1   **Adding fossil occupancy trajectories to the assessment of modern extinction risk**

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9

10   **Abstract**

11   Besides helping to identify species traits that are commonly linked to extinction risk, the fossil record

12   may also be directly relevant for assessing the extinction risk of extant species. Standing geographic

13   distribution or occupancy is a strong predictor of both recent and past extinction risk, but the role of

14   changes in occupancy is less widely assessed. Here we demonstrate, based on the Cenozoic fossil

15   record of marine species, that both occupancy and its temporal trajectory are significant

16   determinants of risk. Based on extinct species we develop a model on the additive and interacting

17   effects of occupancy and its temporal changes on extinction risk. We use this model to predict

18   extinction risk of extant species. The predictions suggest a moderate risk for marine species on

19   average. However, some species seem to be on a long-term decline and potentially at a latent

20   extinction risk, which is not considered in current risk assessments.

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22   Keywords: palaeobiology, extinction risk, geographical occupancy

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1. INTRODUCTION

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

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

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

2. MATERIAL AND METHODS

Occurrences of Cenozoic marine invertebrates were downloaded from the Paleobiology Database (PaleoDB, http://paleobiodb.org) on 22 Jan 2016 and parsed into one of 18 time bins (electronic supplementary material, table S1). The dataset comprised 147,268 fossil occurrences of 39,902 species, 6,651 of which are extant. To be able to assess simultaneously the role of occupancy and the 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: glm(extinct ~ occupancy * occupancy change, family =

66 binomial(link="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 step() function and the amount of deviance explained by each model (D^2) was estimated

69 with the 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* × *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.

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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

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125 more sophisticated methods. We propose autoregressive integrated moving average (ARIMA)

126 forecasting (ESM 1) as the way forward.

Ethical Statement

128 Not applicable

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.

Competing interests

134 We have no competing interests

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.

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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
Entire Cenozoic			
Occupancy (*oc*)	11140	-0.29 (0.005)	15077
Change of occupancy (*ch*)	11140	-0.57 (0.005)	14975
oc+ch	11140	-0.13*oc*-0.50*ch* (0.013)	14964
*oc*ch*	11140	(0.016)	14913
Change of occupancy over two intervals (*ch2*)	3402	-0.56 (0.021)	4591
Change of occupancy over three intervals (*ch3*)	1334	-0.72 (0.044)	1743
*oc*ch*ch2*ch3*	1334	(0.08)	1692
The last 10 myr			
*oc*ch*	5106	(0.07)	7009
oc*ch*ch2*ch3	**893**	**(0.12)**	**1042**[§]

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

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Figure captions
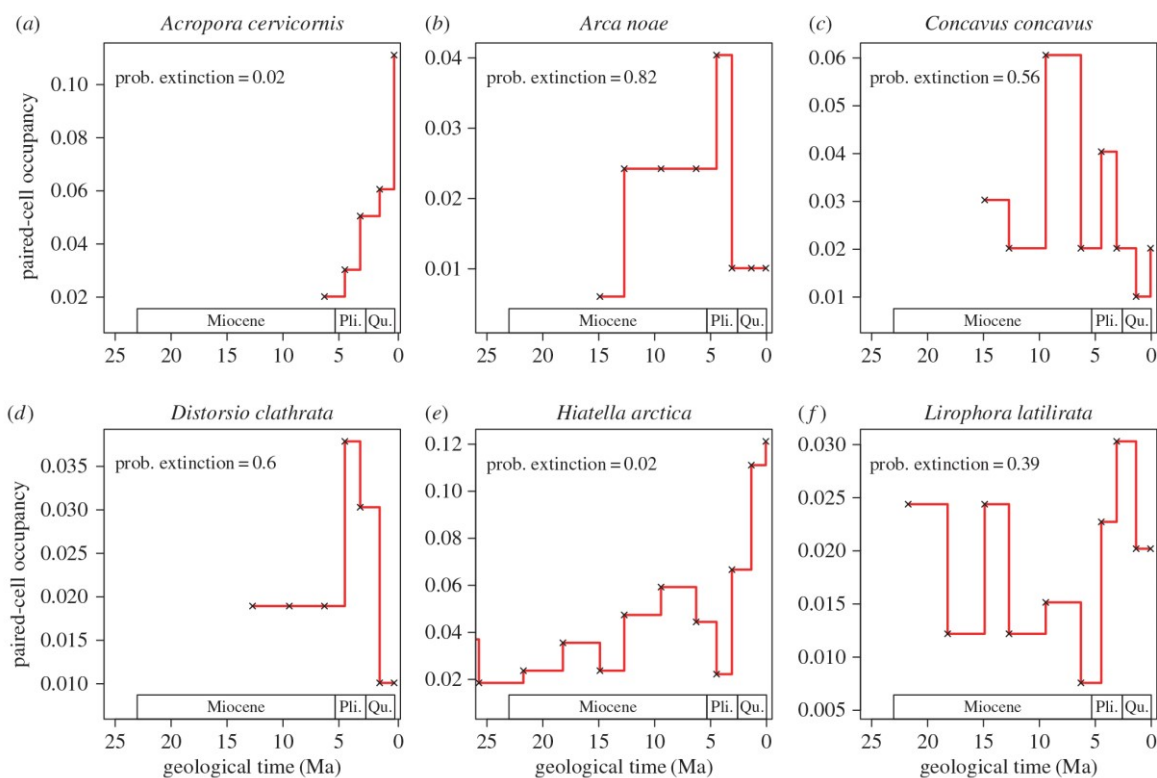

Figure 1. Selected palaeontological trajectories of geographic occupancy for extant marine species.

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

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

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

Pliocene, Qu. = Quaternary.
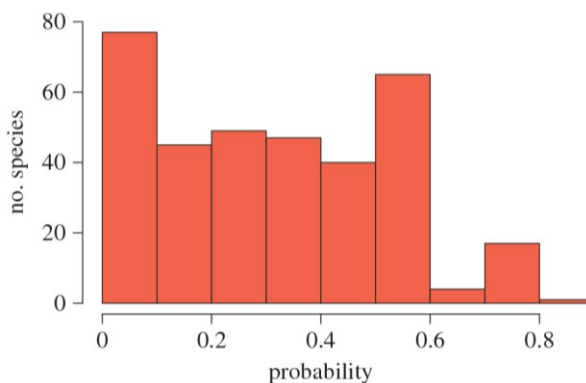
Figure 2. Histogram of extinction probabilities for extant species derived from a model of multiple

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

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