1   **Occupancy history influences extinction risk of fossil marine microplankton groups**

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25 **Abstract**

26   Geographic range has long been acknowledged as an important determinant of extinction

27 risk. The trajectory of geographic range through time, however, has not received as much

28 scientific attention. Here, we test the role of change in geographic range – assessed by a measure

29 of proportional occupancy of grid cells – in determining the extinction risk in four major

30 microplankton groups: foraminifera, calcareous nannofossils, radiolarians, and diatoms. Logistic

31 regression was used to assess the importance of standing occupancy, occupancy change, and

32 sampling probability in the extinction risk of species. We find that while standing occupancy is a

33 major determinant of extinction risk in all microplankton groups, change in occupancy accounts

34 for an average of 52% of the explanatory power of the three analyzed variables, with a maximum

35 value of 92%. Sampling probability was also found to be consistently informative, with an

36 average of 6% and a maximum value of 22%. Our results highlight the importance of

37 incorporating both geographic range and its change through time, as well as sampling

38 probability, into extinction models. The ability of occupancy trajectory to help predict extinction

39 risk underlines the necessity of paleontological data in modern conservation efforts.

40 **1. Introduction**

41   There is a rich literature documenting the effect of smaller geographic range sizes in

42 contemporary and ancient extinctions (e.g. Foote et al., 2016; Foote et al., 2007; McKinney,

43 1997; Payne and Finnegan, 2007; Purvis et al., 2000; Staude et al., 2020). The International

44 Union for the Conservation of Nature (IUCN) uses geographic range size as one of the five key

45 criteria by which the "Red List of Threatened Species" risk status of a species is assessed (Mace

46 et al., 2008). The temporal trajectory of geographic range as a predictor of extinction has been

47 sparingly explored in the paleontological literature (Liow et al., 2010; Foote et al., 2007, Tietje

48   and Kiessling, 2013; Kiessling and Kocsis, 2016), but many studies looking at historic

49   extinctions exclude this factor altogether. Increasing anthropogenic impact on biotic systems has

50   been suggested as a contributing factor to species' extinction risks (Ceballos et al., 2015; De Vos

51   et al., 2015; Payne et al., 2016; Wagler, 2011). Understanding factors that increase a species' risk

52   of disappearance, and how they can be mitigated, is thus more important now than ever before.

53   Based on a data set of Cenozoic marine invertebrates from the Paleobiology Database

54   (https://paleobiodb.org/), Kiessling and Kocsis (2016), suggested that the trajectory of

55   geographic range has the potential to inform extinction risk. However, the coarse stratigraphic

56   resolution of the macroinvertebrate record (geological stages, about 5 million years in duration)

57   puts constraints on the fidelity of any approach that depends on the spatiotemporal distribution of

58   species. Due to their sheer abundance, unicellular groups are less affected by such issues and can

59   be used for finely resolved studies of assemblage changes (e.g., Strack et al. 2024) and

60   biogeography (e.g., Swain et al., 2024). Variations in the material that make up their tests

61   (calcareous or siliceous) are expected to manifest as either differential fossil sampling or as

62   evolutionary patterns, which presents an opportunity to explore the sensitivity of extinction

63   models under a wider range of scenarios. While accounting for sampling, we assess here the

64   importance of geographic range (expressed as proportional grid occupancy) and its temporal

65   trajectory on extinction risk of marine planktonic organisms. By using a temporally finely-

66   resolved dataset of fossil plankton, as well as with the explicit incorporation of fossil sampling

67   into our models, we can better assess whether the trajectory of geographic occupancy actually

68   influences extinction risk in marine life.

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2. Data and Methods

2.1 Sourcing and cleaning of raw data

We downloaded occurrence records of four major marine microplankton groups from the

Neptune Sandbox Berlin ("NSB"; Lazarus, 1994; Renaudie et al., 2020; data downloaded 30

August 2023) using the R package "NSBcompanion" (Renaudie 2019). These groups were

planktonic foraminifera, calcareous nannofossils, radiolarians, and diatoms. The four data sets

were downloaded with the taxonomy resolved using the IODP Taxonomic Name List Project

(Renaudie et al., 2020), a built-in option that we specified prior to downloading. Additionally,

questionably-identified taxa were excluded from the download. Open-nomenclature taxa and

possibly problematic or reworked occurrences were also excluded using the built-in NSB

download options. The NSB holds taxon occurrences stretching back to the late Jurassic, but we

limit our analysis to the Cenozoic record (i.e. the last 66 million years) to ensure a consistent age

range for all for taxonomic groups, since both the diatom and the radiolarian NSB records only

exist for the Cenozoic.

The NSB database includes the estimated age as well as the modern and estimated paleo-

coordinates (longitude and latitude) of each fossil occurrence calculated internally based on the

plate tectonic reconstruction by Boyden et al. (2011, Fig. S1). Each dataset (foraminifera,

calcareous nannofossils, radiolarians, diatoms) was cleaned to remove any occurrences that were

missing age, paleo-coordinate, and/or relevant taxonomic information. The counts of unique

species and the number of occurrence records in each data set (post-cleaning) are provided in

Table 1. All cleaning and subsequent analyses were carried out in R 4.2.2 (R Core Team, 2022).

Data Set Summaries				
	Foraminifera	Calcareous Nannofossils	Radiolarians	Diatoms
Number of unique species	552	737	840	966
Number of occurrences	96 410	154 052	91 240	91 092
Proportion of extant species with usable records (>1 time bin)	0.051	0.015	0.093	0.119
Number of unique species-bin pairings with "gap-omission" approach, excluding first occurrences (*occupancy change* = NA). Bin size = 1 million years.	3 471	4 814	5 626	4 938

Table 1. The number of unique species, the number of total occurrence records, the proportion of species that are extant and occur in more than one bin, and the number of species-bin pairings (post-cleaning).

We assigned occurrences from each data set to time bins of either 0.1, 0.2, 0.5, or 1 million years, noting that 0.1 million years is currently the lower limit for global correlation. For each time bin size, the first bin stretched from the present (0 Ma) to either 0.1, 0.2, 0.5, or 1 million years into the past. Each subsequent bin encompassed the following increment stretching progressively further into the past. Ages are reported in millions of years before present (Ma).

We assessed stratigraphic ranges as defined by the oldest and youngest fossil occurrences. Due to reworking and other processes, the documented raw ranges may not reflect the true durations of species. Therefore, we also applied the recommended "Pacman profiling" (Lazarus et al., 2012), a stratigraphic outlier correction, to reduce the impact of outliers and reworking on the data. The degree of Pacman trimming on the NSB data was determined via a calibration process that used speciation and extinction ages of a given subset of each taxonomic

111   group. Based on this subset, the degree of trimming necessary to restore the "true" temporal

112   ranges of species could be estimated. Calibration ages were sourced from the Triton database

113   (Fenton et al. 2021) for foraminifera, Nigrini et al. (2006, obtained from Lazarus et al., 2012) for

114   radiolarians, the "Barron Diatom Catalog" (Lazarus et al., 2014) for diatoms, and a custom

115   species list constructed from Mikrotax (www.mikrotax.org; Huber et al., 2017) for calcareous

116   nannofossils. Potential trim values ranging from 0% to 16% of the raw ranges, at 1% intervals,

117   were analyzed. Pacman calibration was carried out on datasets after they had been trimmed to the

118   last 66 million years. Trim values were selected such that they minimized the average absolute

119   difference between the actual and the represented speciation or extinction ages of the species

120   present in the calibration set. The best-performing trim values were implemented in this study,

121   although the key results presented here do not change in the absence of Pacman profiling. Those

122   trim values were as follows: foraminifera (top: 15%, bottom 3%), calcareous nannofossils (top:

123   14%, bottom: 4%), diatoms (top: 11%, bottom: 4%), radiolarians (top: 10%, bottom: 6%). Per

124   capita extinction rates were calculated using the formula from Foote (1999).

125

126   **2.2 Analysis of completeness**

127   In order to quantify the degree to which sampling completeness affected downstream

128   analyses, we employed two separate completeness metrics: the simple completeness metric

129   ("SCM"; Benton, 1985) and the three-timer completeness metric (Alroy, 2008). The three-timer

130   completeness metric was calculated from the three-timer and part-timer counts returned by the

131   "divDyn" R extension package (Kocsis et al., 2019).

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2.3 Calculating occupancy

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136   For each data set, paleo-coordinates of samples were assigned to equal-area geographic

137 cells using the R package "icosa" (Kocsis, 2020) for the calculation of proportional grid

138 occupancy. Proportional grid occupancy is a recognized metric for assessing geographic range in

139 the fossil record, where contemporaneous sampling is impossible and incomplete preservation is

140 common (Foote et al., 2007; Darroch et al. 2022). Several cell-sizes were analyzed ranging in

141 edge length between 3.33° to 2°. There was little variation in results within this range, so the

142 highest resolution (4002 cells with 2° edge length, mean area of 1.3×10^5 km^2) was selected for

143 this study. The present-day distribution of samples can be seen in supplementary Fig. S1.

144   As counts of occupied cells tend to be biased by sampling (Kiessling, 2005), we

145 calculated proportional occupancy of each species in every time bin. Proportional occupancy is

146 simply the number of geographic cells occupied by the species divided by the total number of

147 sampled cells in a given time bin. For clarity, we refer to what is actually proportional occupancy

148 as simply *occupancy* from here forward. Furthermore, the number of unique Longhurst (2007)

149 biogeographic planktonic provinces that were occupied by each species in each time bin was

150 calculated, and the Pearson correlation of this value with the raw number of occupied geographic

151 cells was calculated. Autocorrelation was accounted for by differencing temporally consecutive

152 values prior to calculating correlations.

153

2.4 Change in occupancy

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155   In addition to standing *occupancy*, the change in *occupancy* between consecutive time

156 bins was calculated by taking the natural log of the ratio of *occupancy* in time bin *i* to *occupancy*

157 in time bin *i*-1. The log transformation serves to standardize the magnitude of change and

158   produces positive values for increases in *occupancy* (range expansions) and negative values for

159   decreases in *occupancy* (range contractions).

160   Initially, instances where *occupancy* values in bin *i* or *i*-1 were 0 (no occurrences) were

161   coded as missing data for *occupancy change* and removed from the final data set. While

162   removing these records prevents the inclusion of undefined *occupancy* change values in the final

163   data set, it greatly reduces the number of occurrences for a given taxon, especially for species

164   whose sampling is fragmentary. This effect is magnified by the fact that for each time bin with

165   zero occurrences of a given taxon (a "gap" in that taxon's fossil record), two data points are

166   removed from the final data set for that taxon. This overall loss of data becomes more

167   pronounced with smaller bin sizes.

168   To combat this effect, we employed a "gap-omission" approach, whereby the change in

169   *occupancy* was calculated based on the previous occurrence of the taxon (regardless of when that

170   was) rather than the previous time bin, *per se*. Thus, *i* and *i*-1 do not necessarily correspond to

171   sequential time bins in this approach, but rather consecutive positive sampling intervals for each

172   given taxon. With this approach, consecutive taxon occurrences are included even when

173   separated by "gaps", thus retaining more data to the final data set. Although both approaches

174   yield the same basic results (see Tables S1 and S2), we used the "gap-omission" approach for the

175   sake of retaining a larger data set.

176

177   **2.5 Binomial logistic modeling**

178   For every species, a record of each time bin in which that species occurred was included

179   in the final table as a single row. Each unique species-bin pairing (row) is characterized with the

180   *occupancy* and binary extinction indicator in the focal time bin as well as the change in

181   *occupancy* from the previous time bin. An extinction indicator value of 1 was assigned if an

182   occurrence was the last time bin in which a species occurred for the entire data set (the species

183   went extinct or permanently disappeared from the fossil record during this interval). An

184   extinction value of 0 was assigned for all other occurrence records (the species did not go extinct

185   during this interval).

186   Species that are still extant, or those which only went extinct during the most recent time

187   bin (which spans up to the present), would by default be assigned an extinction value of 1 in the

188   most recent time bin (because the most recent bin is the last occurrence of those species in the

189   data set). To avoid this edge effect, all occurrences from the most recent time bin were removed

190   prior to model fitting.

191   Binomial logistic models were constructed to examine the dependency of extinction on

192   *occupancy* and *occupancy change*. Both the additive and multiplicative effects of *occupancy*,

193   *occupancy change*, and *sampling* (represented by the three-timer value calculated for each bin),

194   as well as the impact of each variable independently, were examined with respect to the per-

195   interval probability of extinction. The multiplicative generalized linear model structure of

196   "glm(*extinction ~ occupancy * occupancy_change * sampling*, family = binomial(link =

197   'logit'))," was used. The best model was selected based on its AIC value.

198

199   **2.6 Model performance and predictor importance**

200   We calculated the adjusted amount of deviance (D^2 of Guisan and Zimmermann, 2000)

201   accounted for by each computed logistic model. Deviance in a generalized linear model is

202   analogous to variance of ordinary linear regression. In each of the 16 data sets (four groups with

203   four time resolutions each), the Lindeman, Merenda, and Gold (1980) indices of correlated input

204   relative importance (henceforth referred to simply as "relative importance") were calculated for

205   the *occupancy*, *occupancy change*, and *sampling* terms with respect to predicting the *extinction*

206 term. The relative importance of the *occupancy change* term was standardized as a proportion of

207 "total importance". This statistical approach was used to represent the explanatory power of each

208 model term with respect to one another, an insight that is not directly apparent with simple model

209 coefficients. Additionally, for each of the additive model outputs, the ratio of the standardized

210 *occupancy change* coefficient to the standardized *occupancy* coefficient was calculated to

211 estimate the relative explanatory power of the *occupancy change* term between data sets.

212   For each of these metrics, the standard error was estimated by bootstrapping the species

213 that make up each set of occurrence records. For each of the 1000 bootstrapping iterations, the

214 set of species whose occurrence records were retained in the data set was determined by

215 resampling with replacement. After each resampled set of species and their occurrence records

216 was determined, every model was re-fit and every metric was recalculated. The standard

217 deviation of all bootstrapped values for a single metric approximates the standard error.

218

219 **2.7 Extinction probabilities of extant species**

220   The World Register of Marine Species (https://www.marinespecies.org/), with the

221 assistance of the R package "taxize" (Chamberlain and Szoecs, 2013), was used to identify

222 extant species. These data on extant taxa were downloaded on 25 September 2023.

223   In order to predict the extinction probabilities of extant species, the data sets were

224 reanalyzed and re-fit to models using only the extinct species. Although this technique reduced

225 the overall amount of data used to fit the model, it allowed for the prediction of extinction

226 probabilities of extant species without circularity. Other than removing extant species, all other

227 processes were carried out in the same way as described above.

228   After selecting the best model for each plankton group, that model was used to predict the

229 extinction probability of extant species. Using the fitted models along with the *occupancy* and

230   *occupancy change* values for each extant species in the present bin (that which ends at the

231   present, 0 Ma), a probability of the binary response variable occurring as a 1 (extinction) can be

232   calculated. This represents the probability that the species will *not* appear again during the next

233   time bin of the same length (that which begins at the present, 0 Ma) or in other future time bins.

234   Because three-timer sampling calculations require bins both before and after the target bin, the

235   present bin lacked a three-timer sampling value. Models were thus fitted without the sampling

236   term for future extinction probability predictions. Extinction predictions were made on extant

237   species subsets without upper Pacman trimming, and the average probability of extinction for all

238   extant species were calculated in each data set.

239

240   **2.8 Robustness testing**

241   Further analyses tested the robustness of our results, specifically for the proportional

242   occupancy's utility as a metric of geographic range and for different datasets. The same analyses

243   at a bin size of 1 million years were carried out using latitudinal range and change of latitudinal

244   range instead of proportional occupancy and its change. Additionally, the same analyses were

245   carried out using proportional occupancy of Longhurst (2007) provinces and the change in

246   proportional occupancy of Longhurst provinces for data sorted into 1 million-year bins.

247   Although containing only records of planktonic foraminifers (many of which were

248   sourced from the NSB), the Triton database includes information on the original purpose of each

249   study from which records were sourced, as well as the age of speciation and extinction for each

250   species. With this additional information, the Triton dataset can be used to confirm the suitability

251   of methods used with the Neptune dataset with a different collection of fossil occurrences. Given

252   that some studies may not record every present taxon if it is not a zonal marker or thought to be

253   particularly informative, the Triton dataset was subset to include only studies whose purpose was

254   noted as "community analysis" (Fenton et al. 2021). Because studies whose purpose was to

255   analyze community structure would likely document all present species, by using this subset,

256   studies that potentially excluded some species were removed from the final data set.

257   Additionally, each included species history was subset to exclude any occurrences that occurred

258   before or after the speciation and extinction ages noted in the Triton dataset (Fenton et al. 2021),

259   respectively, reducing the potential impact of reworked fossils in the analysis. Because each

260   species in Triton was trimmed in this manner, these data did not undergo Pacman profiling as the

261   NSB data did. After these additional data-cleaning actions were taken, the Triton dataset had

262   197,871 usable occurrence records and was analyzed in the same way as the NSB data.

263

264   **3. Results**

265   The utilized datasets show all four groups with elevated extinction rates coming out of

266   the K-Pg and returning to relative stasis approximately 5-15Ma after the K-Pg boundary (Fig. 1).

267   Shortly thereafter, all groups, but especially the siliceous groups, undergo decreases in diversity,

268   corresponding with the Paleocene-Eocene Thermal Maximum (PETM, Fig. S4). Both

269   foraminifera and calcareous nannofossils retain relatively low and stable extinction rates (<0.2)

270   for the rest of the Cenozoic (Fig. 1).

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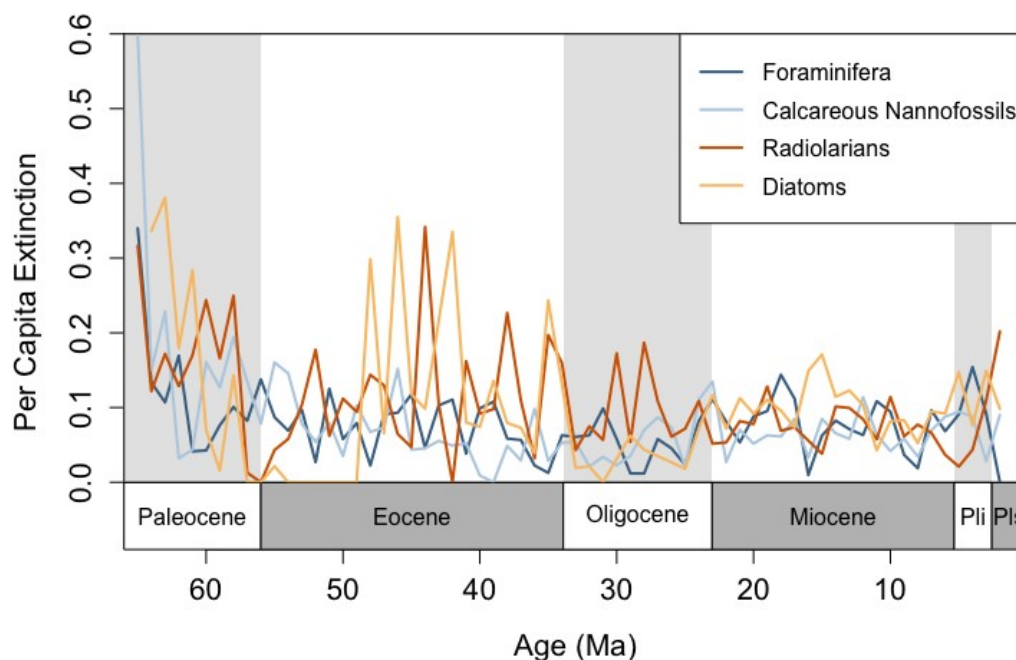
Figure 1. Per capita extinction rates calculated using the formula in Foote (1999) for each of the
four taxonomic groups during the Cenozoic, calculated for 1-million-year bins. The timescale of
Gradstein et al. (2012) was used here to match age assignments in the NSB.

276

277   The extinction rates (Fig. 1) and diversity patterns (Fig. S4) of each plankton group

278   match those of previous analyses of Neptune data (Jamson et al., 2022), and various biotic events

279   in the Cenozoic can be detected. In all analyzed combinations of taxonomic group and bin size,

280   standing *occupancy, occupancy change*, and *sampling* were all retained in the AIC-selected

281   models as informative (Table 2). When considering strictly the simpler additive models, both

282   *occupancy* and *occupancy change* were determined significant in all models (*p = 0.05*).

283   S*ampling* was deemed significant across all bin sizes for calcareous nannofossils, at 0.2 and 1.0

284   Ma for foraminifera, at 0.2 and 0.5 Ma for diatoms, and never for radiolarians.

285

Bin size (Ma):	0.1	0.2	0.5	1.0
Foraminifera	*multiplicative*	*additive*	*multiplicative*	*multiplicative*
Calcareous Nannofossils	*multiplicative*	*multiplicative*	*multiplicative*	*multiplicative*
Radiolarians	*multiplicative*	*multiplicative*	*multiplicative*	*multiplicative*
Diatoms	*multiplicative*	*multiplicative*	*multiplicative*	*multiplicative*

286 **Table 2.** The AIC-selected model formula for each group and bin size combination, on data that
287 was processed with the "gap-omission" approach. "*multiplicative*" refers to the model with the
288 formula: *ex ~ oc * ch * p* , and "*additive*" refers to the model with the formula: *ex ~ oc + ch + p.*
289 "*ex*" represents the binary response variable *extinction*, "*oc*" represents the *occupancy* term, "*ch*"
290 represents the *occupancy change* term, and "*p*" represents three-timer sampling probability.
291

292   The signs of the *occupancy* and the *occupancy change* coefficients were always negative

293 in single-term models, meaning that smaller instantaneous geographic range sizes and more-

294 negative changes in geographic range size both correspond to larger extinction probabilities (Fig.

295 2). The D^2 values and AIC values of each analyzed model combination for each 1-million-year

296 binned data set are depicted in Fig. 3. The maximum D^2 for any model was 0.129, occurring for

297 the multiplicative foraminifera model at a bin size of 1.0 Ma (Table 3). The relative importance

298 of the *occupancy change* term averaged 52.0%, with higher values being achieved with larger

299 bin sizes.

300
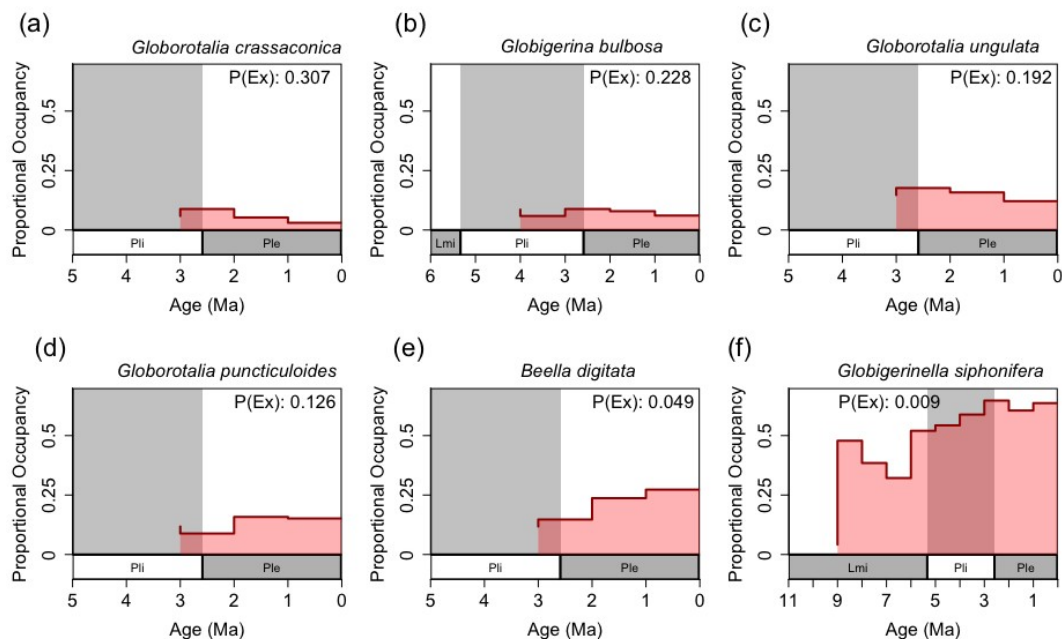
Figure 2. A selection of proportional occupancy through time plots for 6 species of foraminifers
sourced from the NSB in one-million-year bin size. In each panel, the current extinction
probability of that species—predicted using that species' historical geospatial records with the
model that was fit using extinct species of the same taxonomic grouping— is shown. Panels A
through F are ordered according to decreasing current extinction probability. Notice the
association of relatively small standing occupancy values and relatively large occupancy
decreases with increased probability of extinction.
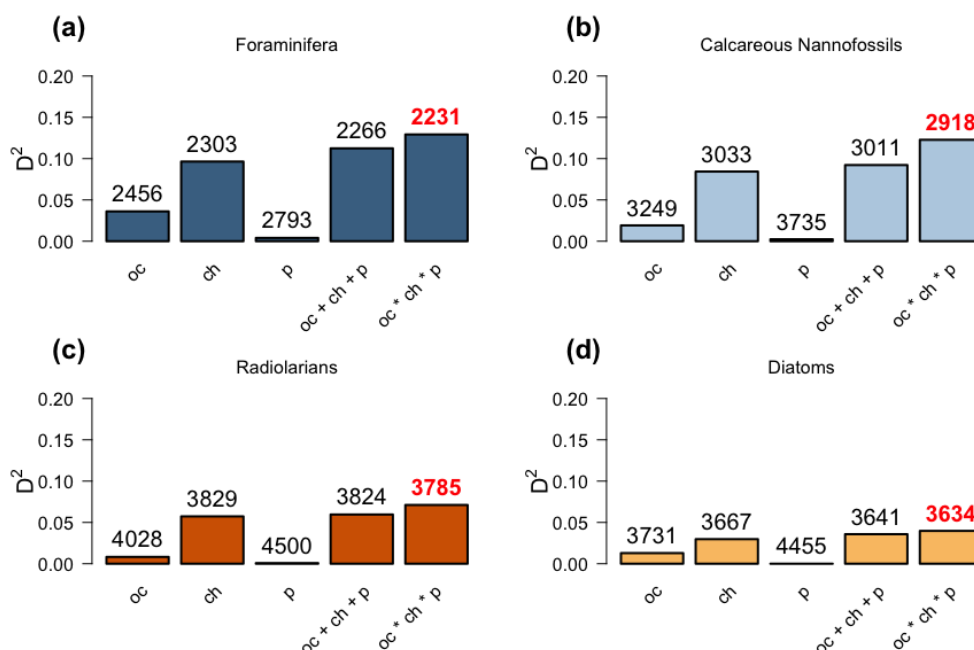
Figure 3. D^2 values (bars) and AIC values (numbers displayed above each bar) for each examined model formula. Shown for each of the NSB data sets with bin size = 1 million years. The lowest AIC value for each data set is shown in red.

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312
313

Bin size (Ma):	0.1	0.2	0.5	1.0
Foraminifera	0.042	0.053	0.079	0.129
Calcareous Nannofossils	0.053	0.053	0.090	0.123
Radiolarians	0.015	0.025	0.060	0.071
Diatoms	0.021	0.030	0.027	0.040

314   **Table 3.** The D^2 of each best-fit model (see Table 2) for each data set at each bin size.
315

316   D^2 values increase systematically with bin size, and calcareous organisms tend to have

317   higher D^2 values than siliceous organisms for their best-fit model (Table 3), indicating better

318   overall explanatory power in calcareous organisms. A maximum relative importance value of

319   91.9% was achieved for radiolarians binned to 1.0 million years (the D^2 of this particular

320   multiplicative model was 0.071). In all but the smallest bin size, radiolarians consistently have

321   the highest standardized coefficient ratios and relative importance values of the *occupancy*

322   *change* term. Not surprisingly, sampling completeness increases with larger temporal grain.

323   Foraminifera and calcareous nannofossils had consistently higher three-timer sampling

324   completeness than the siliceous groups across all bin sizes (Table 4).

325

326

Three-Timer Completeness				
Bin Size (million years)	**0.1**	**0.2**	**0.5**	**1.0**
Foraminifera	0.821 ± 0.006	0.899 ± 0.006	0.928 ± 0.007	0.933 ± 0.009
Calcareous Nannofossils	0.874 ± 0.004	0.899 ± 0.005	0.925 ± 0.006	0.936 ± 0.008
Radiolarians	0.792 ± 0.005	0.825 ± 0.006	0.886 ± 0.007	0.926 ± 0.008
Diatoms	0.729 ± 0.006	0.781 ± 0.007	0.838 ± 0.008	0.861 ± 0.010

327   **Table 4.** Three-timer completeness scores (Alroy 2008) calculated for each full data set at each
328   of the four examined bin sizes. Shown with 95% confidence intervals.
329

330   When fit to extinct-only data subsets, AIC-selected models were still either the additive

331   or multiplicative three-term models for all groups at all bin sizes (Table S4). Extant diatoms

332   showed a significantly higher probability of extinction than all other groups, followed by extant

333   radiolarians, and then by the two calcareous groups. Extinct radiolarians had a significantly

334   lower extinction probability than calcareous nannofossils and diatoms (Table 5). Extinction

335   values through time for each group are visualized in Fig. 1.

336

337

	Species	
	Extant	**Extinct**
Foraminifera	0.097± 0.051	0.219 ± 0.034
Calcareous Nannofossils	0.060 ± 0.038	0.240 ± 0.016
Radiolarians	0.122 ± 0.011	0.187 ± 0.013
Diatoms	0.141 ± 0.009	0.256 ± 0.020

338   **Table 5.** Mean of all extant-organism extinction probabilities (left) and extinct-organism
339   extinction probabilities (right) produced for each data set. Means are shown with 95%
340   confidence interval.
341

342   The raw number of cells occupied by each species during each time bin showed a strong

343   positive correlation with the number of occupied Longhurst provinces for each taxonomic group

344   at each bin size, even when autocorrelation was removed (Table S5). The same analyses

345   conducted on proportional occupancy of Longhurst provinces and the change in proportional

346   occupancy of Longhurst provinces, as well as on the latitudinal range of species and the change

347   in latitudinal range of species, yielded best-fit models that related all three model terms

348   multiplicatively (Figs. S2 and S3). When the logistic modeling was applied to the Triton data, the

349   three-term multiplicative or additive models always performed the best (Fig. S6).

350

351   **4.   Discussion**

352   **4.1 Geographic range as a driver of microplankton diversity**

353   Our observations agree with the findings of Jamson et al. (2022), which observed

354   increased extinction rates for siliceous organisms during the PETM. Additionally, the authors

355   found a net diversification rate of around 0, as well as a stable extinction rate, for calcareous

356   groups between the PETM and the modern. Our results show diatoms and radiolarians having

357   several spikes in extinction between 40-50 Ma, which may indicate the termination of the Early

358   Eocene Climatic Optimum. There is another localized spike in extinction for the siliceous groups

359   around 35Ma, perhaps corresponding with the end of the Middle Eocene Climatic Optimum.

360   Jamson et al. (2022) observed a brief increase in diatom extinction rate during this event.

361   While absolute geographic range size is an informative predictor of extinction risk,

362   various other factors relating to geographic range also play an important role in global

363   biodiversity patterns. Powell and Glazier (2017) found that in the same four groups of

364   microplankton analyzed in this study, latitudinal diversity gradients are produced by asymmetric

365   shifts in geographic range, rather than variations in diversification rate with respect to latitude.

366   On the contrary, Raja and Kiessling (2021) found that the extratropics had higher average

367   origination rates than the tropics. Supporting Powell and Glazier's (2017) finding that

368   asymmetric shifts in geographic range are key drivers of latitudinal diversity gradients, Raja and

369   Kiessling (2021) showed that dispersal was more likely to occur from the extratropics towards

370   the tropics. Both studies suggest that latitudinal diversity gradients, and thus the geographic

371   distribution of a species, are closely linked to paleoclimate regimes. Indeed, changes in global

372   circulation patterns as well as water column stratification and temperature are the key influences

373   on global plankton diversity (Lowery et al., 2020)

374   As paleoclimate regimes shift over geologic time, marine microplankton ranges often do

375   not shift to follow changes in temperature; instead, populations may simply go extinct as local

376   temperatures become inhospitable without a comparable range expansion into more-hospitable

377   zones (Trubovitz et al., 2020). Trubovitz et al. (2023) found that radiolarian abundance is not a

378   significant predictor of extinction risk and that external drivers (such as climate) are more likely

379   to predict extinctions. Thus, larger geographic ranges may provide species with a geographic

380   cushion: as local temperatures change, more widespread species undergo a more drawn-out

381   series of local extirpations before global extinction occurs. This agrees with the well-established

382   phenomenon, and that which we also report here, that larger instantaneous geographic occupancy

383   reduces a species' risk of extinction.

384   Additionally, the trajectory of a species' geographic range through time might indirectly

385   reflect shifts in regional or global climate. As paleoclimate zones shift, geographic cells may

386   become inhospitable to a species, and the species may undergo extirpation in that geographic

387   cell. A more rapid change in a species' occupancy through time may reflect a more rapid change

388   in paleoclimate and hospitable regions of Earth. Continued reduction in occupancy over time can

389   thus provide insight into the effects of long-term climatic, geographic, or biological trends on the

390   extinction probability of marine microplankton.

391

392   **4.2 History of occupancy / legacy effects**

393   The trajectory of various ecological variables through time has been shown to impact the

394   current and future direction of species diversity trends. These legacies may include past climatic

395   events or geographic range shifts influencing modern distributions or extinctions of species

396   (Svenning et al., 2015). The interaction of historic information with current information can

397   provide insight about ecological processes that neither historic nor current information could

398   provide on its own.

399   The historic trajectory of climate change impacts the probability of extinction occurring

400   with a short-term change in climate. A warming event occurring after a long-term warming trend

401   leads to greater extinction rates (Mathes et al., 2021a) and lower origination rates (Mathes et al.,

402   2021b) than a warming event occurring after a long-term cooling trend. Understanding the

403   historical conditions leading up to a study period of interest thus may be essential to

404   understanding the key drivers as to what goes extinct versus what survives.

405   Although the effect of climate and geographic range legacies on instantaneous

406   geographic range itself is well-studied (Svenning et al., 2015), the effect of geographic range

407   legacies on instantaneous extinction probability has not received as much attention. Kiessling

408   and Kocsis (2016) found that the legacy of geographic range (represented as its change to the

409   present from the previous bin) is an informative predictor for extinction risk in marine

410   macroinvertebrates. Our results build upon those of Kiessling and Kocsis (2016), demonstrating

411   both that these findings hold true for marine microplankton, as well as that temporal scale (bin

412   size) is a key variable in detecting the importance of geographic legacy effects.

413

414   4.3 Scale dependency of extinction drivers:

415   Although previous studies have analyzed various drivers of extinction through geologic

416   time, relatively little research has gone into understanding the scale-dependency of these

417   extinction drivers. Scale-dependency in extinction studies manifests in various variables, such as

418   area (Fagan et al., 2005; Guardiola and Rodá, 2013) or taxon age (Diaz et al., 2019). Analyzing

419   data at different temporal scales is also imperative to detect true ecological signals (Hewitt et al.,

420   2010). We find here that as temporal resolution decreases (bin size increases), the relative

421   explanatory power of the occupancy change variable increases while the relative explanatory

422   power of the other two variables decreases (Fig. 4).

423
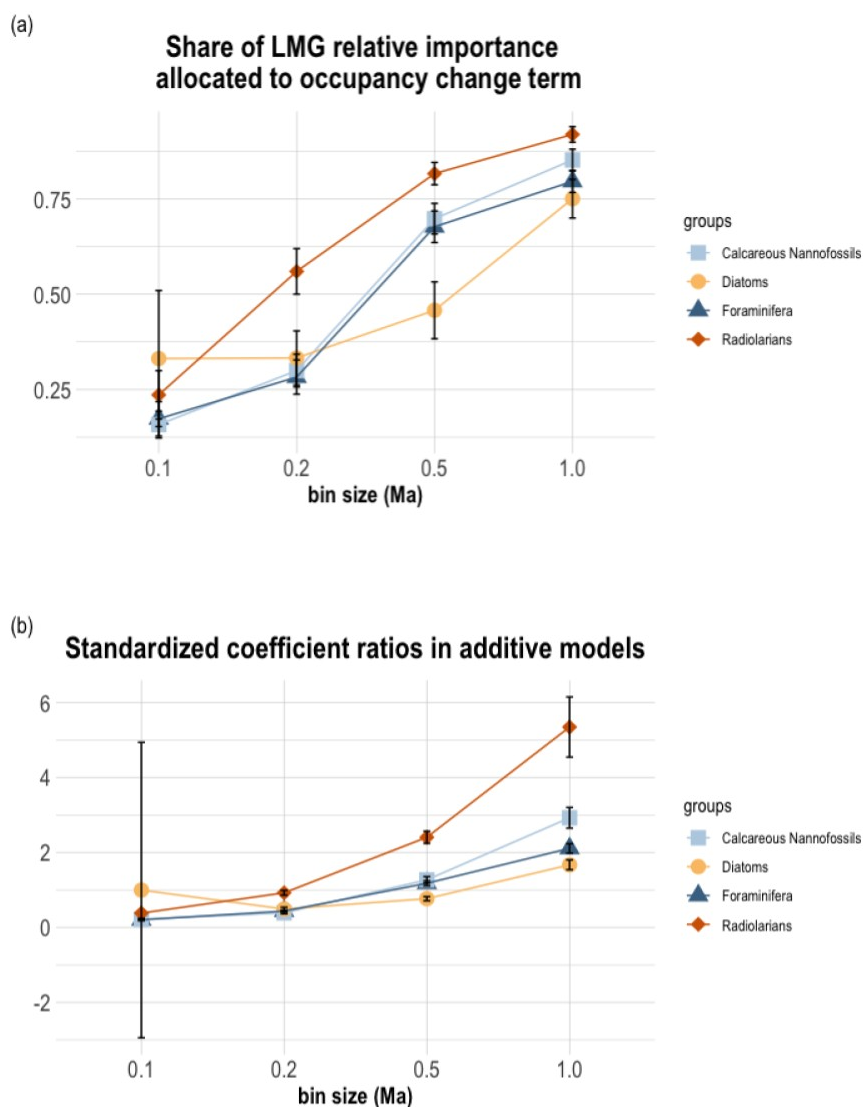
Figure 4. A.) Share of the Lindemann, Merenda and Gold relative importance (1980) allocated
to the *occupancy change* term, taken as a proportion of "total importance". Shown for each data
set at each bin size. **B.)** Standardized coefficient ratios in AIC-selected models for each bin size.
Error bars represent the bootstrap-estimated standard error. Note that as bin size increases
(temporal resolution decreases), the relative importance of the occupancy change term as well as
the standardized coefficient ratio (occupancy change : standing occupancy) both increase.

430   This could result from there being more records in a single temporal bin as bin size

431   increases, thus creating a more complete set of data in any given time bin. This may be

432   especially true when working with fragmentary fossil data, such as that which we analyze here.

433   With larger bin sizes, it is easier to detect biological signals that may otherwise be lost in the

434   noise of fragmentary data. The temporal scale by which we analyze these data can influence our

435   understanding of extinction risk in marine microplankton. We show here that the seemingly-

436   arbitrary selection of temporal bin size can have major impacts on conclusions drawn about

437   microplankton diversification.

438

439   **4.4 Calcareous vs siliceous microfossils**

440   In general, the explanatory power of each of the model terms is smaller in the siliceous

441   groups than in the calcareous groups. Although *occupancy* and *occupancy change* were found to

442   be informative across all groups, the signals are weaker in diatoms and radiolarians (Table 3). As

443   both siliceous and calcareous organisms are sensitive to nutrient limitation (Kamikuri et al.,

444   2005; Lazarus et al., 2009; Bristow et al., 2017), this discrepancy likely results from minor

445   variations in sampling, as evidenced by lower 3-timer completeness values for the two siliceous

446   groups. Furthermore, the *sampling* term was found to be significant in the three-term additive

447   model across all bin sizes for calcareous nannofossils, in two bin sizes for both foraminifera and

448   diatoms, and never for radiolarians. The greater importance of the *sampling* term in the

449   calcareous groups suggests that fossil preservation and sampling rate has a greater influence on

450   when a species disappears from the fossil record, a piece of information that is crucial to

451   distinguishing "true" from "apparent" extinction. This discrepancy may be a result of variable

452   taphonomic pathways between the calcareous and siliceous organisms (Boltovskoy 1994).

453   Nonetheless, both *occupancy* and *occupancy change* are important predictors of extinction

454 regardless of the group, and these findings further underscore the importance of accounting for

455 sampling when analyzing paleontological data.

456

457 **4.5 Robustness testing**

458   There is a strong correlation between the number of occupied Longhurst provinces and

459 the number of individual occupied geographic cells for each species-bin pairing. This

460 demonstrates that, although the locations of the various drilling expeditions that sourced much of

461 the data in the Neptune database are not entirely random, when taken together they still account

462 for a diverse spread of planktonic biogeographic regions around the globe. This supports the idea

463 that the collection of data contained in the Neptune database, while only a snapshot of the global

464 microplankton fossil record, is comprehensive enough to study large-scale biogeographic trends.

465 Additionally, AIC-selected models contained both the *occupancy* and *occupancy change* terms

466 even when geographic range was measured as latitudinal expanse or as a proportion of occupied

467 Longhurst provinces. This suggests that the significance of proportional occupancy change in

468 predicting extinction is not merely an artifact of data processing.

469   The AIC-selected model for each bin size in the Triton data set was either the three-term

470 additive or multiplicative model. Although the Triton dataset has substantially more occurrence

471 records after preprocessing, it has consistently lower diversity compared to the other taxonomic

472 groups from the NSB (Fig. S4). This could indicate a greater propensity for "lumping" in the

473 Triton dataset than in the NSB, which in turn could change how spatio-temporal signals

474 manifest. The similar results obtained from the Triton dataset further confirms the suitability of

475 these methods with an alternative data set and reaffirms the importance of *occupancy* and

476 *occupancy change* when modeling extinction.

477   Taken together, our findings suggest that the change in geographic occupancy is an

478   important metric for predicting extinction across the tree of life. Kiessling and Kocsis (2016)

479   looked exclusively at skeletal macroinvertebrates, whereas here we analyzed several protist

480   lineages of marine plankton. The broad taxonomic scope of these findings emphasizes the

481   fundamental importance of the trajectory in geographic range as a biological metric, which can

482   be a key aspect of taxon dynamics through time. Although the explanatory power of the model

483   may seem low (up to 12.9%), it is an important factor given the many other variables that

484   influence extinction risk (McKinney 1997)

485   Although modern studies can track geographic occupancy change over the course of

486   decades (if there is a history of consistent data collection), estimates of marine species durations

487   average between 5-10 million years (Foote and Raup, 1996; Raup, 1991), much longer than

488   human-collected records can encompass. To fully understand the change of occupancy through a

489   species' duration, records extending beyond those which could have been manually recorded by

490   conservation biologists are needed. Although some modern conservation practitioners have been

491   hesitant to fully embrace long-term paleontological data, this study provides yet another

492   argument for the incorporation of historical perspectives and fossil evidence in conservation

493   efforts (Dietl et al., 2019; Kiessling et al., 2019; Smith et al., 2018).

494   While for simplicity's sake, this study only looked at the interaction of *occupancy* and the

495   first degree of *occupancy change* (bin number *i* to *i*-1), future iterations could incorporate entire

496   occupancy histories into model fitting using even more advanced techniques. This may help the

497   model overcome variations in sampling intensity or localized paleoenvironmental events, and let

498   the models provide information not only on decline, but information on *continued* decline —

499   another hallmark of increased extinction risk.

500

5. Conclusion

In providing evidence that the geological history of species distributions plays a significant role in species extinction risk, our study demonstrates the importance of paleontological data for assessing modern species extinction risk. Incorporating paleontological range data may allow for more-informed decisions about how to spend limited conservation funding in the future. We also demonstrate here the importance of temporal grain in detecting biological signal in fragmentary fossil data.

Data availability statement

All data and code is currently accessible at the reserved stable repository DOI: 10.5281/zenodo.7745607 (Smith, 2024).

Author contributions

WK and AK developed the conceptual framework. IS constructed the analytical pipeline and carried out analyses and drafted manuscript. All authors contributed to the development of the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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