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Reef coral traits predict extinction risk
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Abstract:	<p>The responses of life history traits to the spatial variation in environmental conditions and biotic interactions influence the fitness of organisms and shape their ecological niches. We performed a quantitative assessment of the link between reef coral traits and species extinction risk as reported by the International Union for Conservation of Nature (IUCN). We selected four traits based on their relevance to predict the IUCN extinction risk and the proportion of missing data in the original trait dataset: geographic range, maximum water depth, typical growth form and corallite size. Missing trait values were estimated using phylogenetic multiple imputation. An artificial neural network model based on these four traits derived from 661 coral species yielded 75.8% accuracy in predicting the IUCN threat status. We used this model to predict the threat status of 77 data deficient coral species and derive the threat status of late Pleistocene corals. Removing geographic range from the predictors slightly lowered the explanatory power and resulted in 64.3% prediction accuracy. Even a limited compilation of traits can provide valuable information for the extinction risk assessment of reef coral species.</p>	
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Dear Editors of *Coral Reefs*,

Please consider our manuscript "*Reef coral traits predict extinction risk*" for publication as a Research Report in your journal.

We apply machine-learning techniques on recent reef coral life history and spatial traits to derive an explicit model of threat statuses as proposed by the International Union for Conservation of Nature (IUCN). With our model, which is based on just four traits, we are able to predict the threat status of modern reef corals with a 76% accuracy. This performance led us to suggest a threat status for so far data deficient species. As our traits can be inferred in fossil corals, we also applied the model to coral occurrences of the Last Interglacial Episode. Results for recent global patterns, including increased susceptibility in the Malay Archipelago and moderate susceptibility in the Caribbean, are congruent with previously proposed patterns. We conclude that coral traits represent a valuable tool for estimating threat levels of coral species and their geographic distribution, both today and the past.

All authors have agreed to the final submitted version, and all persons entitled to co-authorship have been so named. None of the material has been published or is under consideration elsewhere. Supporting information is included in a separate file.

We look forward to hearing from you about this submission.

For all co-authors

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Reef coral traits predict extinction risk

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4 23 **Abstract**
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9 25 interactions influence the fitness of organisms and shape their ecological niches. We performed a
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11 26 quantitative assessment of the link between reef coral traits and species extinction risk as reported
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13 27 by the International Union for Conservation of Nature (IUCN). We selected four traits based on
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15 28 their relevance to predict the IUCN extinction risk and the proportion of missing data in the
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30 34 geographic range from the predictors slightly lowered the explanatory power and resulted in
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32 35 64.3% prediction accuracy. Even a limited compilation of traits can provide valuable information
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34 36 for the extinction risk assessment of reef coral species.
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38 37 **Introduction**
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44 38 Coral reefs are under increasing pressure from climate change and direct human impacts
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46 39 (Harborne et al. 2017; Hughes et al. 2017; Perry et al. 2018). A third of extant reef coral species
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48 40 are considered vulnerable to extinction or endangered due to these combined stressors (Carpenter
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50 41 et al. 2008). The International Union for Conservation of Nature (IUCN) has standardized the
51
52 42 criteria for assessing the extinction risk of species. For coral species, extinction risk is mainly
53
54 43 based on trends in population size (Criterion A), with only six species assessed under Criterion B
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56 44 (range size) and three under Criterion D, which is a special category for species with already
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58 45 restricted populations (Carpenter et al. 2008). These criteria are well established (Mace et al.
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4 46 2008) but information on them is often hard to gather, which is one of the reasons why many
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6 47 marine species remain ‘data deficient’.
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10 48 Trait-based approaches are widely used in population and community ecology from
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12 49 species to whole ecosystem scales (Violle et al. 2007; Suding et al. 2008; Chown 2012; Darling
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14 50 et al. 2012; Madin et al. 2016a). Species life-history traits may be linked with extinction risk due
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16 51 to climate change (Foden et al. 2013; Pearson et al. 2014) and their formal incorporation into the
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18 52 assessment of extinction risk may help improve the assessment of risk status of currently
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20 53 unevaluated species. Among a plethora of life-history traits, habitat breadth, maximum water
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22 54 depth, larval temperature tolerance, association with particular symbiont clades, growth rates, and
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24 55 dispersal capacity have been associated with climate change vulnerability for corals (Foden et al.
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26
27 56 2013).

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32
33 57 Reef corals have a range of additional physiological, morphological, and reproductive
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35 58 traits that might explain variance in their resilience to increasing sea-surface temperatures (SST)
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37 59 (Mizerek et al. 2018). Here we use trait information from the Coral Trait Database (Madin et al.
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39 60 (2016b) and assess its capacity to predict the IUCN Red List threat status of reef corals. While
40
41 61 comprehensive, the Coral Trait Database (CTD) contains abundant missing data entries. To
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43 62 improve the taxonomic coverage and predictive capacity of our model, we estimated expected
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45 63 trait expressions with a phylogenetic imputation approach (Kim et al. 2018). After exploring the
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47 64 predictive power of individual traits, we use a machine-learning algorithm to create a model of
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49 65 combined traits assessing the Red List status. We apply this model to previously data-deficient
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51 66 species of reef corals and to Pleistocene corals of the Last Interglacial (ca. 130 kyr) in order to
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53 67 track the long-term evolution of threat status at the regional level.

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4 69 **Methods**
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8 70 Coral trait data were downloaded on 4th of October 2018 from the CTD (coraltraits.org),
9 and species occurrence data were extracted from the Ocean Biogeographic Information System
10 (OBIS, iobis.org) on the same date. The trait dataset comprised information for 136 coral traits of
11 1548 species. For our analyses, we initially limited the dataset to 13 traits for 661 zooxanthellate
12 coral species (those with symbiotic dinoflagellates). Several traits had a large proportion of
13 missing data with skewed taxonomic coverage (Supplementary table 1). Previous studies
14 commonly treated missing entries in trait datasets by removing taxa with missing information
15 (e.g. Shipley et al. (2006); Bernard-Verdier et al. (2012)). However, such reduction in a dataset is
16 likely to impair downstream analyses (Nakagawa and Freckleton 2008; Van Buuren 2018). Other
17 studies showed the benefit of single imputation approaches (Penone et al. 2014; Schrodt et al.
18 2015). While single imputation approaches may reduce bias in downstream analyses, they
19 produce overly optimistic standard error ranges (Newman 2014; Van Buuren 2018). To resolve
20 statistical issues associated with other approaches, we selected multiple imputation as the basis
21 for our phylogenetic imputation framework, following Kim et al. (2018). In particular, we chose
22 multiple imputation by chained equations with the recursive partitioning to minimize errors
23 stemming from highly dimensional data with nonlinear structures, which are common among trait
24 data (Santini et al. 2013; Doove et al. 2014). Phylogenetic information was extracted from coral
25 supertrees (Huang and Roy 2015). For recursive partitioning, we fitted ten decision trees, each
26 with 500 iterations to build a Bayesian network. This process was replicated ten times to achieve
27 our multiple imputation framework. We performed multiple imputation using the ‘randomForest’
28 and ‘mice’ packages (Liaw and Wiener 2002; Buuren and Groothuis-Oudshoorn 2010) in R (R
29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 CoreTeam 2018).

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4 92 We chose traits known to be sensitive to temperature and other stressors (van Woesik et
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6 93 al. 2012; Foden et al. 2013). Although the initial selection resulted in 13 traits, we only used traits
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8 94 with a total percentage of less than 5% missing data in the CTD. For traits that underlie similar
9 function, such as multiple growth form traits in the CTD, we selected those that showed a better
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11 95 rank-order correlation with extinction risk or had less missing data. As a result, we selected four
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13 96 traits for downstream analyses: (1) typical growth form, (2) maximum water depth, (3) maximum
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15 97 corallite width, and (4) geographic range. Importantly, these traits can be assessed or inferred in
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17 98 fossils (water depth can be estimated from sedimentological criteria), rendering the model
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19 99 applicable in the near-recent fossil record. Analyses with more traits yielded the same basic
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21 100 results (Figure S2 and Supplementary Text).

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24 102 Typical growth form has a total of 12 categories, yet we reduced it to a binary variable to
25
26 103 highlight the most striking forms of coral growth morphology: branching and non-branching. For
27
28 104 maximum water depth and maximum corallite width, we used directly the values provided in the
29
30 105 CTD. Geographic range size was measured as the maximum great circle distance of observed
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32 106 species occurrences in the OBIS dataset. Geographic range size measurements were subsequently
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34 107 normalized using the largest range size among all taxa. We used this measure of geographic
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36 108 range size instead of the geographic area size in the CTD because area measurements are not
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38 109 possible in the Pleistocene dataset, and the normalized range size is less sensitive to the reduced
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40 110 sampling of fossil corals. Range area and normalized range size are significantly correlated for
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42 111 modern corals ($\rho = 0.74$, $p < 0.001$) and yield nearly the same statistical relationship with modern
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44 112 threat status (Table S2).

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47 113 At the core of our analysis is a machine-learning algorithm to predict the IUCN Red List
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49 114 status from trait combinations, considering potential interactions among variables. We created an
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4 115 artificial neural network based model with the ‘nnet’ package in R (Ripley et al. 2016). The
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6 116 IUCN status was the response variable and the four trait data listed above were the predictor
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8 117 variables. IUCN status comprised five ordinal values: Least Concern (LC), Near Threatened
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10 118 (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR). The traditional
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12 119 separation between non-threatened and threatened categories falls between NT and VU (Mace et
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14 120 al. 2008).

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19
20 121 Artificial neural networks can handle categorical response variables (e.g. IUCN status) by
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22 122 transforming them to a binary representation (Garson 1998). Numeric predictors were scaled to
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24 123 account for different ranges and variabilities. The input variables were fed into a system of
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26 124 hidden layers containing a range of nodes that generate different linear combinations of these
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28 125 variables. A logistic function switches nodes on and off, which generates different logistic
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30 126 regression models. The best combination of these is chosen by back-propagation where the best
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32 127 model is fitted using maximum likelihood. To get an estimate of the variation between different
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34 128 imputation results, we used the median absolute deviation (Figure S4).

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40 129 In order to assess the performance of our neural network models we performed three tests.
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42 130 The first was run on data comprising the modelled IUCN statuses as five discrete variables (LC
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44 131 to CR). We compared the number of cases in which the modelled status differed from the actual
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46 132 status proposed for a species. The number of correct results resulting from iterating the analyses
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48 133 over the 10 imputation tables is divided by all ten cases to provide an accuracy value, which is
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50 134 reported in percent. In the second test we used the R package ‘pROC’ (Robin et al. 2011) to
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52 135 calculate an “Area Under the Curve (AUC)” value of a "Receiver Operating Characteristic
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54 136 (ROC)" which is a measure of performance of a model in signal detection theory. AUC and ROC
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56 137 can also be calculated with not-binary variables (multiclass AUC/ROC as defined by Hand and

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4 138 Till (2001)). In the third test AUC values are based on IUCN statuses treated as binary variables
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6 139 (LC/NT as 0, VU/EN/CR as 1).
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10 140 The model was then applied to predict the IUCN status of data-deficient extant corals.
11
12 141 There were 77 corals listed as data deficient, which was equivalent to 10.4% of all coral species
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14 142 in our dataset. A threat status was assigned to a species only if the status was supported by greater
15
16 143 than 60% probability in the model prediction. The dominant data-deficient genus was *Acropora*
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18 144 (32.5% of the data deficient-species).
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23 145 We also modeled the threat status of late Pleistocene (Last Interglacial, LIG, ca. 130 kyr)
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25 146 corals with the aim to check if areas with high concentrations of threatened species have changed
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27 147 through time. The modeled threat status of the two extinct Caribbean species *Pocillopora*
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29 148 *palmata* and *Orbicella nancyi* (Pandolfi et al. 2001) was used to determine whether predicted
30
31 149 extinction risk was actually greater than average for these species. A species was assigned to one
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33 149 of the categories if at least six out of ten matches were reached within the 10 imputation runs.
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37 151 Geographic ranges of LIG species were derived from the Paleobiology Database (paleobiodb.org,
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39 152 downloaded 4th of October 2018), again using the maximum great-circle distance per species
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41 153 normalized to the global maximum.
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46 154 To permit comparisons with previously published results (Carpenter et al. 2008), we
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48 155 compiled species occurrence data from OBIS and mapped our modelled threat status in equal
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50 156 area hexagonal grid cells using the ‘icosah’ package (Kocsis 2017) in R. We then compared the
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52 157 distributions of percentages of modeled threat status in grid cells with those of Carpenter et al.
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54 158 (2008) using Spearman rank-order correlation. Comparisons were made for critically endangered
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56 159 (CR) species first and then sequentially adding less endangered IUCN categories.
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4 160 **Results**
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8 161 Individual traits showed significant rank-order correlations with the IUCN threat status
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10 162 (Table S2). Geographic range and the maximum water depth a species could inhabit exhibited
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12 163 best correlations with the threat status. Growth rate, growth form and corallite width also showed
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14 164 significant correlations with IUCN threat status in all 10 imputation runs. Although Kruskal-
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16 165 Wallis tests confirm different distributions of trait values among threat statuses ($p < 0.001$)
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18 166 relationships can be complex (Fig. 1).

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24 167 **Figure 1**
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27 168 The ANN model comprising all four traits explained the IUCN status with 75.8%
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29 169 accuracy. Excluding geographic range resulted in 64.3% accuracy after 1000 iterations. Running
30
31 170 the model with each trait separately showed the highest predictive power for maximum water
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33 171 depth with 49.3% accuracy, followed by corallite size (48.3%), geographic range (48.1%), and
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35 172 typical growth form (9.1%). The AUC was 0.86 for all traits and 0.76 without the geographic
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37 173 range for binary response (threatened versus non-threatened). The multiple class AUC was 0.92
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39 174 for all and 0.72 without the geographic range.

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45 175 A comparison of our model output with the empirical data of Carpenter et al. (2008)
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47 176 yielded significant correlations. The correlation was strongest ($\rho \approx 1$, $p < 0.001$) in the most
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49 177 threatened category (CR; Fig. 2a), but the other categories also showed significant (all: $p < 0.001$)
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51 178 correlations in overlapping grid cells: CR+EN (Fig. 2b): $\rho = 0.83$, CR+EN+VU (Fig. 2c): $\rho = 0.77$
52
53 179 and CR+EN+VU+NT (Fig. 2d): $\rho = 0.73$. In the Caribbean, the high proportions of highly
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55 180 endangered species (Fig. 2a) resulted from only two critically endangered species (*Acropora*
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57 181 *palmata* and *A. cervicornis*). The Caribbean vulnerability hotspot vanished when all threatened

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4 182 species were considered (CR, EN and VU). Adding near-threatened species to the community per
5 grid cell identified the Indo-Pacific as more vulnerable region, whereas the Caribbean (as with
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7 183 the entire Atlantic) showed moderate extinction risk (Fig. 2d). Grid cells with less than 25%
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9 184 threatened species were evident in all geographic regions and appear to be randomly distributed.
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Figure 2

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18 187 Of the 77 data deficient (DD) reef coral species in the Red List (Table 1), seventeen
19 species showed no linkages to compilations of trait expressions that clearly delineated the threat
20 status, and thus remained as data deficient. The remaining species were similarly distributed
21 among threat categories as previously assigned species ($\rho=0.87$, $p=0.0538$), with LC=15.6%,
22
23 188 NT=10.4%, VU=27.3%, EN=10.4%, and CR=0%. Modelled prediction of the IUCN status for
24 data-deficient corals showed moderate (mostly <40%) global extinction risks, except for the
25
26 189 Caribbean, and limited cases of isolated areas (e.g. Hawaii, Galápagos Islands, and Kiribati)
27 where regional extinction risks did not change (Fig. 3). In contrast, the Coral Triangle and the
28
29 190 Philippines showed exceptionally high extinction risks among DD corals. Corals from the genus
30
31 191 *Acropora* contributed to 57.1% of the vulnerable and 62.5% of the endangered categories. In
32 contrast, they only accounted for 25% of the least concern and near threatened categories, which
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34 192 emphasizes the general vulnerability of *Acropora* species.
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Figure 3

Table 1

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4 204 west coast of Mexico. In models with geographic range included, the total proportion of non-
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6 205 threatened species (least concern and non-threatened) was 10.2% lower in the LIG than today.
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8 206 These differences were mainly caused by the lower number of least concern species in the LIG
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10 207 (Table 2).
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15 208 **Figure 4**
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18 209 **Table 2**
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21 210 The modeled threat statuses for the two now extinct Caribbean species *Orbicella nancyi*
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23 and *Pocillopora palmata* showed low and high extinction risk, respectively (Fig. S3). The
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25 modeled predictions of the IUCN status for *O.nancyi* did not result in the vulnerable categories
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27 (VU, EN or CR), whereas *P. palmata* was always categorized in one of the threatened statuses.
28
29 213 (VU, EN or CR), whereas *P. palmata* was always categorized in one of the threatened statuses.
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31 214 The most common outcome was LC for *O. nancyi* (99.9% of all cases yielding >60% the same
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33 result in this category) and VU for *P. palmata* (89.8%).
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37 216 **Discussion**
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41 217 **Prediction accuracy**
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44 218 Previous studies revealed linkages between coral traits and extinction vulnerability (van Woesik
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46 et al. 2012; Foden et al. 2013), but our goal was to go beyond the simple separation of two
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48 categories such as low and high risk of extinction. We aimed instead at predicting from reef coral
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50 traits their precise IUCN category and wanted our approach to be applicable to fossil data by
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52 choosing traits preservable in fossils. A 76% accuracy in our predictions is way above what
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54 would be expected by chance (one out of five = 20%). Our multi-class AUC with all four traits
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56 yields 0.92. This high AUC value is especially remarkable because we have only used four
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58 variables in our model. Although our binary AUC value is lower (0.86) it is in the range of trait-
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61 225 variables in our model. Although our binary AUC value is lower (0.86) it is in the range of trait-
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4 226 based prediction performance for terrestrial amphibians and reptiles, which yielded AUC values
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6 227 of 0.80-0.86 (Pearson et al. 2014).
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10 228 **Relevance of single traits for threat status assessment**
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13 229 Although the ANNs with all traits were better suited to predict the species-specific Red
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15 230 List categories, individual rank-order correlations also depicted direct relationships between trait
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17 231 expressions and extinction risk. The negative association between geographic range and
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19 232 extinction risk is unsurprising given the universality of geographic range as an insurance against
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21 233 extinction (Cooper et al. 2008; Harris and Pimm 2008; Davidson et al. 2009), which also is
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23 234 expressed in the fossil record (Kiessling and Aberhan 2007; Payne and Finnegan 2007; Finnegan
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25 235 et al. 2015). Geographic range size is already used in the IUCN assessment (Criterion B, 6
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27 236 species out of 827, Carpenter et al. (2008) SOM), albeit only as a supplementary criterion to
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29 237 population size trends over time (IUCN criterion A, 695 species, Carpenter et al. (2008) SOM).
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31 238 Although abundance and geographic distribution are weakly linked in reef corals (Hughes et al.
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33 239 2014), geographic range is still the strongest individual predictor of extinction risk in our study.
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35 238 Although abundance and geographic distribution are weakly linked in reef corals (Hughes et al.
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37 239 2014), geographic range is still the strongest individual predictor of extinction risk in our study.
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39 240 However, the relatively small Caribbean range sizes coincide with a proportionally larger number
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41 241 of species in the non-threatened categories compared to the rest of the world.
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45 242 Our findings also showed a negative correlation between maximum water depth and
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47 243 extinction risks. Previous studies argued that the uppermost 20m of the water column are heavily
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49 244 affected by anthropogenic and climatic stressors, whereas deeper marginal reef habitats or off-
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51 245 reef areas are often less influenced by these stressors (Carpenter et al. 2008; Foden et al. 2013).
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53 246 Although mesophotic environments may also contain threatened communities (Rocha et al.
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55 247 2018), research in the mesophotic zone is limited, and our results support the established
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57 248 knowledge about the degree of anthropogenic and climatic stress over depth.
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4 249 Most interesting from a fossil perspective is the negative association between extinction
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6 250 risk and corallite size. This life-history trait figures prominently in the ANN model and can be
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8 251 linked to nutrition. Smaller corallites are commonly associated with higher autotrophy, whereas
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10 252 species with large corallites tend to be more heterotrophic (Porter 1976). Therefore, small
11
12 253 corallites enhance photosymbiotic autotrophy and are more beneficial under normal conditions.
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14 254 However, large corallites facilitate heterotrophic nutrient cycle under thermal stress, and can
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16 255 reduce mortality during breakdown of the symbiosis (Hughes and Grottoli 2013). Furthermore, a
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18 256 larger coral polyp can store more energy, which might support resilience to disturbances (van
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20 257 Woesik et al. 2012). Our results support the notion that extinction risk is reduced in species with
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22 258 larger-sized corallites.
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29 259 Growth form is strongly linked to linear extension rates, with branching species growing
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31 260 nearly an order of magnitude faster than massive species (Renema et al. 2016). Fast growing
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33 261 species in the families Acroporidae, Euphylliidae and Dendrophylliidae tend to occur in the higher
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35 262 extinction risk categories (Carpenter et al. 2008). Massive growth forms prevalent in Poritidae,
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37 263 on the other hand, are mostly of least concern. This observation is confirmed by our results
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39 264 showing lower extinction risk for massive than for branching corals, although the importance of
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41 265 growth form was relatively low in the ANN model. Surprisingly, fast growth (associated with
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43 266 branching species) was qualified as low climate change vulnerability in Foden et al. (2013).
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50 267 **Last Interglacial – Recent comparison**

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53 268 The LIG – Recent comparison highlights two interesting points. First, the Caribbean
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55 269 shows a different behavior than other ecoregions. The proportion of non-threatened species was
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57 270 10.2% lower in the LIG (Table 2). Second, the differences between models comprising all traits
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59 271 and those without geographic range are much larger in the Caribbean than in other ecoregions,
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4 272 suggesting a larger influence of geographic range on extinction risk in the region. Two well-
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6 273 studied Caribbean species are confirmed extinct: *Orbicella nancyi* and *Pocillopora palmata*. The
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8 274 extinction of these two and perhaps other endemic Caribbean species might be the reason for the
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10 275 shift to a proportionally less threatened species pool in the region since the LIG. Major
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12 276 advantages of Caribbean species today are their potentially higher thermal resistance due to high
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14 277 symbiont diversity and their high trait redundancy (Huang and Roy 2015). Strong, cyclic sea
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16 278 level changes preceded the LIG, when sea level is thought to have reached up to 6.6 m higher
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18 279 than today (Kopp et al. 2009). This history of sea level changes, coupled with advantageous life-
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20 280 history characteristics, is suggested to have resulted in a dominance of *Acropora* (Renema et al.
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22 281 2016) in most reef sites. *Acropora* can cope with fast sea level changes because its growth and
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24 282 calcification rates are among the highest of all coral species (Gold and Palumbi 2018) and it has
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26 283 the ability to regenerate upon fragmentation. However, these traits, coupled with a branching
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28 284 morphology, indicate a higher extinction risk and thermal susceptibility, which today caused the
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30 285 collapse of the two highly threatened acroporid species in the Caribbean and a dominance of
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32 286 massive corals (Green et al. 2008).
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13 299 **Author contributions statement**
14
15 300 A.L performed the analyses and wrote the manuscript, W.K. wrote the manuscript and assisted
16
17 301 with the analyses. J.M.P. provided conceptual ideas and reviewed the manuscript. K.S.W.
18
19 302 performed the imputation analysis, and provided technical advice.
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23 304 **Additional information**
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25 305 ***Conflict of interest statement***
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27 306 On behalf of all authors, the corresponding author states that there is no conflict of interest.
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4 430 **Figure Legends**
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8 431 Figure 1: Combined box/bean plots of the IUCN status against the four numeric traits used in the
9 analyses. Threat categories are color coded from dark green (LC) to red (CR) representing
10 increasing threat categories from left to right. Vertical size of the beans represents number of
11 species with values on the y-axis, horizontal width is a not to scale representation of the number
12 of data points at a certain value on the y-axis. Black bars in the boxes within the beans show
13 interquartile range in white and the median as a vertical bar. Outliers not shown.
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27 438 Figure 2: Trait-modelled percentages of reef coral species IUCN Red List category in equal-area
28 grid cells (mean global edge length about 2.5° , area of 200,790 km²) comprising 343,293
29 occurrences. Models derived from artificial neural network (ANN). (A) Critically endangered
30 species (CR); (B) Critically endangered (CR) plus endangered (EN) species; (C) Critically
31 endangered (CR), endangered (EN) and vulnerable (VU) species; (D) Critically endangered (CR),
32 endangered (EN), vulnerable (VU) and near threatened (NT) species.
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46 445 Figure 3: Trait-modelled percentages of coral threat statuses for previously data-deficient coral
47 species in equal-area grid cells (mean global edge length about 2.5°) comprising 3,184
48 occurrences, modelled with ANN. The value in each grid cell shows the summed percentage of
49 critically endangered, endangered and vulnerable coral species.
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4 450 Figure 4: Trait-modeled percentage of coral threat statuses for Last Interglacial (LIG; ~125 ka)
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6 451 coral species in equal-area grid cells (mean global edge length about 4.4°). The value in each grid
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8 452 cell shows the summed percentage of critically endangered, endangered and vulnerable coral
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10 453 species.
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Figure 1

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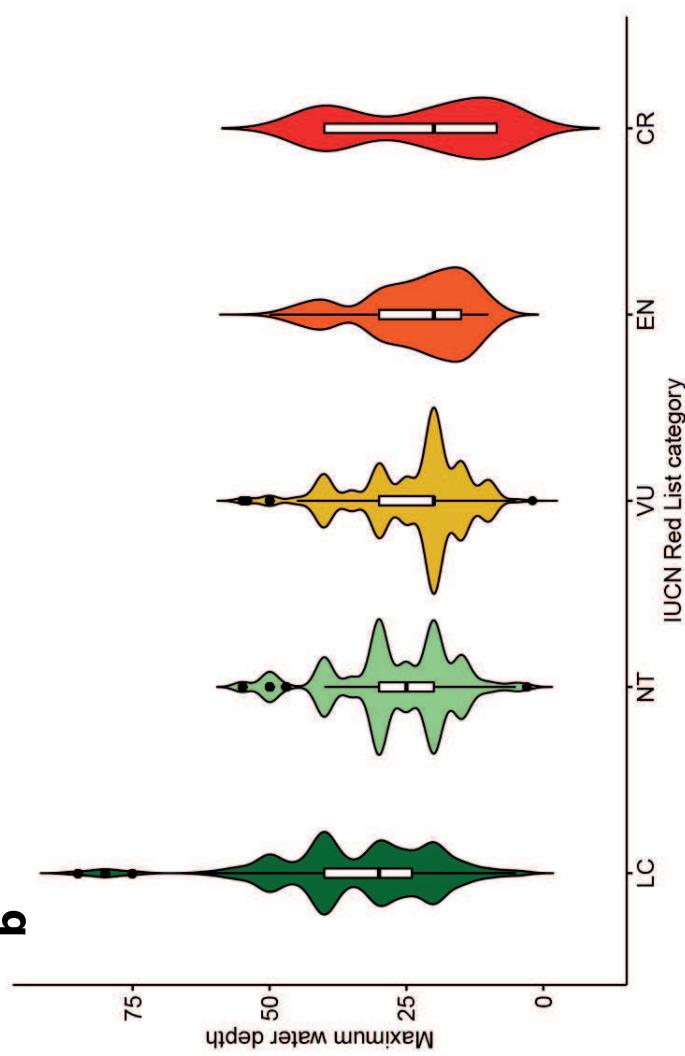
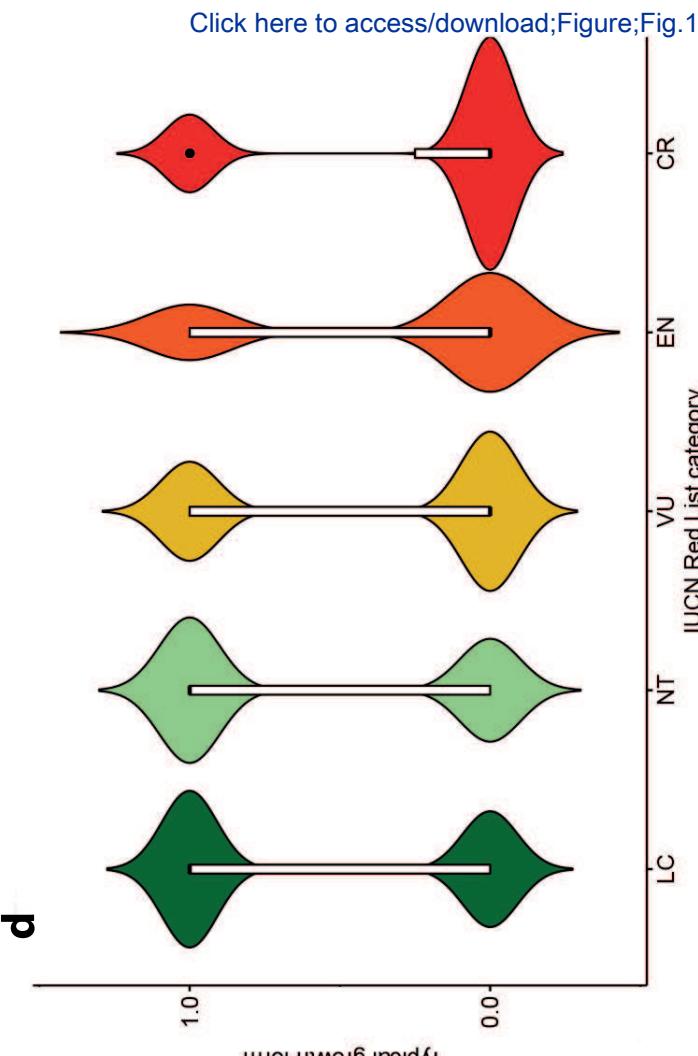
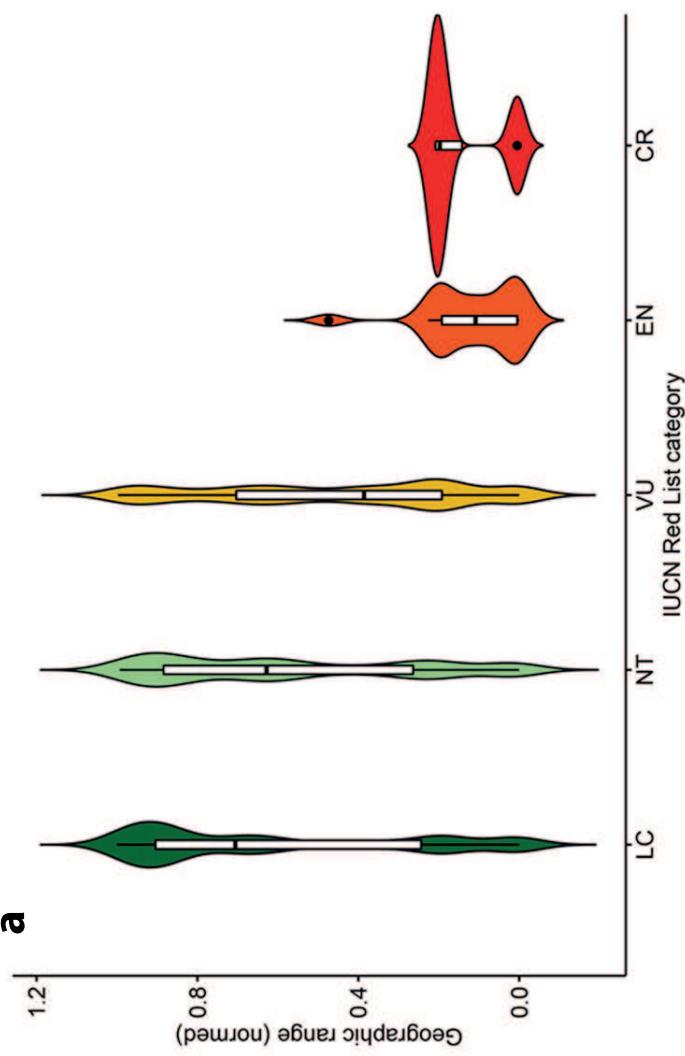
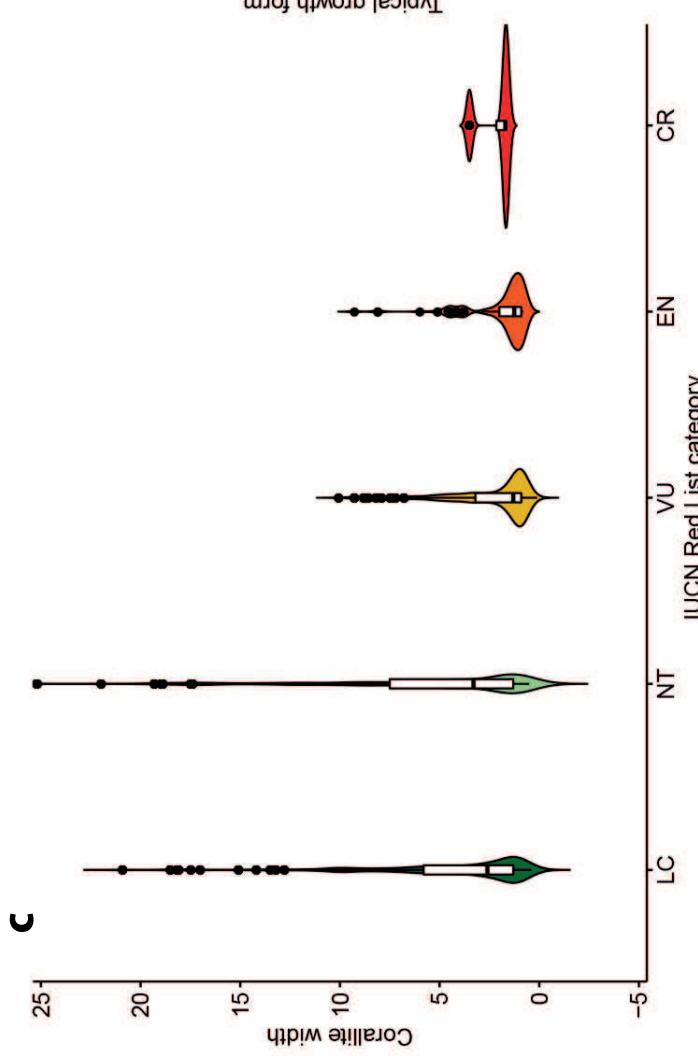
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Figure 2

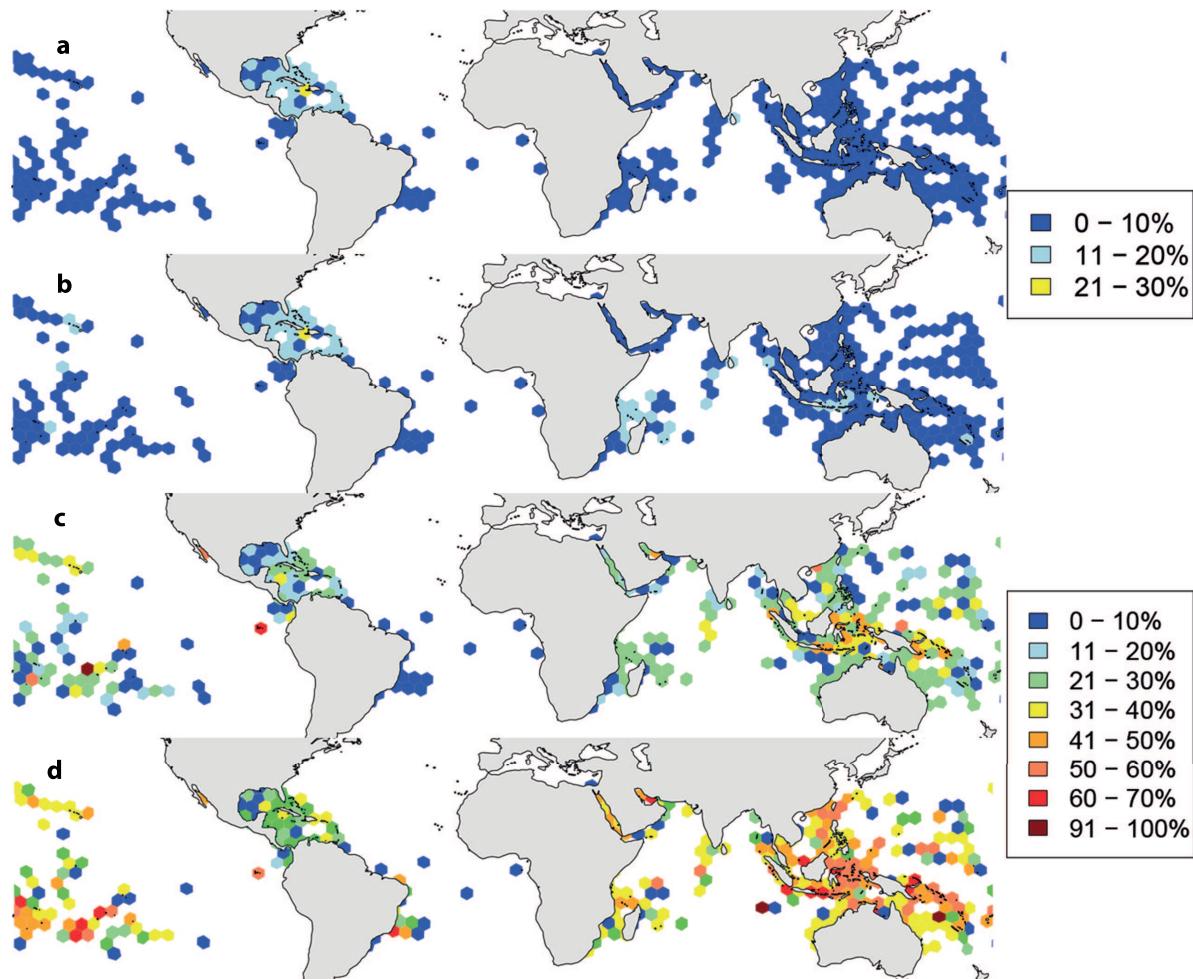
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Figure 3

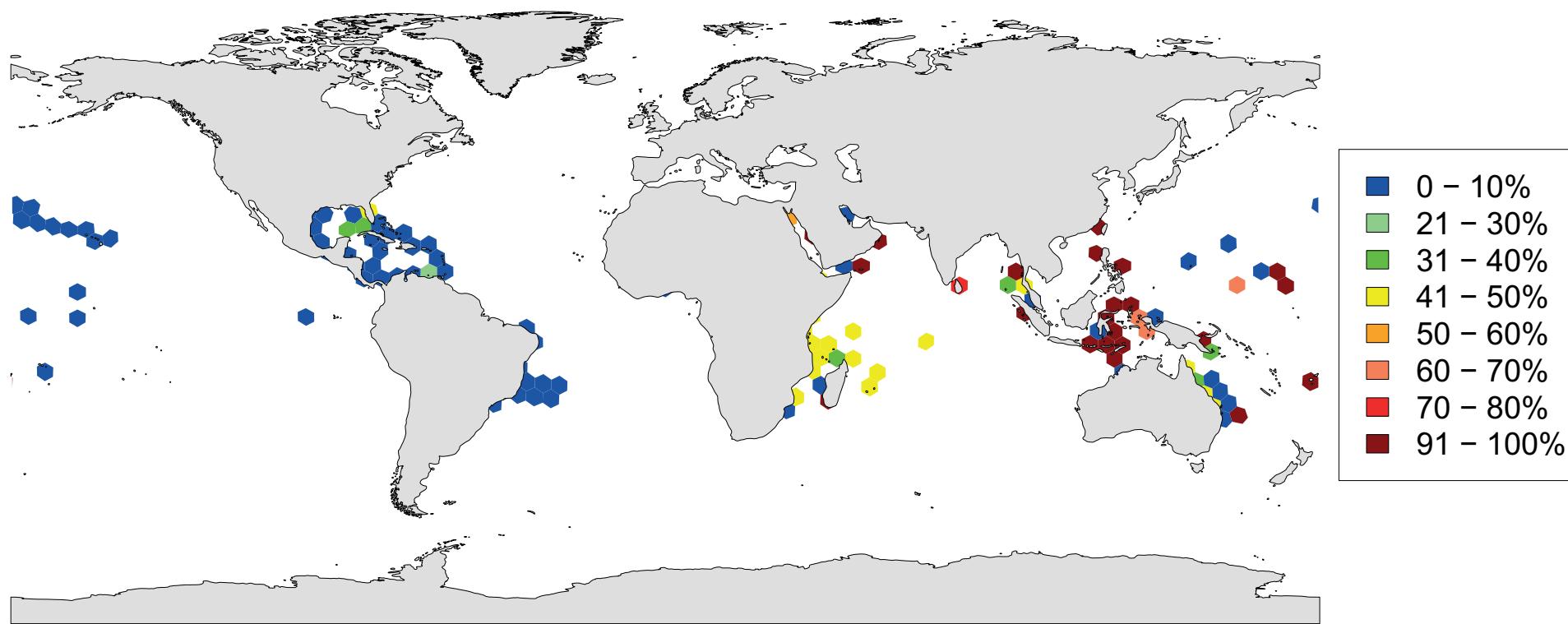
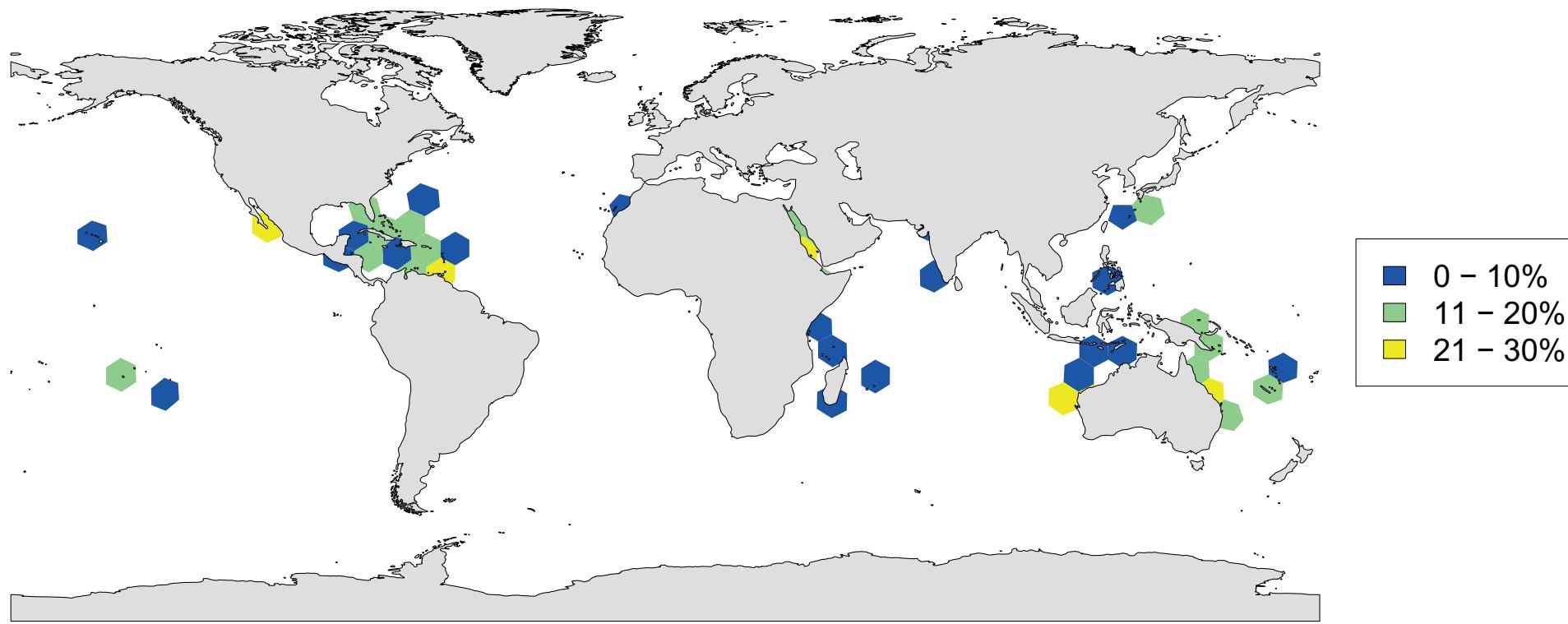
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Figure 4

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1 Table 1: IUCN threat status classification (LC for “least concern”, NT for “near threatened”, VU
 2 for “vulnerable”, EN for “endangered”) of formerly data-deficient (DD) coral species, inferred
 3 from an artificial neural model comprising preservable species traits. Species with a match of less
 4 than 60% or ambiguous results (50% match for two categories) are listed as still data deficient
 5 (DD). Letters in parentheses indicate Atlantic (A), Pacific (P), Indian (I), Caribbean (C), Indo-
 6 Pacific (IP) and Caribbean/Atlantic (CA) habitat. Red Sea is Included in I.

LC	NT	VU	EN	still DD
<i>Acropora cardenae</i> (IP)	<i>Acropora plantaginea</i> (I)	<i>Acropora branchi</i> (I)	<i>Acropora fastigata</i> (IP)	<i>Acropora fennieri</i> (IP)
<i>Acropora eurystoma</i> (IP)	<i>Acropora ridzwani</i> (P)	<i>Acropora halmaherae</i> (IP)	<i>Acropora filiformis</i> (IP)	<i>Acropora gomezi</i> (IP)
<i>Acropora torihalimeda</i> (IP)	<i>Mussismilia harttii</i> (A)	<i>Acropora japonica</i> (P)	<i>Acropora navini</i> (IP)	<i>Acropora natalensis</i> (I)
<i>Agaricia fragilis</i> (CA)	<i>Cladocora caespitosa</i> (A)	<i>Acropora lamarcki</i> (I)	<i>Acropora parahemprichii</i> (IP)	<i>Acropora tanegashimensis</i> (P)
<i>Agaricia undata</i> (CA)	<i>Oculina valenciennesi</i> (C)	<i>Acropora maryae</i> (IP)	<i>Acropora parapharaonis</i> (I)	<i>Alveopora ocellata</i> (IP)
<i>Cynarina macassarensis</i> (P)	<i>Oxypora convoluta</i> (I)	<i>Acropora minuta</i> (IP)	<i>Montipora hemispherica</i> (I)	<i>Anacropora pillai</i> (IP)
<i>Echinophyllia pectinate</i> (IP)	<i>Pectinia crassa</i> (P)	<i>Acropora pectinata</i> (IP)	<i>Oculina robusta</i> (C)	<i>Boninastrea boninensis</i> (IP)
<i>Madracis carmabi</i> (C)	<i>Porites flavus</i> (P)	<i>Acropora rongelapensis</i> (P)	<i>Podabacia sinai</i> (RedSea)	<i>Echinopora tiranensis</i> (I)
<i>Montipora verrilli</i> (P)		<i>Acropora rufa</i> (I)		<i>Enigmopora darveliensis</i>
<i>Mycetophyllia reesi</i> (C)		<i>Acropora seriata</i> (IP)		<i>Isopora elizabethensis</i> (P)
<i>Schizoculina fissipara</i> (A)		<i>Acropora sukarnoi</i> (IP)		<i>Montipyra kenti</i> (I)
<i>Schizoculina africana</i> (A)		<i>Acropora torresiana</i> (P)		<i>Montipora kellyi</i> (I)
		<i>Anacropora spumosa</i> (I)		<i>Montipora taiwanensis</i> (P)

		<i>Echinopora irregularis</i> (I)		<i>Mussismilia braziliensis</i> (A)
		<i>Micromussa diminuta</i> (IP)		<i>Mussismilia hispida</i> (A)
		<i>Montipora aspergillus</i> (IP)		<i>Mycedium spina</i> (P)
		<i>Montipora echinata</i> (I)		<i>Plerogyra multilobata</i> (IP)
		<i>Montipora pachytuberculata</i>		<i>Plerogyra diabolotus</i> (IP)
		<i>Pavona xarifae</i> (P)		<i>Pocillopora effusa</i> (P)
		<i>Plerogyra cauliformis</i> (P)		<i>Pocillopora molokensis</i> (P)
		<i>Porites decasepta</i> (I)		<i>Porites baueri</i> (P)
				<i>Porites colonensis</i> (C)
				<i>Porites evermanni</i> (IP)
				<i>Psammocora albopicta</i> (IP)
				<i>Siderastrea stellata</i> (A)
				<i>Simplastrea vesicularis</i>
				<i>Stylaraea punctata</i> (IP)
				<i>Oxypora egyptensis</i> (I)

9 Table 2: Recent - Pleistocene comparison of proportions of coral species in the five threat
 10 categories. Positive values indicate an increase of proportions from the Pleistocene to the Recent,
 11 negative ones a decrease. Traits used for the analyses comprise maximum water depth, growth
 12 form, geographic range and corallite size. In the bottom panel, geographic range was excluded
 13 from analyses.

Traits analyzed including geographic range												
	Worldwide		Indo-Pacific		Coral Triangle		Caribbean					
LC	11.8 %	→ 10.2 %	-5.4 %	→ 5.1 %	2.6 %	→ 3.6 %	48.2%	→ 10.4 %				
NT	-1.6 %		10.5 %		1 %		-37.8 %					
VU	-14.5 %	→ -12.8 %	-5.5 %	→ -5 %	-3.6 %	→ -3.6 %	-26.7 %	→ -10.6 %				
EN	0.4 %		0.5 %		0 %		0.3 %					
CR	3.7 %		0%		0%		16.1 %					
Traits analyzed without geographic range												
	Worldwide		Indo-Pacific		Coral Triangle		Caribbean					
LC	17.3 %	→ 33.8 %	-15 %	→ 9.9 %	-8 %	→ 11 %	68.4 %	→ 52.3 %				
NT	16.5 %		24.9 %		17 %		-16.1 %					
VU	-38.1 %	→ -34.4 %	-10.5 %	→ -9.9 %	-9.1 %	→ -9.1 %	-68.8 %	→ -52.6 %				
EN	0.5 %		0.6 %		0 %		0.3 %					
CR	3.7 %		0%		0%		16.1 %					



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