly used to measure the performance of classification models as it has the desirable characteristic of comparing the model's true positive rate with its false positive rate, as opposed to accuracy which only considers true positives. AUC ranges between 0.5 and 1, with 0.5 indicating no difference in classification from random and 1 indicating perfect classification. AUC can be interpreted as the probability that our model correctly ranks the relative extinction risks of a randomly selected extinct-extant species pair [39, 40]. AUC values of approximately 0.8 or greater can be considered "good" [41], so we interpret values between 0.7 and 0.8 could then be considered "fair," and values between 0.6 and 0.7 as "poor."

See our code repository at <https://github.com/psmits/trident> for full code details. This entire analysis was coded in R and uses tidyverse and tidyverse adjacent tools such as `dplyr` [42], `purrr` [43], and `tidybayes` [44]. Additionally, all of our models were written using the `brms` [45, 46] R package, which implements Stan-based Bayesian models which are fit via Hamiltonian Monte Carlo [47].

3 Results

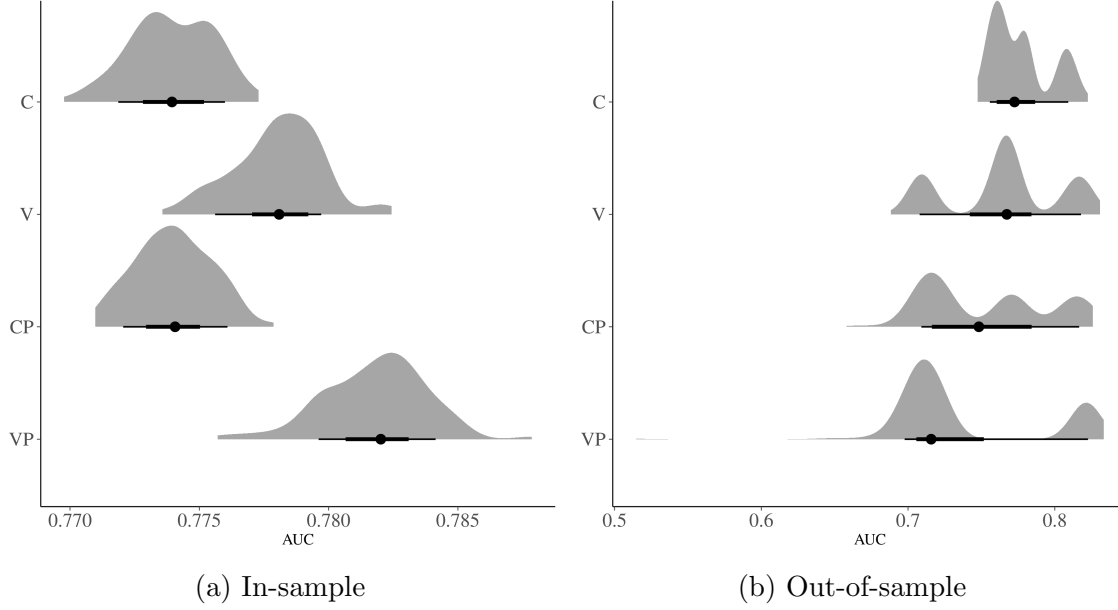


Figure 1: In-sample (1a) and out-of-sample (1b) AUC estimates for each of our four models. These estimates are calculated from the models posterior predictive distribution or from predictions made to new data, respectively. Models with a higher AUC values indicate better performance over models with lower AUC values. AUC is bounded between 0.5 and 1. See Table 1 for a description of each of the four models.

3.1 In-sample forecasting adequacy

The in-sample model comparisons are useful for comparing the relative ability of our models to represent the data they were fit to. Comparison between the posterior distributions of in-sample AUC for each of the four models demonstrates that all of our models have approximately equal in-sample forecasting performance (Fig. 1a). The parameter rich model VP has the greatest median in-sample AUC when compared to the other three models, but there is substantial overlap in their posterior distributions. Additionally, while our parameter rich model VP is possibly the most adequately performing model, the difference or improvement to performance is minimal at best – all four models have approximately equal in-sample AUC posterior distributions. All the in-sample AUC estimates from our models are concentrated on an AUC value of 0.77. It is therefore hard to conclude that there is one “best” model which we can rely upon as they are all nearly functional equivalent.

Depending on the taxon-model combination, there are between zero and 4 time intervals where our posterior distribution of in-sample AUC has a median value less than or equal to 0.5 (Fig. 2). However, this pattern is absent for the posterior estimates of in-sample AUC for Foraminifera and Radiolaria as fit by the VP model. In contrast, there are fewer periods of

low model performance for calcareous nannoplankton and Dinoflagellates as estimated from
 174 our VP model than in those estimates from the other three model variations.

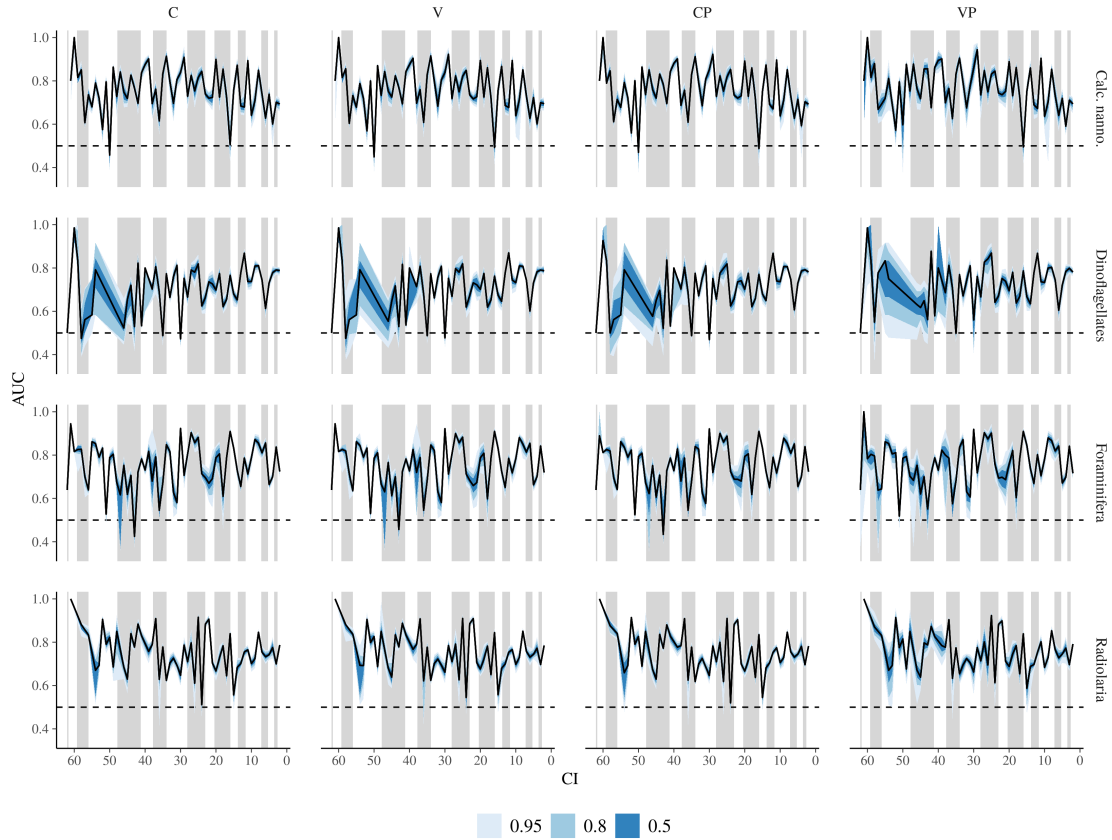


Figure 2: Comparison of in-sample forecasting performance measured by AUC for each of the four models, arranged over time and by taxonomic group. These estimates reflect each model’s fit to the various taxonomic groups over time. The black line corresponds to the median AUC value, while the envelopes correspond to multiple credible intervals as indicated in the legend. In all cases, higher AUC values indicate greater predictive performance versus lower AUC values. See Table 1 for a description of each of the four models.

3.2 Out-of-sample forecasting performance

Expected out-of-sample forecasting performance was estimated using five-fold cross-validation
 177 for time series [37, 38]. The resulting distribution when all folds are combined is highly
 multimodal as expected given that they are fit to and estimated from different data sets with
 different numbers of observations [36]. This multimodality increases with model complexity
 180 (Fig. 1b), most likely because the complex models allow for predictor effects to vary with
 time, allowing a greater range in possible parameter values which in turn yield a greater
 range of posterior predictions.

183 Comparison the in-sample AUC estimates to the expected out-of-sample AUC estimates

reveals a similar range in performance for all models (Fig. 1a, 1b). Interestingly, the differences in posterior predictive distributions of AUC between the four model variations is reduced in out-of-sample prediction. For example, the VP model no longer has the greatest median AUC of the four models (Fig. 1b). For this reason the rank order of median out-of-sample AUC is different from the rank order of median in-sample AUC. However, making interpretations based only on the median AUC estimates is incorrect – our estimates are the full posterior, not individual points. Because of this, the four models are effectively indistinguishable in their out-of-sample forecast performance (Fig. 1b).

The posterior predictive distribution of expected out-of-sample AUC over time and across taxonomic groups are nearly identical for each of the four models (Fig. 3).

In the analysis of the in-sample forecast performance of the four models, we noted that there were time intervals where our predictions were no better than random (Fig. 2). This occurrence is generally much rarer for the posterior distribution of AUC from the out-of-sample forecasts. The major exception to this pattern are our estimates for the Dinoflagellates, which have at least one time interval for all four models in which the median AUC of the out-of-sample forecasts were no better random. The only other group for which median posterior predictive estimate of out-of-sample AUC reaches 0.5 is calcareous nannoplankton, and then only with the V model.

We compared the difference in our AUC estimates from the out-of-sample forecasts to the AUC estimates from our in-sample forecasts by subtracting the in-sample AUC estimates from the out-of-sample AUC estimates (Fig. 4). A difference in AUC close to 0 indicates complete congruence between the in-sample and out-of-sample forecasts. A positive difference indicates that our out-of-sample forecasts are actually higher performing than our in-sample forecasts, while negative difference indicates poorer out-of-sample performance than in-sample forecast. Divergences between our out-of-sample and in-sample forecasts are rare and tend to not form multimillion year patterns, consistent with the broad visual congruence between the in-sample and out-of-sample forecast performance (Fig. 2, 3). The only major multimillion year pattern indicating significantly poorer out-of-sample forecast performance than in-sample forecast performance is for Radiolaria based on the VP model concentrated around 30 Mya (Fig. 4).

4 Discussion

We find that all of our models are expected to correctly forecasting the rank order of extinction probability for a randomly selected extinct-extant pair of future observations between 70% to 80% of the time (Fig. 1b). One of the most striking aspects of these results is the similarity in forecasting performance for in-sample and out-of-sample observations. A slight decrease in performance when dealing with out-of-sample observations makes sense: each of the models fit during cross-validation is based on fewer data than the model fit on the full data (between 1/5th to 4/5ths of the original). Additionally, a potential decrease in precision when forecasting the future of extinction risk is to be expected as the future will always differ from the past in some respect. However, the similarity between the in-sample and out-of-sample results indicates that our model is fairly robust to variation in extinction intensity over the

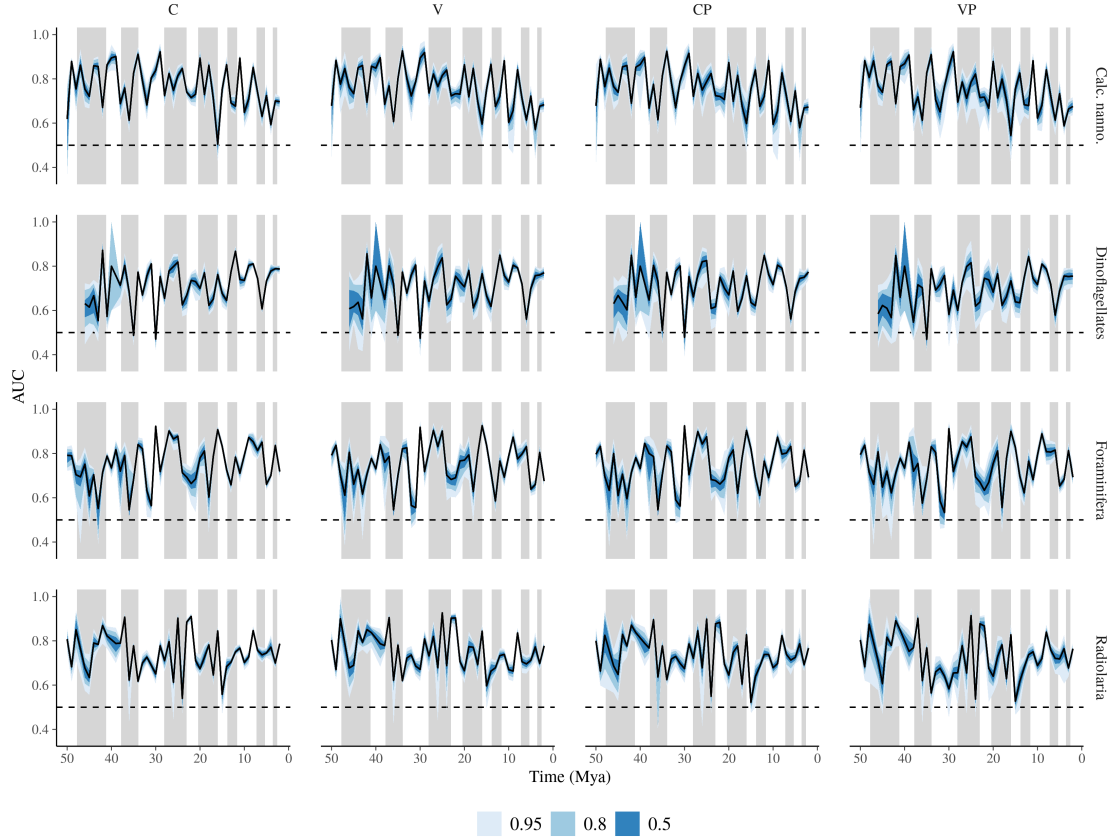


Figure 3: Comparison of out-of-sample AUC values over time as aggregated by taxonomic group for each of the four models. The AUC of the individual My intervals within each fold is plotted to highlight the heterogeneity in performance within and between folds. This presentation decomposes each of the 12-million year folds by each of the taxonomic groups into the predictions made for each of the million-year intervals. The black line corresponds to the median AUC estimate, with the envelopes corresponding to multiple credible intervals as indicated in the legend. See Table 1 for a description of each of the four models.

Cenozoic. A extremely important caveat, of course, is that human impacts may substantially alter present and future extinction risk dynamics relative to the average Cenozoic state, so that the future may become less predictable than it has been in the past [1, 48].

We also find that our four models are practically identical in their ability to make in-sample and out-of-sample forecasts. Although the in-sample AUC estimates differ between models, all of these estimates are in a narrow range of possible AUC values (Fig. 1a). While the “best” model does include the historical covariates and allows all covariate effects to vary over time, its practical difference in performance versus the other models is negligible (Fig. 1b). Thus even though the VP model has a statistically greater AUC for in-sample forecasts than the other three models, this result is not practically or scientifically significant. The results of the out-of-sample forecasts illustrate this point in full, as all four models have functionally identical out-of-sample performance. This including geographic range trajectory results in only very minor improvements in forecasting accuracy. This contrasts with findings from coral

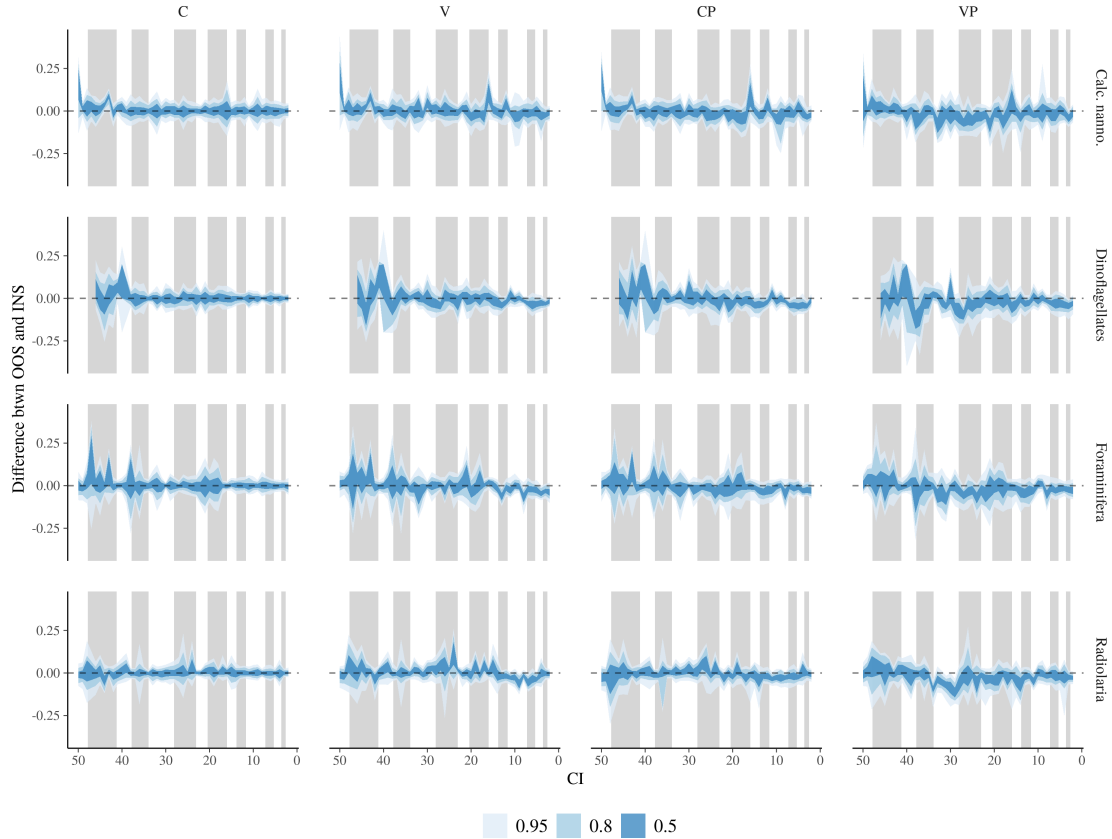


Figure 4: Comparison between our out-of-sample forecasts and in-sample forecasts for all models. This value is calculated as the values presented in Figure 3 minus those values presented in Figure 2. A differences close to 0 indicate complete congruence between in-sample and out-of-sample forecasts, while a positive difference indicates that our out-of-sample forecasts are actually higher performing than our in-sample forecasts, and a negative difference indicates poorer out-of-sample performance than in-sample forecast. See Table 1 for a description of each of the four models.

genera [2] and suggests that further investigation of other taxa, timescales, and environments may help to elucidate the conditions under which past geographic range trajectories are most informative about future extinction risk.

The relative quality and consistency of our models out-of-sample forecasting performance is encouraging given that its estimates are based on very limited biological and environmental information about the taxa. Even our most complex models only account for a few simple aspects of geographic range, prior history, and taxonomy. The principal reason we were not able to include more biological information in our models is that we lack suitably detailed life history or ecological information for many marine micro- and nannoplankton. Foraminifera are an exception to this problem as aspects of life history, ecology, and physiology are known for many foram species [8]. However, comparable information does not exist all foram species, nor does this type of data exist for the other three taxonomic groups studied here. Future analyses including this type of information and focused more narrowly on the foraminifera

may be informative.

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