Adding fossil occupancy trajectories to the assessment of modern extinction risk

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Abstract

Besides helping to identify species traits that are commonly linked to extinction risk, the fossil record may also be directly relevant for assessing the extinction risk of extant species. Standing geographic distribution or occupancy is a strong predictor of both recent and past extinction risk, but the role of changes in occupancy is less widely assessed. Here we demonstrate, based on the Cenozoic fossil record of marine species, that both occupancy and its temporal trajectory are significant determinants of risk. Based on extinct species we develop a model on the additive and interacting effects of occupancy and its temporal changes on extinction risk. We use this model to predict extinction risk of extant species. The predictions suggest a moderate risk for marine species on average. However, some species seem to be on a long-term decline and potentially at a latent extinction risk, which is not considered in current risk assessments.

Keywords: palaeobiology, extinction risk, geographical occupancy
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
recorded in at least two consecutive time intervals and attaining occupancy values of greater than zero. This resulted in 85,110 occurrences of 8,270 species [16].

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

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

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

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

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

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

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

Although the Cenozoic fossil record in the PaleoDB is currently too patchy at the species level to assess risk with great accuracy, the methods developed here may be used in future studies pending better geographic coverage and stratigraphic resolution of fossil data. With a finer temporal resolution, the capacity for prediction of fossil occupancy trajectories is likely to be improved with
more sophisticated methods. We propose autoregressive integrated moving average (ARIMA) forecasting (ESM 1) as the way forward.

Ethical Statement

Not applicable

Data accessibility

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

Competing interests

We have no competing interests

Authors’ contributions

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

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Anthropogenic mortality on coral reefs in Caribbean Panama predates coral disease and bleaching.

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

<table>
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<tr>
<th>Input</th>
<th>d.f.</th>
<th>Parameter estimates for individual or additive models (D^2)</th>
<th>AIC</th>
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<td></td>
<td></td>
</tr>
<tr>
<td>Occupancy (oc)</td>
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<td>-0.29 (0.005)</td>
<td>15077</td>
</tr>
<tr>
<td>Change of occupancy (ch)</td>
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<td>-0.57 (0.005)</td>
<td>14975</td>
</tr>
<tr>
<td>oc+ch</td>
<td>11140</td>
<td>-0.13oc-0.50ch (0.013)</td>
<td>14964</td>
</tr>
<tr>
<td>oc*ch</td>
<td>11140</td>
<td>(0.016)</td>
<td>14913</td>
</tr>
<tr>
<td>Change of occupancy over two intervals (ch2)</td>
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<td>-0.56 (0.021)</td>
<td>4591</td>
</tr>
<tr>
<td>Change of occupancy over three intervals (ch3)</td>
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<td>-0.72 (0.044)</td>
<td>1743</td>
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<tr>
<td>oc<em>ch</em>ch2*ch3</td>
<td>1334</td>
<td>(0.08)</td>
<td>1692</td>
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<tr>
<td>oc*ch</td>
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<td>(0.07)</td>
<td>7009</td>
</tr>
<tr>
<td>oc<em>ch</em>ch2*ch3</td>
<td>893</td>
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</table>

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