

RESEARCH ARTICLE

Morphological traits of reef corals predict extinction risk but not conservation status

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Abstract

Aim: The current assessment of extinction risk in reef corals by the International Union for Conservation of Nature (IUCN) has been criticized, because coral life-history traits associated with resilience are not reflected in the conservation status. We aimed to carry out a quantitative assessment of the link between reef coral traits and species extinction risk informed by extinctions of reef corals observed in the fossil record.

Location: Global.

Time period: Plio-Pleistocene and present day.

Major taxa studied: Scleractinian reef corals.

Methods: We used morphological traits, phylogenetic information and evidence of extinction during the Plio-Pleistocene to predict the extinction risk of contemporary reef corals. Our model was trained using 138 Caribbean fossil coral species and an automatic machine learning algorithm. We then used this model to predict the extinction risk of 674 modern coral species.

Results: Model validation confirmed 77% accuracy in predicting extinction risk of fossil corals. Extinction risk predicted by our model showed a near-random (57%) match with the IUCN conservation status. Our model also suggested that corals in the Least Concern or Near Threatened categories might be at higher risk of extinction than currently believed.

Main conclusions: Morphological traits of fossil corals linked to their extinction risk in the Plio-Pleistocene Caribbean Sea are known to reflect the vulnerability of extant corals. However, the results from our fossil-calibrated model do not match the IUCN assessment of reef corals, with increased overall extinction risk. This does not necessarily indicate near-future extinction risk, because fossil extinctions are spread over thousands of years. However, we show the applicability of using fossil data to inform the extinction risk of modern corals and recommend that future assessments of extinction risk of reef corals should consider incorporating the relationship between morphological traits and resilience, calibrated by fossil data, to maximize the utility of the extinction risk assessment.

KEYWORDS

extinction risk, fossil record, predictive modelling, Red List, reef corals, traits

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1 | INTRODUCTION

Coral reefs are increasingly threatened by a combination of anthropogenic stressors and climate change (Harborne et al., 2017; Hughes et al., 2017; Perry et al., 2018). Understanding the degree to which coral species are prone to extinction is a central goal for the conservation of coral reef habitats. The International Union for Conservation of Nature (IUCN) Red List of Threatened Species is widely regarded as the global standard for assessing extinction risk (Hoffmann et al., 2008; Mace et al., 2008). In the IUCN Red List, species are classified in five categories, referred to hereafter as “conservation status”, each with a probability of extinction over time (a period of 10 years or three generations up to a maximum of 100 years; Akçakaya et al., 2006).

The conservation status of 845 reef corals was assessed in a single publication (Fig S1; Carpenter et al., 2008). Given that long-term monitoring data are not widespread, criteria used to assign the conservation status of reef coral species are based primarily on the estimates of reef area dynamics and the extent of geographical distribution (Carpenter et al., 2008). However, abundance and geographical distribution are both known to be weakly linked with the extinction risk of reef corals (Hughes et al., 2014). The assessment by Carpenter et al. (2008) has been criticized recently, because coral life-history traits associated with stress tolerance, fecundity and habitat specialization do not align with the current conservation status for several species (Bridge et al., 2020). These traits have shown high correlations with extinction risk in other groups (Pearson et al., 2014; Purvis et al., 2000) and therefore have a similar potential to affect the extinction risk of reef corals.

Trait-based approaches are widely used in population and community ecology, from species to whole ecosystem scales (Chown, 2012; Darling et al., 2012; Madin, Hoogenboom, et al., 2016; Suding et al., 2008; Violle et al., 2007), and previous assessments of multiple organisms have shown that the life-history traits of species can help to predict extinction risk as a result of climate change and direct human impacts (Collen et al., 2011; Dulvy & Reynolds, 2002; Foden et al., 2013; Murray & Hose, 2005; Pearson et al., 2014; Purvis, 2008; Purvis et al., 2000; Ribeiro et al., 2016; Tingley et al., 2013). Trait-based approaches have also been applied to other groups to predict the extinction risk of data-deficient species and to test the accuracy of the IUCN assessments (Bender et al., 2013; Ceretta et al., 2020; González-del-Pliego et al., 2019; Mattila et al., 2008).

Fossil data can also provide important information on the resilience of species to environmental change (van Woesik et al., 2012). Extinctions observed in the fossil record provide unique opportunities to test for the correspondence between life-history traits and extinctions. One such example is the regional extinction of reef corals observed in the Caribbean Sea during the Plio-Pleistocene. Climatic and tectonic changes caused 18 coral genera to disappear from the region, including six that went globally extinct (Budd et al., 1994; Johnson et al., 1995; van Woesik et al., 2012). Although the IUCN Red List criteria do not include evolutionary facets, there is

an increasing body of evidence that showcases phylogenetic conservatism of extinction risks and benefits of incorporating evolutionary information in the prediction of extinction risks (Cantalapiedra et al., 2019), including for corals (Huang, 2012). In light of these issues, there remains a need for a new framework for the assessment of extinction risk of reef corals that can inform coral reef conservation practices.

Reef corals have a range of physiological, morphological, ecological and reproductive traits that are linked to their variable vulnerabilities to climate-driven stressors (Bridge et al., 2020; Darling et al., 2012; Foden et al., 2013; Madin, Hoogenboom, et al., 2016). Among a plethora of traits, habitat breadth, maximum water depth, larval temperature tolerance, association with particular symbiont clades, growth rates and dispersal capacity have previously been associated with climate change vulnerability for corals (Foden et al., 2013). Although several biological traits are not preserved in fossils, morphological characters such as corallite size or growth form are usually well preserved and can provide crucial insights into the resilience of reef corals under climate change (Darling et al., 2012). Given their linkage to species resilience under climate change, the incorporation of life-history traits in the assessment of extinction risk of reef corals is likely to improve the assessment of the risk status of reef corals.

Here, we use fossil coral data from the Caribbean Sea to construct a trait-based model of extinction risk of reef corals using machine learning algorithms. We apply this model to contemporary corals, including data-deficient corals to: (a) predict their extinction risk; and (b) compare model-derived extinction risk with the IUCN Red List conservation status.

2 | MATERIALS AND METHODS

2.1 | Coral species data

Caribbean fossil occurrences of coral species during the Plio-Pleistocene (5.3–0.017 Ma) were obtained from the Paleobiology Database (PBDB, <https://paleobiodb.org/>) and merged with the dataset previously described by van Woesik et al. (2012), which included high-resolution time-range data. In total, we collated data on 138 species (80 extinct and 58 extant). In addition, a list of 887 modern coral species and their conservation status was obtained from the IUCN Red List. To allow for comparison with the fossil data, the IUCN categories were divided into two categories: non-threatened [i.e., having low extinction risk (Least Concern or Near Threatened)] and threatened [i.e., having high extinction risk (Vulnerable, Endangered or Critically Endangered)].

Taxonomic uncertainty is one of the problems exacerbating the current assessment of the extinction risk of reef corals. There is evidence from genetic studies of cryptic speciation, convergent evolution, phenotypic variability and other complex patterns in morphological variations that have shed some light on the uncertainty in the systematics of reef corals (Forsman et al., 2015; Keshavmurthy

et al., 2013; Richards et al., 2016; Schmidt-Roach et al., 2014). As such, taxonomic names were cross-validated against the PBDB, the World Register of Marine Species (WoRMS; <http://www.marin.especies.org/>) and the coral genus compilation by Kiessling and Kocsis (2015). We limited our analysis to zooxanthellate coral species (those with symbiotic dinoflagellates, commonly termed “reef corals”), because they are known to be sensitive to climate-related stressors (Foden et al., 2013; van Woesik et al., 2012). The final dataset for modern corals comprised 674 species.

2.2 | Trait data

We focused on morphological traits that could be assessed or inferred in fossils: corallite integration, maximum corallite diameter, typical growth form and budding type (Supporting Information Figure S2). These traits were initially chosen because they are some of the morphological traits that are well preserved in the fossil record and have been hypothesized to have a relationship to extinction risk (Table 1). High corallite integration, smaller corallite widths, higher degree of branching and extracalicular budding are all characteristics that have previously been associated with lower stress tolerance and higher extinction risk. To assess the importance of clade membership, we also incorporated the Linnaean family (Supporting Information Figure S3) in the model.

Trait information was obtained directly from the Neogene Marine Biota of Tropical America (NMITA) taxonomic database (<https://fossils.its.uiowa.edu/>; Budd et al., 2001) for extinct species and from the Coral Traits Database (CTD, <https://coraltraits.org/>; Madin, Anderson, et al., 2016) for extant species. Family information

for extinct species was obtained from the compilation by Kiessling and Kocsis (2015) and WoRMS for extant species. Corallite integration was in eight categories based on the level on integration from solitary to meandroid (Supplementary Materials Table S1). The typical growth form has a total of 12 categories in the CTD, which we reduced to four categories, from high branching to no branching (Supplementary Materials Table S2), using volume compactness as a measure (Zawada et al., 2019). The same principle was applied to the data obtained on fossil corals from NMITA. Budding was categorized into three groups: intracalicular (occurring within the tentacle ring of the parent polyp), extracalicular (occurring outside the tentacle ring, with daughter corallites forming on the side of the parent corallite), or both.

2.3 | Training and validation of machine learning tools

We implemented an automatic machine learning algorithm (AutoML) using an open-source machine learning platform, the H2O framework (<https://www.H2O.ai>). H2O's AutoML can be used to automate machine learning workflows, including automatic learning and tuning of multiple models within a user-specified time limit (8 h in this case). All the analyses were conducted in R v.4.0.1 (R Core Team, 2019) using the “h2o” package v.3.8.0.2 (LeDell et al., 2020).

Machine learning models are parameterized such that their learning process can be tuned for a given problem. Hyperparameters are properties that determine the model structure and control the learning process (Feurer & Hutter, 2019). These hyperparameters

TABLE 1 Traits used in the machine learning model and their role in affecting extinction risk

Trait	Relationship to extinction risk
Corallite integration	Communication pathways between highly integrated polyps might facilitate the dissemination of toxic byproducts created during the bleaching response; hence, highly integrated coral species might be more vulnerable to thermal stress Swain et al. (2018)
Maximum corallite diameter	Smaller corallites are commonly associated with higher photosymbiotic autotrophy, whereas species with larger corallites tend to be more heterotrophic Crabbé and Smith (2006). Large corallites also facilitate heterotrophic nutrition during thermal stress and can reduce mortality during breakdown of the symbiosis Hughes and Grottoli (2013)
Typical growth form	Growth form is strongly linked to linear extension rates, with branching species growing nearly an order of magnitude faster than massive species Huston (1979), (1985a), (1985b) and Renema et al. (2016). Higher growth rates require higher energy investment, which has been shown to have a significant impact on their ability to respond to stressors Pinzón et al. (2014). Growth form can also be used as a partial proxy for demographic strategies, as a trade-off between reproductive investment and mechanical stability. Branching species have the tendency to invest more energy in reproductive investment Álvarez-Noriega et al. (2016) but generally have higher mechanical instability that leads to increased mortality rates Madin et al. (2014)
Budding type	The type of budding (intracalicular versus extracalicular) can affect light transmission across the coral skeleton and, as such, the light absorption by coral symbionts, which can affect coral vulnerability to climate perturbations Enríquez et al. (2017). Organisms with extracalicular budding tend to have significantly higher light-scattering abilities than those with intracalicular budding. However, the mode of budding has also been linked to sexual maturity, in that organisms with intracalicular budding share the same developmental stage as the parent polyp, whereas new polyps from extracalicular budding are developmentally “young” and not sexually mature Sakai (1998). Late sexual maturity in several organisms has been shown to be related to population extinctions, because they are less able to compensate for increased mortality Purvis et al. (2000)
Family	Extinction risk exhibits considerable phylogenetic signal Finnegan et al. (2015) Huang (2012)

need to be tuned in order that model can solve the given machine learning problem and provide optimized results. The AutoML searches continuously for hyperparameter choices and produces models by optimizing a user-specified accuracy metric. All available algorithms within the H2O framework were considered: distributed random forest, generalized linear model, gradient boosting machine, naive Bayes classifier and XGBoost. Multi-model stacked ensembles (i.e., the combination of two or more models) were also generated to obtain the optimal combination of the prediction algorithms and to improve predictive performance in comparison to the individual algorithms.

The AutoML was applied to find an optimal model [referred to hereafter as the fossil morphological model (FMM)] using fossil data to predict the extinction risk of modern reef corals. For comparison, we also trained two additional models using modern coral data to predict conservation status, one using the same morphological traits as FMM [hereafter modern morphological model (MMM)] and one using additional information on species distribution, namely geographical range and maximum water depth [hereafter modern distributional and morphological model (MDMM); see Supplementary Materials]. Compiled data were divided into a 75% training set and a 25% validation set according to standard practice (Müller & Guido, 2017). We applied a fivefold cross-validation on the training set to optimize the model tuning parameters by maximizing the area under the receiver operating characteristic curve [area under the curve (AUC); a measure of the ability of the model to distinguish between classes]. Values for the AUC range between zero and one, where $AUC = 1$ corresponds to a perfect predictor (Mandrekar, 2010). An AUC of .5 corresponds to a random classifier, whereby the model is not able to discriminate between classes. Values of $AUC > .7$ indicate a good fit of the model to the data (Mandrekar, 2010; Pearce & Ferrier, 2000).

The final model for predicting extinction risk was chosen from the best models found by the AutoML by comparing AUC values of the tuned models on both the training and test datasets. For each of these models, we identified a probability threshold (decision threshold), above which species were identified as extinct, by maximizing the Youden index ($Y = \text{sensitivity} + \text{specificity} - 1$; Perkins & Schisterman, 2006; Youden, 1950). The Youden index in this case lends an equal weight to detecting extinct and extant species while accounting for differences in the number of observations in both classes. The final probability threshold was computed as the average of the training and test thresholds that provided the highest AUC for the respective datasets (Cook, 2016).

In addition to the AUC, the F1 score, a measure of accuracy that takes into account both false positives and false negatives (Müller & Guido, 2017), was calculated for each model using the optimal threshold as a measure of overall accuracy. The final model was then used to predict the extinction risk of modern reef coral species. Maps were generated using the "icos" v.0.10.0 package (Kocsis, 2020) to assess the geographical distribution of species at risk of extinction. The predicted extinction risk for the modern taxa was compared with the conservation status assigned in the IUCN Red List by calculating the proportion of species whose predicted extinction risk did

not match the binary categorization of the IUCN conservation status considered above.

2.4 | Evaluating variable importance

We applied two methods to illustrate the role played by predictor variables in the machine learning model. First, the variable importance of the predictor variables was computed, which represents the statistical significance of each variable with respect to its effect on the generated model (Breiman, 2001). We implemented a permutation-based variable importance computation using the "DALEX" v.2.0 package (Biecek, 2018), whereby the values for each of the predictor variables are randomly shuffled, and the increase in the root mean squared error (RMSE) for the trained model is then calculated for each permutation. We applied a total of 1,000 permutations.

Second, partial dependence plots were used to show the effect of one variable on the predicted outcome of a machine learning model while averaging the effects of all the other variables used to train the model (Friedman, 2001). In essence, predictions using the model are made using the input values of the variable of interest from the given dataset while other variables are kept at their average values. Partial dependence profiles were calculated using the *partial_dependency()* function of the "ingredients" v.0.5.0 package (Biecek et al., 2019).

3 | RESULTS

3.1 | Machine learning performance

Out of the 98 fossil models trained by the AutoML, the optimal model included a deep learning algorithm and showed an AUC of .77 on the training dataset and .78 on the test dataset, and F1 scores of .72 on the training dataset and .76 on the test dataset, with a decision threshold of .54 (Supporting Information Figure S4). Models using other algorithms, such as boosting algorithms, also performed well, achieving both AUC and F1 scores $> .7$ (Supplementary Materials Table S3). The optimal model correctly classified 87% and 71% of extinct species for the training and test dataset, respectively, with an overall accuracy of 78% and 77%, respectively, on the training and test datasets. The AUC values for the MDMM are comparable to that of FMM (Supplementary Materials Table S4). However, MDMM had higher F1 scores (.88 on the training dataset and .79 on the test dataset), suggesting higher accuracy. MMM had the worst performance, especially on the test dataset ($AUC = .61$).

In general, corallite diameters of extinct species were smaller than the global median value (Supporting Information Figure S2a). Extinct species also had higher degrees of branching and higher corallite integration in comparison to their extant counterparts (Supporting Information Figure S2b,d). No distinction between extinct and extant species could be made for budding type (Supporting

Information Figure S2c). Corallite integration was the dominant predictor for extinction risk, followed by the degree of branching morphology and maximum corallite diameter (Figure 1). Budding type was the least important variable in the machine learning model. In spite of its multivariate nature, with potential interactions among variables, the machine learning results followed the general pattern observed in the original data; species with higher corallite integration, a higher degree of branching and smaller corallite diameters were predicted to show a higher probability of extinction (Figure 2). In contrast to FMM, budding type was the most important variable for MDMM, followed by corallite diameter and geographical range (Supporting Information Figure S5).

3.2 | Predicted conservation status of modern coral species

FMM showed a 43% mismatch with currently assigned conservation status of the Red List; c. 50% of mismatch species are currently classified as Least Concern or Near Threatened, but > 75% of fossil extinct species were correctly predicted to be at risk of extinction (Figure 3). This model was therefore not better than a random classifier, which would have an expected match of 50%. A greater mismatch (58%) was observed when MDMM was used to infer the extinction risk of Pleistocene corals. The model trained on modern data was also unable to predict real extinctions of corals in the fossil record.

FMM predicted that 49% of modern reef coral species, including data-deficient species, were at risk of extinction (Figure 4). It also predicted that 51% of coral species in the Indo-Pacific were at risk of extinction; an increase by 35% when compared with the IUCN assessment (31%; Figure 4). Likewise, 63% of reef corals were predicted to be at risk of extinction in the Caribbean by FMM; an increase by 40% when compared with the IUCN assessment (16%;

Figure 4). Isolated reef aggregations in the Southwestern Atlantic, in the Central Pacific and the Western Indian exhibit a high proportion of species at risk of extinction (> 60%) and might therefore be more vulnerable to regional extinctions, in contrast to regions with dense reef aggregations.

4 | DISCUSSION

4.1 | Model performance and constraints

The high AUC values of our models (Supplementary Materials Tables S3 and S4) indicate that extinction risk is indeed linked to morphological traits of reef corals. However, our methodology is constrained by: (a) the number of variables used; and (b) the dataset size. Studies that adopt modelling approaches to assess the extinction risk of species generally use more than five (6–36) variables in their assessments (Bland et al., 2015; Keller et al., 2011; Luiz et al., 2016; Pearson et al., 2014; Trull et al., 2018). The incorporation of more variables in our model would be likely to provide additional information on the importance of certain life-history traits with regard to resilience and extinction risk. Although a comprehensive compilation of coral traits is available for modern corals in the CTD, fossil corals preserve only morphological traits of their skeletons. Despite the limited number of traits, our models suggest that morphological traits, namely corallite integration, corallite size and growth form, are useful indicators of the extinction risk of reef corals.

Dataset size is also known to affect the performance of machine learning models (e.g., Ajiboye et al., 2015; Raudys & Jain, 1991). However, the error rates of machine learning models have also been shown to decrease for sample sizes of > 100 observations (Ajiboye et al., 2015). Similar analyses applied using a range of datasets show that accurate results can be achieved for groups with small sample

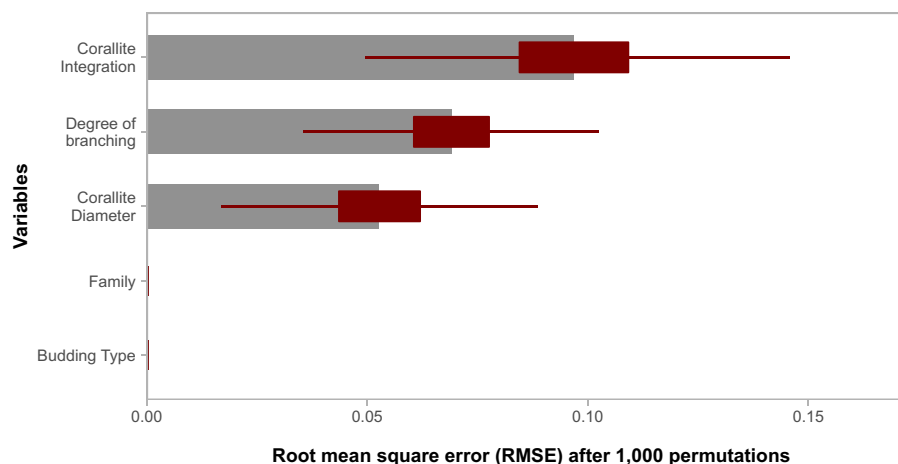


FIGURE 1 Permutation-based variable importance of the predictor variables in the final machine learning model (random forest) using the root square mean error (RMSE) as the loss function. The higher the RMSE value, the greater the increase in overall error rates by the machine learning model when the values for the particular variables are randomized. The grey bars show the mean error and the red boxplots the range of error values for 1,000 permutations.

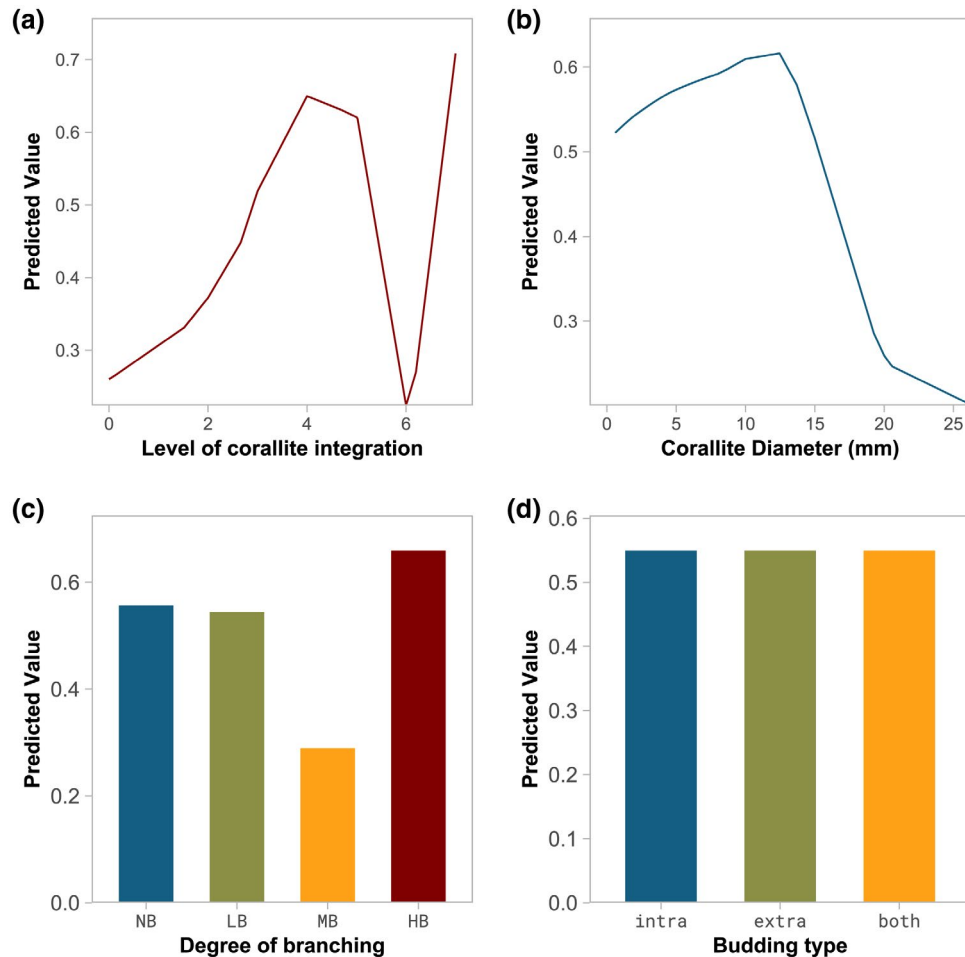


FIGURE 2 Partial dependence plots of the predictor variables: (a) corallite integration, with higher values showing increasing corallite integration; (b) corallite diameter; (c) degree of branching; and (d) budding type (intra = intracalicular; extra = extracalicular) in the fossil model used to compute the predicted values of threat status. The predicted values are computed based on the original data. HB, high degree of branching; LB, low degree of branching; MD, medium degree of branching; NB, no branching.

sizes (Bland et al., 2015). Setting aside 25% of the data for validation purposes reduced our sample size to 105 observations. The biggest issue with small datasets is that of class imbalances, where the dataset is biased towards one of the classes (Mazurowski et al., 2008). Initially, our data were relatively well balanced (59 extant species and 81 extinct species). In addition, we used the built-in oversampling algorithm to achieve balanced classes within the H2O framework and a custom decision threshold to overcome any possible issues with imbalances in our dataset. As such, our model is unlikely to be affected by either dataset size or class imbalances.

4.2 | Extinction of reef corals in the fossil record

The fossil record of reef ecosystems provides a source of data to understand the range of responses of reef corals to different environmental pressures, and this information is useful to project future responses of coral reefs to climate change (Pandolfi et al., 2011;

Pandolfi & Kiessling, 2014). Several examples of global reef crises, defined as a significant reduction in reefal calcium carbonate production, are thought to have been driven by climate warming (Kiessling & Simpson, 2011), and global projections suggest that modern reefs face a similar threat (Spalding & Brown, 2015).

Rapid changes in sea level during the Plio-Pleistocene are thought to have favoured fast-growing corals, such as *Acropora* (Renema et al., 2016). However, *Acropora* is also particularly susceptible to bleaching, ocean acidification, predation and pollution (Renema et al., 2016). This vulnerability is already documented in the decline and high threat status of the two Caribbean acroporids (Jackson et al., 2014) and a dominance of massive corals (Green et al., 2008). Although several reef corals were not able to keep up with changing environments during the Pleistocene, resulting in extinctions (Pandolfi et al., 2001), most reef corals were able to survive, partly as a result of migration to higher latitudes (Greenstein & Pandolfi, 2008; Kiessling et al., 2012). The traits that show resilience in our study (i.e., lower corallite integration, larger corallite sizes and

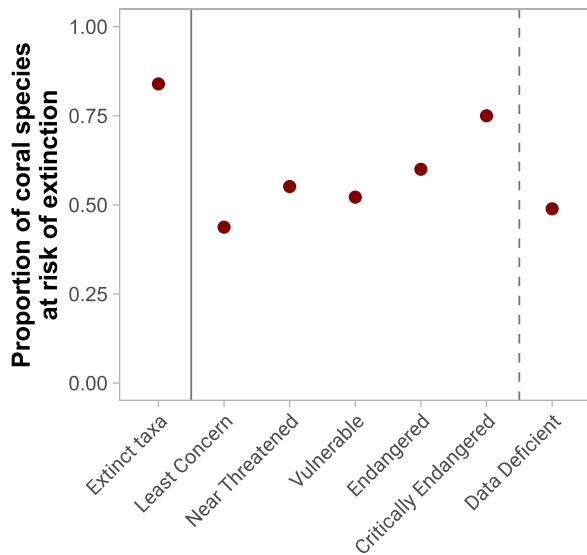


FIGURE 3 Proportion of taxa predicted to be at risk of extinction, for extinct and modern taxa (categorized according to the IUCN Red List classification), by the machine learning model.

lower degree of branching) also align with previous studies on traits of reef corals conferring resilience against climate-driven stressors (van Woesik et al., 2012).

The match between predicted extinction risk and the current conservation status in the IUCN Red List was poor for reef corals, with FMM correctly classifying the extinction risk category of only 43% of examined species. One potential reason for the poor match is the incompleteness of the fossil record, which can lead to truncation of the true time of extinction. This is unlikely in this case, because the sampling of Caribbean fossil reef corals is particularly good, which is the reason that we limited our fossil data to the Caribbean region. Limiting the fossil data to the Caribbean region also means that most species considered for training the model have relatively small range sizes in comparison to modern-day Indo-Pacific coral species (Veron et al., 2015). However, there is a good correspondence between the extinctions of Caribbean coral genera in the Plio-Pleistocene and the measured vulnerability of modern Indo-Pacific coral genera, suggesting that the Caribbean Plio-Pleistocene might also reflect contemporary trends in the Indo-Pacific region (van Woesik et al., 2012). In addition, a widespread distribution does not

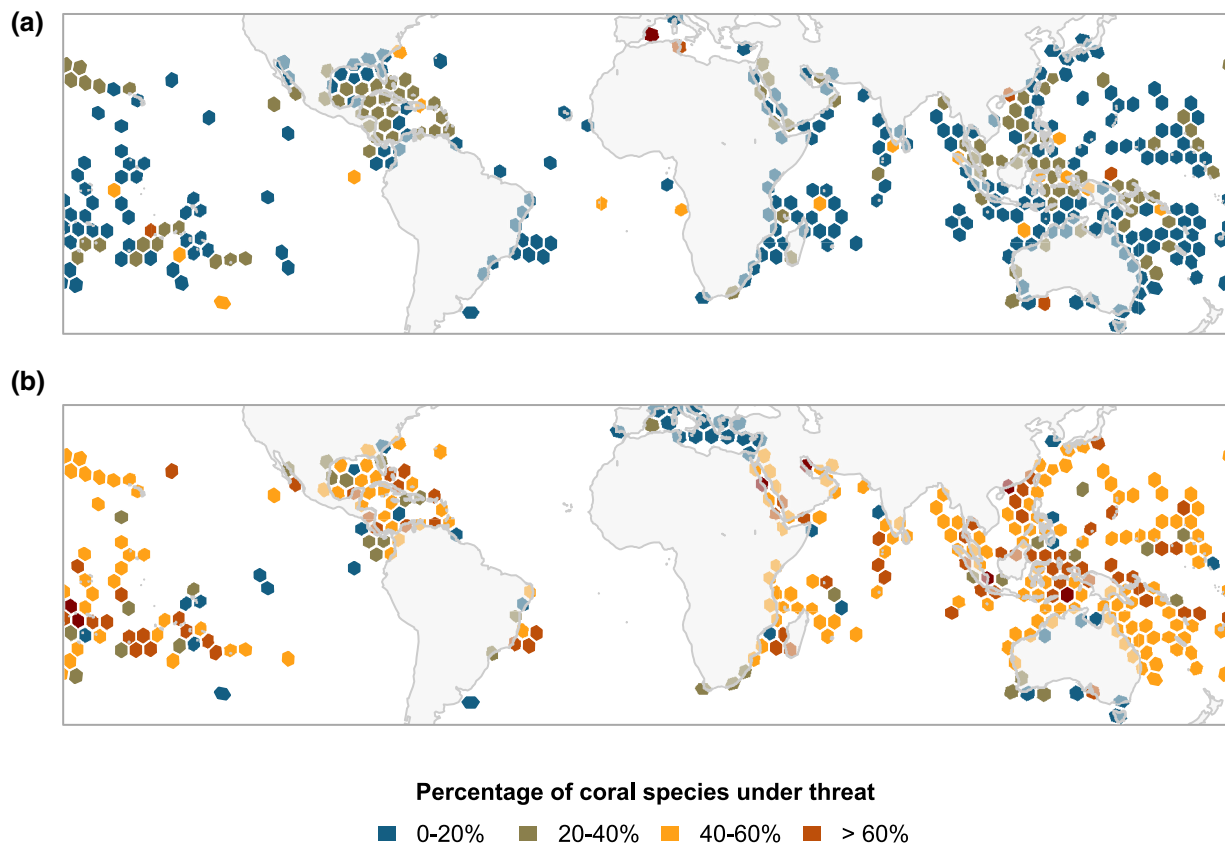


FIGURE 4 Global distribution of modern corals at risk of extinction as a percentage of the total number of reef coral species (a) according to the IUCN Red List, excluding data-deficient coral species (Carpenter et al., 2008), and (b) according to the trait-based models of extinction risk informed from the Plio-Pleistocene fossil record. Fossil extinctions during the Plio-Pleistocene were spread over > 1 Myr; hence, values in (b) do not necessarily indicate near-future extinction risk. The hexagon grids represent a mean global edge length of c. 2.5°.

automatically translate into resilience against regional extinctions. Caribbean extinctions were mostly driven by chronic environmental changes, including but not limited to the closure of the Isthmus of Panama causing changes in circulation patterns (Budd et al., 2011; O'Dea et al., 2007; Roff, 2021). This multitude of drivers is reminiscent of today, when direct anthropogenic stressors and climate change interact (Carpenter et al., 2008). The corals that survived the Plio-Pleistocene extinction were those resilient to environmental fluctuations (Johnson et al., 1995; van Woesik et al., 2012), showing the strong relationship between past and present vulnerability.

4.3 | Traits are a good predictor of extinction risk but not of IUCN conservation status

We can legitimately ask whether the IUCN Red List correctly identifies threat status for reef corals. There are a number of significant issues in the IUCN assessment of reef corals. First and foremost, the assessment by Carpenter et al. (2008) used reef area as a surrogate for population trends. The fossil record of reefs and reef corals shows that this approach is not justified. Prolific reef growth can occur with reduced coral diversity (Johnson et al., 2008), and coral reef growth was negligible during the peak diversity of reef corals in the late Early Cretaceous (Kiessling & Kocsis, 2015). The Cretaceous was marked by depressed reef growth, although the diversity of reef corals remained high (Kiessling, 2009; Kiessling & Baron-Szabo, 2004), suggesting that these organisms might have lost their reef-building capacity during that time as a result of a warming ocean (Kiessling & Kocsis, 2015). This shows that coral species have the ability to survive outside of reef systems, and as such, reef area is not a reliable proxy for population sizes and diversity. Likewise, the Paleocene–Eocene Thermal Maximum (PETM; 56 Ma), which marked a period of rapid warming, coincided with one of the most significant reef collapses in the fossil record (Kiessling & Simpson, 2011), although no extinction event for corals is recorded (Zamagni et al., 2012). Reef growth is therefore decoupled from diversity and probably from population sizes and is instead dependent on species with the capacity to create reef structures in sustained warming conditions.

Second, geographical range was another variable used in the IUCN assessment of corals (Carpenter et al., 2008). Geographical range has been universally documented as an insurance against extinction, not only for modern taxa (Cooper et al., 2008; Davidson et al., 2009; Harris & Pimm, 2008), but also in the fossil record outside of mass extinction episodes (Finnegan et al., 2015; Kiessling & Aberhan, 2007; Payne & Finnegan, 2007). Although the use of geographical range as a criterion in the IUCN assessments is well founded for many taxa, it might be less so for reef corals. This is partly attributable to the fact that the IUCN is based on traditional taxonomy (e.g., Veron, 2000) and does not account for cryptic speciation that is evident across many coral taxa (Forsman et al., 2015; Keshavmurthy et al., 2013; Richards et al., 2016; Schmidt-Roach et al., 2014), resulting in a discrepancy between the identity of a species and its geographical range (Bridge et al., 2020). Our use

of morphological traits circumvents this issue and provides an alternative to traditional taxonomy-based approaches (Menezes et al., 2010; Spitz et al., 2014), such as the one used by the IUCN, by providing a general framework to identify the relationship between life-history traits and extinction risk.

Our model suggests that the extinction risk of modern corals might be underestimated. Almost half of modern coral species are at elevated extinction risk (Figure 4), most of which are currently assessed as Least Concern or Near Threatened (Figure 4). However, our model was trained by coral extinctions, which occurred over hundreds of thousands of years. Although our model is likely to identify vulnerable coral species correctly, the severity of near-time extinction risk is unclear. Irrespective of the modelled extinction risk or assessed conservation status, the extinction of reef corals is unlikely to be severe in the near future, simply because population sizes of even “rare” species are way above typical extinction-prone species (Dietzel et al., 2021), although this could change rapidly as thermal stress intensifies (Hughes et al., 2018). Practitioners in conservation science are, of course, more interested in decadal changes (Kiessling et al., 2019). However, experimental studies that are carried out on smaller temporal scales (hours to weeks) have similar scaling concerns but still provide valuable information on the stress tolerance of organisms (e.g., Pörtner, 2010). Moreover, the sensitivity of organisms to climate-related stressors has been shown to conform across time-scales, from sub-annual experiments to decadal shifts to extinction patterns in the fossil record (Reddin et al., 2020).

The incongruence of the IUCN classification of conservation status of modern reef corals and life-history traits related to resilience is also documented in the literature (Bridge et al., 2020; Huang, 2012). We therefore concur with Bridge et al. (2020) that the current conservation status of coral species set by the IUCN might not reflect extinction risk accurately. As such, any model trained using the IUCN classifications to infer extinction risk of corals is also likely to be inaccurate, despite the high performance of such models (Supplementary Materials Table S4). Instead, the extinction risk of reef corals should be calibrated using life-history traits known to confer resilience against climate warming and against real extinction as observed in the fossil record (e.g., Finnegan et al., 2015). We show in the present study that the fossil record not only provides information on resilient or vulnerable traits with regard to extinction, but also can be used to infer the extinction risk of modern corals. The IUCN assessments inform conservation policy and practice in several countries (Bland et al., 2019). Unreliable assessments of the extinction risk of reef corals, whereby extinction risk might be severely underestimated for some species, can therefore impact these management practices. Elucidation of the relationship between reef coral extinction risk and species traits can be applied as a rapid and inexpensive approach for assessing the conservation status of species and geographical regions with data deficiency. The investment in collecting such data for both fossil and modern corals coupled with machine learning represents one way forward to quantify risk in the response of reef corals to environmental change.

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CONFLICT OF INTEREST

The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

N.B.R. performed the analyses, wrote the manuscript and drafted the figures. A.L. performed analyses and drafted an earlier version of this manuscript. N.B.R., A.L. and W.K. developed the concept. W.K. contributed to writing and data cleaning. J.M.P. provided conceptual ideas and reviewed the manuscript. S.W.K. contributed technical advice. A.F.B. aided in data acquisition and curation, and also contributed to the interpretation of the results.

DATA AVAILABILITY STATEMENT

Data and code for the analyses are available on the Open Science Framework (<https://doi.org/10.17605/osf.io/gb5ty>).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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