

24 **1. INTRODUCTION**

25 The world's biodiversity is in decline, and some scientists argue that we have already entered a time
26 of mass extinction similar in magnitude and rate to the greatest mass extinctions recorded in the
27 fossil record [1, 2]. Current extinctions against which historical or prehistorical extinctions are
28 assessed are usually informed by the International Union of Conservation of Nature (IUCN). The IUCN
29 Red List of Threatened Species has good coverage of terrestrial vertebrates but lacks data for most
30 marine invertebrates, except reef corals [3]. The IUCN criteria for assessing extinction risk are clear
31 and successful [4] but the lack of data for many invertebrate taxa render the assessments incomplete
32 and potentially unrealistic [5].

33 Novel ways of defining palaeontological baselines for evaluating extinction risk at the genus level
34 have recently been developed [6, 7], and here we add a species-level perspective by assessing the
35 trajectories of geographic occupancy of extant marine species over geological time scales.
36 Geographic distribution is universally accepted as a strong predictor of extinction risk, both in the
37 past [7-11] and today [4, 12-15]. Much less is known about the role of change in geographic
38 distribution, especially on geological time scales.

39 Here we first assess the relative impact of occupancy and change of occupancy on extinction risk
40 in extinct Cenozoic species and then use the palaeontological trajectories of occupancy in extant
41 species to evaluate their current extinction risk.

42

43 **2. MATERIAL AND METHODS**

44 Occurrences of Cenozoic marine invertebrates were downloaded from the Paleobiology Database
45 (PaleoDB, <http://paleobiodb.org>) on 22 Jan 2016 and parsed into one of 18 time bins (electronic
46 supplementary material, table S1). The dataset comprised 147,268 fossil occurrences of 39,902
47 species, 6,651 of which are extant. To be able to assess simultaneously the role of occupancy and the
48 change of occupancy in extinction risk, this dataset was filtered further to comprise only species

49 recorded in at least two consecutive time intervals and attaining occupancy values of greater than
50 zero. This resulted in 85,110 occurrences of 8,270 species [16].

51 Occupancy and its temporal change were assessed using the proportion of equal area
52 palaeogeographic grid cells occupied by each species in a time interval (see electronic supplementary
53 material file 1, ESM1). To circumvent the problem of heterogeneous spatial sampling, the
54 denominator of the proportion is the number of matching grid cells sampled in two consecutive time
55 intervals (ESM1). The change in occupancy is the log ratio of the occupancy at time i divided by the
56 occupancy at time $i-1$. Suppose that 100 grid cells are sampled in two consecutive time intervals and
57 a species is found in 10 of them in the younger interval and 5 in the older. The corresponding change
58 would thus be $\log(0.1/0.05) = 0.693$. We tested different geographic resolutions, but only report
59 results for a resolution in which the average edge length was 8.64 degrees along arcs of great circles,
60 because this resolution retained the most information.

61 Extinct species were used to assess the combined impact of occupancy and its changes on
62 extinction risk. The time of extinction was estimated as the time of last occurrence in the matching
63 cell assessment. All analyses were carried out in R [17]. In a generalized linear model, the additive
64 and multiplicative effects of occupancy and its change were tested against the probability of
65 extinction in each time interval in the form: $\text{glm}(\text{extinct} \sim \text{occupancy} * \text{occupancy change}, \text{family} =$
66 $\text{binomial}(\text{link} = \text{"logit"}))$. For longer time series, we have also tested to see if a change of occupancy
67 over longer stretches of time (e.g., 2-3 intervals) improves the model. The best model was sought
68 with R's $\text{step}()$ function and the amount of deviance explained by each model (D^2) was estimated
69 with the $\text{Dsquared}()$ function [18]. We used a model of moderate complexity to assess the extinction
70 risk of extant marine species based on their previous history of occupancy in the Late
71 Pleistocene/Holocene bin, which has been 125 kyr in duration.

72

73 3. RESULTS

74 The individual trajectories of occupancy for extant species can be very volatile and multimodal (figure
75 1 and ESM 2), but both occupancy (*oc*) and the first derivative of change (*ch*) are significantly
76 associated with extinction risk (table 1). Based on all Cenozoic species which have their last fossil
77 occurrence before the late Pleistocene/Holocene bin, change in occupancy is an even better
78 predictor of extinction than occupancy, both individually and in the additive model. In addition, the
79 additive model has stronger support than the individual models, suggesting that both terms are
80 important. Adding a multiplicative term ($oc \times ch$) improves the model further, suggesting that the
81 interaction between occupancy and its change is important. Incorporating consecutive changes in
82 occupancy into the model leads to a dramatic loss in sample size but a better model fit and a better
83 explanation of deviance (table 1).

84 The parameters of the multiple regressions are time-variant, with more negative estimates
85 towards the Recent (ESM 1). As our intention is to assess the extinction risk of modern species, we
86 developed our final model on species that became extinct within the last 10 million years. This model
87 comprised 893 species-interval combinations of 495 extinct species with occupancy data spanning at
88 least four consecutive time intervals. From this model of four parameters and their interactions, the
89 final model was chosen based on the Akaike Information Criterion (AIC). This final model has four
90 significant parameters and explains 12% of the deviance (ESM1, figure S8).

91 Applying the model to extant species with a corresponding length of past trajectories permits an
92 assessment of their extinction risk based on occupancy history (figures 1, 2, ESM2). Based on the
93 average duration of intervals from which our model was derived, the probabilities refer to roughly
94 the next two million years. The three major clades in our dataset (corals, bivalves and gastropods)
95 have significantly different median risks (Kruskall-Wallis test, $p < 0.001$) with corals having the lowest
96 (0.03) and gastropods the greatest (0.35) median risk.

97

98 **4. DISCUSSION**

99 We confirm the significant effect of occupancy or geographic distribution on extinction risk, which
100 has been noted so often in fossil and extant organisms [4, 7-15]. However, we also find that changes
101 of occupancy are an even stronger predictor of extinction. We attribute this outcome to the fact that
102 some species never gain high occupancy in their duration without being at elevated risk, whereas a
103 decline over longer stretches of time combined with low occupancy puts the species at greater risk.
104 Our new findings suggest that the palaeontological history of occupancy may contribute to the
105 assessment of extinction risk in extant marine species, for which monitoring data are hardly
106 available. The explanatory power (12% of deviance) of our model may appear low but is remarkable
107 given the many additional biotic and abiotic factors that contribute to extinction risk [19].
108 Nevertheless, it is surprising that corals appear to be at a lower risk of extinction than molluscs. Most
109 reef corals have been on rising trajectories over millions of years but are considered especially
110 vulnerable today [3].

111 We emphasize that a rising occupancy on geological time scales is no guarantee of lower
112 extinction risk in the modern ocean. This fact is best illustrated by the two Caribbean coral species
113 *Acropora cervicornis* (figure 1a) and *A. palmata*, which are both categorised as critically endangered
114 by the IUCN Red List but have been steadily rising in occupancy on geological time scales. The two
115 species have been under strong human pressure for decades [20], which undermined their past
116 success. Life-history traits and sensitivity to current anthropogenic and climate-induced stressors
117 may be more relevant for the short-term fate of marine species. However, we argue that species
118 considered to be in a good state today or not assessed at all may be at a hidden risk if on a long-term
119 decline, especially if species are both sensitive to current stressors and on a long-term trajectory
120 declining occupancy.

121 Although the Cenozoic fossil record in the PaleoDB is currently too patchy at the species level
122 to assess risk with great accuracy, the methods developed here may be used in future studies
123 pending better geographic coverage and stratigraphic resolution of fossil data. With a finer temporal
124 resolution, the capacity for prediction of fossil occupancy trajectories is likely to be improved with

125 more sophisticated methods. We propose autoregressive integrated moving average (ARIMA)
126 forecasting (ESM 1) as the way forward.

127 **Ethical Statement**

128 Not applicable

129 **Data accessibility**

130 The taxonomically vetted raw occurrence file of fossil Cenozoic species can be accessed through
131 Dryad <http://dx.doi.org/10.5061/dryad.h5b45/1>. The data matrix used for modeling is provided in
132 table S2.

133 **Competing interests**

134 We have no competing interests

135 **Authors' contributions**

136 WK designed the project, vetted the data and drafted the text. Both authors analysed the data,
137 developed R scripts, contributed intellectually and revised the text. Both authors agree to be held
138 accountable for the content therein and approve the final version of the manuscript.

139

140 **Acknowledgements**

141 We thank the organizers of WoRMS for providing us their full dataset of marine species. The authors
142 are indebted to James Crampton, three anonymous reviewers and guest editor John Alroy for their
143 valuable and constructive criticism. John Alroy is additionally thanked for suggesting the paired cell
144 approach. This is Paleobiology Database Publication # and MTA-MTM-ELTE Paleo contribution #.

145 **Funding**

146 This work was supported by the Deutsche Forschungsgemeinschaft (KI 806/12-1 and KO 5382/1-1).

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201

202 Table 1. Predictors of extinction risk based on (multiple) logistic regression between the binary
 203 response variable (1 = extinct, 0 = survive) and measures of occupancy and its changes in pre-late
 204 Pleistocene intervals.

Input	d.f. (null)	Parameter estimates for individual or additive models (D ²)	AIC
<hr/> Entire Cenozoic <hr/>			
Occupancy (<i>oc</i>)	11140	-0.29 (0.005)	15077
Change of occupancy (<i>ch</i>)	11140	-0.57 (0.005)	14975
<i>oc+ch</i>	11140	-0.13 <i>oc</i> -0.50 <i>ch</i> (0.013)	14964
<i>oc*ch</i>	11140	(0.016)	14913
Change of occupancy over two intervals (<i>ch2</i>)	3402	-0.56 (0.021)	4591
Change of occupancy over three intervals (<i>ch3</i>)	1334	-0.72 (0.044)	1743
<i>oc*ch*ch2*ch3</i>	1334	(0.08)	1692
<hr/> The last 10 myr <hr/>			
<i>oc*ch</i>	5106	(0.07)	7009
<i>oc*ch*ch2*ch3</i>	893	(0.12)	1042[§]

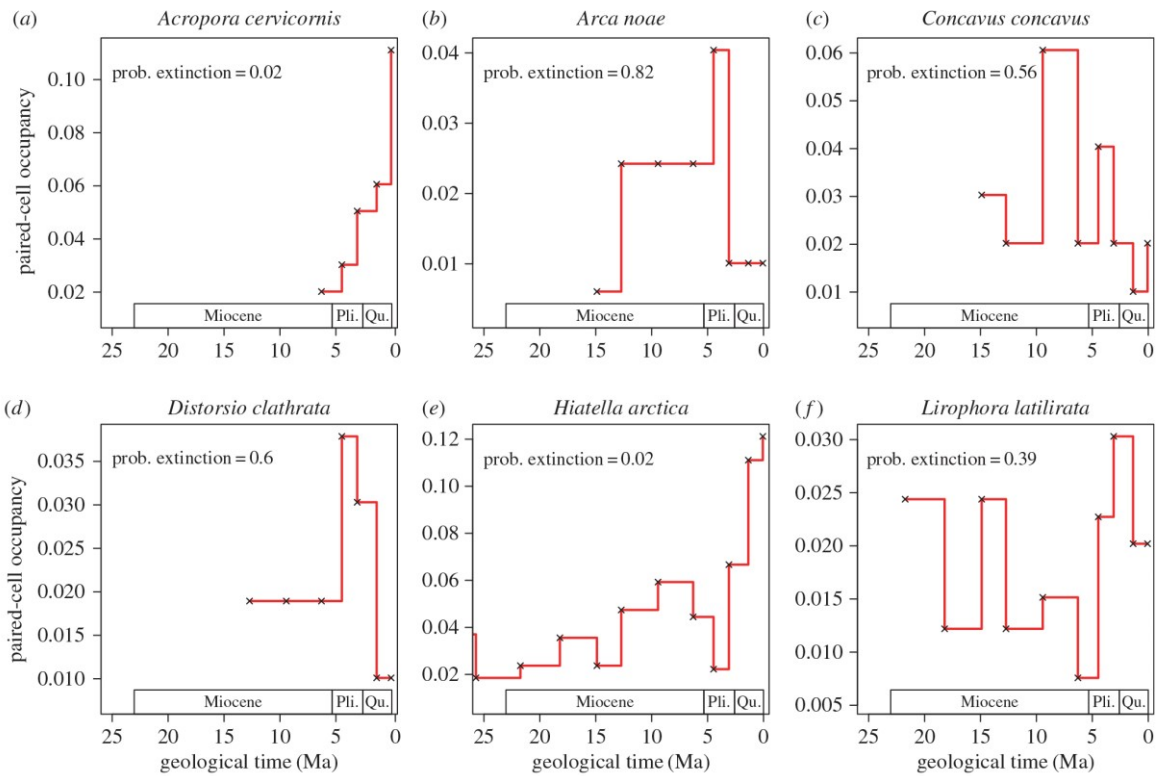
205 d.f., degrees of freedom; AIC, Akaike Information Criteria; [§], chosen model for prediction

206

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208

209 **Figure captions**



210

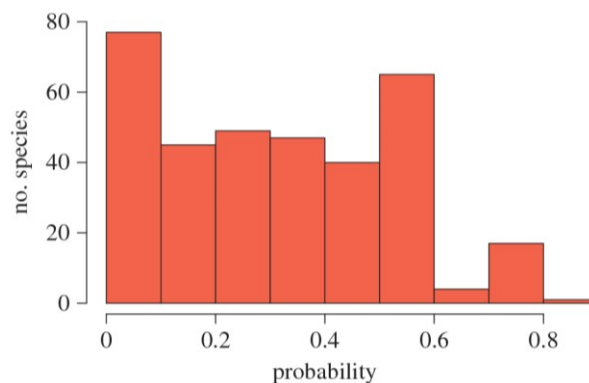
211 Figure 1. Selected palaeontological trajectories of geographic occupancy for extant marine species.

212 The probabilities of extinction in the current geological time interval are indicated. (a) Caribbean reef

213 coral. (b) Eastern Atlantic/Mediterranean bivalve. (c) Barnacle considered extinct in the Quaternary.

214 (d) Western Atlantic gastropod. (e) Widespread myoid bivalve. (f) Caribbean venerid bivalve. Pl. =

215 Pliocene, Qu. = Quaternary.



216

217 Figure 2. Histogram of extinction probabilities for extant species derived from a model of multiple

218 measures of past occupancy (bold print in table 1). The median probability of extinction is 0.32.