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## Incongruence between life-history traits and conservation status in reef corals

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1 **Title: Incongruence between life history traits and conservation status in reef corals**

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16

17 **Keywords:** coral reefs, Scleractinia, Red List, biodiversity; boosted regression trees;  
18 cumulative link model; conservation, management

19

## 20 **Abstract**

21 Comparative lists of species extinction risk are increasingly used to prioritise conservation  
22 resources. Extinction risk is most rigorously assessed using population trajectories, but in the  
23 absence of such data assessments may rely on qualitative estimates based on expert opinion  
24 of species abundances, distributions and threats. For example, one-third of coral species are  
25 classified as threatened and another third as near-threatened on the IUCN Red List, despite a  
26 lack of data at the population level for the vast majority of species. Since many taxonomic  
27 groups show a strong correlation between species traits and extinction risk, a more  
28 theoretically-grounded approach is to examine traits associated with extinction risk. Here, we  
29 examine whether life history traits or species abundance are correlated with Red List  
30 conservation status in reef corals. We found no relationship between conservation status and  
31 life history traits or abundance, suggesting that either traits identified as important predictors  
32 of extinction risk in other taxa are not important in corals, or that conservation status does not  
33 accurately reflect species' relative extinction risk. Recent research revealing that traditional  
34 morphological taxonomy does not accurately reflect species boundaries or evolutionary  
35 relationships highlights further problems with using global-scale extinction risk assessments  
36 to inform conservation of coral reefs, including a high risk of 'silent extinctions' of endemic  
37 species in peripheral geographic regions . We argue that the conservation status for the vast  
38 majority of coral species should be "data deficient" and is likely to remain so for the  
39 foreseeable future, and that assessments of the status and trends of coral populations can only  
40 be reliably assessed at relatively small scales.

41

## 42 **Introduction**

43

44 The abundance and diversity of life on Earth are declining rapidly as species become extinct  
45 at approximately 1000 times the ‘background’ rate (Barnosky et al. 2011; Ceballos et al.  
46 2017). Evidence from past and present extinctions shows that extinction risk is not distributed  
47 randomly across taxa, but is instead phylogenetically conserved because closely related  
48 species tend to share inherited traits that influence their vulnerability to extinction (Purvis et  
49 al. 2000a). For example, ‘slow’ life history traits (e.g. slow growth rates, late sexual maturity,  
50 low fecundity), low population density and small geographic range size are correlated with  
51 elevated extinction risk among the world’s carnivores and primates (Purvis et al. 2000b). The  
52 fossil record also shows that species with small geographic ranges are considerably more  
53 likely to become extinct than large-ranged species (Payne and Finnegan 2007; Harnik et al.  
54 2012; Tietje and Rode 2018).

55

56 Species extinction is generally preceded by declines in population abundance or geographic  
57 range size (Ceballos et al. 2017). Identifying declines before populations fall below critical  
58 thresholds can allow for management actions to be implemented to safeguard a species  
59 against extinction. However, collecting data on population trajectories over spatial and  
60 temporal scales sufficient to identify species at risk of extinction is unrealistic for the vast  
61 majority of species on Earth, particularly as species’ distributions are shifting due to climate  
62 change (Scheffers et al. 2016; Pecl et al. 2019). Consequently, prioritization of species most  
63 in need of conservation actions must be conducted using alternative methods.

64

65 Given that extinction risk within a clade is non-random, species traits can be used to predict  
66 extinction vulnerability in the absence of empirical data on population trends (Foden et al.  
67 2013; Howard and Bickford 2014; Luiz et al. 2016; Tietje and Rode 2018). Comparative

68 rankings of species' extinction risk (e.g. the IUCN Red List) are increasingly being used to  
69 prioritise biodiversity conservation (Rodrigues et al. 2006; Cardillo and Meijaard 2011).  
70 However, the capacity to correctly identify species at risk of extinction is influenced by data  
71 quality and availability, and is therefore most effective for well-studied groups (Possingham  
72 et al. 2002). As the taxonomic and geographic breadth of the IUCN Red List continues to  
73 expand, assessments of lesser-known taxa are inevitably based on a reduced quantity (and  
74 often quality) of data (Bland et al. 2017). This problem particularly acute among marine taxa,  
75 which have double the proportion of Data Deficient species compared to non-marine  
76 counterparts (Webb and Mindel 2015). Assessing extinction risk in groups lacking reliable  
77 empirical data on population trends due to factors such as large geographic ranges or large  
78 effective population sizes could therefore be aided by examination of species traits (Howard  
79 and Bickford 2014; Luiz et al. 2016).

80

81 Reef-building scleractinian corals ('corals' hereafter) are the primary ecosystem engineers on  
82 coral reefs, the most diverse marine ecosystems on Earth. The abundance of corals on reefs is  
83 declining globally due to a range of local to global-scale stressors, with severe consequences  
84 for both biodiversity and human societies dependent on goods and services provided by coral  
85 reefs (Hughes et al. 2017). One-third of coral species are currently classified as threatened  
86 according to the IUCN Red List, and another third as near-threatened (Carpenter et al. 2008).  
87 Despite declines in the abundance and diversity of corals at local scales, assessing the actual  
88 extinction risk of individual species is difficult because 1) there are no confirmed extinctions  
89 of corals in modern times; and 2) many coral species are thought to exhibit traits that should  
90 make them unlikely to become globally extinct, such as large geographic ranges and large  
91 effective population sizes (Hughes et al. 2014; DeVantier and Turak 2017). Therefore, few

92 coral species are considered to be in ‘double jeopardy’ due to small range size and low  
93 abundance (Hughes et al. 2014).

94 Given the lack of reliable information to inform species-level assessments, there is a need to  
95 develop alternative, quantitative methods for identifying corals at risk of extinction. For  
96 example, identifying functional traits associated with extinction risk could provide a better  
97 indication of which species are most vulnerable to extinction, irrespective of the considerable  
98 uncertainties surrounding the taxonomic identity of corals at the species level (Kitahara et al.  
99 2016). Here, we use a newly-developed global database of coral species traits (Madin et al.  
100 2016) to examine whether corals considered by the Red List to be at elevated risk of  
101 extinction share life history traits that could inform the conservation status of data-deficient  
102 species. Specifically, we test whether Red List conservation status can be explained by 1)  
103 quantitative, species-specific life history traits status for 658 reef coral species (excluding  
104 those classified as data deficient) assessed using Red List criteria.

105

## 106 **Methods**

### 107 *Data collection*

108 We collected data on 11 ecological and morphological traits considered likely to influence  
109 species’ susceptibility to population decline (Table 1). Traits were divisible into four  
110 categories indicative of different life history strategies for 1) energy acquisition (growth rate,  
111 number of polyps per unit area); 2) stress tolerance (maximum colony width, skeletal  
112 density); 3) reproduction (reproductive output, fecundity per polyp, reproductive mode,  
113 sexual system); and 4) habitat specialisation (depth range). We also included family as an  
114 explanatory variable to examine the extent to which IUCN classifications could be explained

115 purely by phylogenetically-conserved traits. Geographic range size was not included as an  
116 explanatory variable because some species on the Red List were assessed on this basis,  
117 precluding range size as an independent test of conservation status. Similarly, the qualitative  
118 estimates of global abundance used in Red List assessments do not account for the  
119 considerable variability in species abundances across multiple spatial scales (DeVantier and  
120 Turak 2017; Karlson et al. 2011). Therefore, we used empirical measurements of species'  
121 abundances from surveys along the length of the GBR (Fig. S1) collected at three hierarchical  
122 scales: *transect*, *site* and *reef*.

123

124 Although life-history traits have not been measured empirically for all coral species, many  
125 traits are highly conserved (Kerr et al. 2011). Therefore, we used a phylogenetic infilling  
126 approach (Madin et al. 2016b; McWilliam et al. 2018) to estimate trait values for species  
127 where empirical data were unavailable (see Kuo (2017) for details). Trait infilling involved a  
128 two-step process: Firstly, a species  $\times$  trait matrix was created using data from coraltraits.org  
129 (Madin et al. 2012a). When multiple empirical values were available for a given trait, we  
130 used either the maximum value (e.g. for maximum colony size) or the average value as  
131 appropriate to represent the global estimate for that species. Empirical data were log-  
132 transformed prior to the infilling procedure to improve normality of trait values. Secondly,  
133 we visually explored the empirical data for correlations among traits in order to choose the  
134 best variables used in each regression analysis. Model summaries and additional information  
135 on each infilling procedure are presented in Kuo (2017). Of the 779 species assessed for  
136 which trait data were available either through empirical measurements or infilling, 121 were  
137 classified as Data Deficient, leaving 658 species in our analysis.

138



139 *Data Analysis*

140 We used boosted regression trees (BRTs) (Elith et al. 2008) to examine how well the 11 traits  
141 predicted conservation status for the 658 coral species for which trait data were available.  
142 BRTs are machine-learning algorithms that incorporate multiple individual trees and use a  
143 staged approach where the largest deviation in the response variable is explained by the  
144 primary split in the tree, with remaining trees built using the residual data. This process  
145 enables identification of lower-order interactions in the predictor variables, which is not  
146 possible under other approaches that use multiple trees but average the results (Elith et al.  
147 2008). Unlike other regression approaches such as generalised linear mixed-effects models,  
148 BRTs do not demand exclusion of species where data are absent for explanatory variables.  
149 This functionality was important because although the trait infilling process greatly increased  
150 data coverage for each trait, the lack of information for any species in some lineages  
151 precluded infilling. Consequently, BRTs allowed us to include a far greater number of  
152 species in our analysis than would have been possible using regression-based models.

153

154 We built three BRT models with different response variables: unweighted (i.e. Red List status  
155 as an ordered numerical variable ranging from 1 [Least Concern] to 5 [Critically  
156 Endangered]); weighted (ordered numerical variable, but weighted such that species  
157 considered at higher risk of extinction received an increasingly higher weighting Howard and  
158 Bickford 2014); and binary (i.e. extinction risk classified as either ‘threatened’ [Vulnerable,  
159 Endangered and Critically Endangered] or ‘non-threatened’ [Near Threatened and Least  
160 Concern]). Red List status for each species was derived from Carpenter et al. (2008) and  
161 [iucnredlist.org](http://iucnredlist.org). Tree complexity, i.e. the number of splits in each tree, was set at 5 to prevent  
162 over-fitting but to allow identification of interactions between variables, while learning rate

163 was set to 0.001 to reduce the influence of the initial set of trees on the models. These values  
164 ensured an equivalent number of trees (~2000) in each model to allow for comparison among  
165 models. Predictive performance of each model was compared using the total amount of  
166 deviance explained by the predictor variables, calculated by dividing the difference between  
167 the mean total deviance (td) and the estimated ten-fold cross-validated deviance (cvd) by the  
168 mean total deviance (deviance explained =  $1 - [cvd/td]$ ). The proportion of the total deviance  
169 explained by each predictor variable was assessed using partial dependency plots. All models  
170 were fitted using the 'gbm' package (Ridgway 2006) with extensions provided by Elith et al.  
171 (2008) in R.

172

## 173 **Results**

174 Total deviance explained by BRT models was low (10, 16 and 17% for the binomial,  
175 weighted and unweighted models, respectively) (Table 2), indicating that life history traits  
176 explain only a small proportion of the variation in conservation status. The vast majority of  
177 the total deviance explained for all models was attributable to just two variables: family and  
178 depth range (Appendix 2; Fig. 1). The families Acroporidae, Dendrophylliidae and  
179 Euphylliidae had the highest proportion of species listed as threatened, with over half of all  
180 species in each family listed in 'threatened' categories (Fig. 2). Species that occur over a  
181 greater depth range were more likely to be classified in less-threatened categories.

182

183 The five species listed as critically endangered are split amongst three families: Acroporidae,  
184 Poritidae and Siderastereidae. The families Euphylliidae, Fungiidae, Lobophylliidae,  
185 Merulinidae, Plesiastreidae and Pocilloporidae all contained species listed as Endangered.

186 The highest proportions of threatened species were in the families Euphyllidae (52.9%),  
187 Acroporidae (50.5%) and Dendrophyllidae (50.0%). All five families containing no species  
188 classified as threatened (Astrocoeniidae, Caryophylliidae, Diploastraeidae, Montastraeidae  
189 and Rhizaniidae) either had only one species assessed, because the family is monospecific  
190 (e.g. Diploastraeidae) or because most species are azooxanthellate (e.g. Caryophylliidae).

191

## 192 **Discussion**

193 Irrespective of the response variable used (weighted, unweighted or binomial), the  
194 conservation status for 658 coral species classified using the Red List criteria did not align  
195 with life history traits including key demographic variables, such as growth and fecundity,  
196 that are widely accepted as determinants of extinction risk in other taxa. Similarly, we found  
197 no relationship between conservation status and species abundance along the GBR at any of  
198 the three spatial scales examined. We explore two alternative explanations for this pattern: 1)  
199 factors identified as important predictors of extinction risk in other clades are not important  
200 predictors of extinction risk in corals; 2) conservation status assessments made without  
201 sufficient quantitative data do not accurately assess extinction risk.

202

203 Population-level data on key demographic processes such longevity and particularly  
204 recruitment have previously been used to explain how species-specific differences in life  
205 history traits influence corals' vulnerability to population declines (Hughes et al. 2000a). For  
206 example, the long-lived Caribbean coral *Orbicella annularis* can survive long periods with  
207 minimal larval input and is therefore far less vulnerable to population declines due to  
208 recruitment failure than two species with shorter generation times (*Agaricia agaricites* and

209 *Leptoseris cucullata*). This data highlights how declines in species abundances, and therefore  
210 extinction risk, can be context-specific: while the underlying assumption of the Red List is  
211 that longer generation times increase vulnerability, this is not likely to be the case where  
212 declines are due to recruitment failure. Given that small changes in coral fecundity (e.g. due  
213 to sublethal stress) can result in substantial variations in recruitment and that recruitment  
214 success is a key factor in population sustainability (Hughes et al. 2000a, b), greater detail on  
215 population-level traits supported by empirical data could greatly improve predictions of  
216 extinction risk among coral species.

217

218 Given the demonstrated link between traits and extinction risk in other taxonomic groups  
219 (Purvis et al. 2000b; Payne and Finnegan 2007; Harnik et al. 2012; Tietje and Rode 2018;  
220 Howard and Bickford 2014; Luiz et al. 2016), it seems unlikely that traits associated with key  
221 demographic processes such as growth and fecundity would be unrelated to extinction risk in  
222 corals. Improving the quality of the trait data used to inform species-level assessments may  
223 provide far greater capacity to delineate species-specific differences in extinction risk. For  
224 example,

225

226 Recruitment limitation e.g. declines in fecundity

227

228

229 The only variables that provided any predictive power in our models were family and depth  
230 range. Previous studies of past coral extinctions have revealed non-random extinctions among  
231 coral genera (Johnson et al. 1995; van Woesik et al. 2012); however, our results suggest the

232 Red List process provides little additional capacity to distinguish extinction risk among  
233 species. Previous research has suggested that although species classified as threatened on the  
234 Red List are not clustered on the scleractinian phylogeny, vulnerability to particular  
235 disturbances is phylogenetically conserved (Huang 2012). Consequently, phylogeny could be  
236 used to approximate susceptibility to particular disturbances e.g. an acroporid is likely to be  
237 more susceptible to *Acanthaster* predation than a Euphylliid. While phylogeny may provide  
238 some insight into relative extinction risk, it still explained only a small proportion of variation  
239 in conservation status. Since phylogenetic clustering of extinction risk occurs in many other  
240 taxa (Purvis et al. 2000a; Russell et al. 1998), our results are likely attributable to a lack of  
241 species-level data to inform conservation assessments.

242

243 There are several additional issues with the accuracy of the data underlying conservation  
244 status assessments in corals that likely limit their utility for informing conservation. For  
245 example, corals with broad depth ranges are generally considered at lower risk of extinction  
246 due to deeper habitats being less exposed to disturbances (Carpenter et al. 2008). However,  
247 depth range also explained very little variation in conservation status. Moreover, there is little  
248 empirical data on the composition of coral communities below ~20 m depth, and the data that  
249 do exist suggest that estimates based on expert opinion are highly inaccurate (Roberts et al.  
250 2019) and that many ‘rare’ deep-specialists (e.g. *Acropora tenella*) are more widespread than  
251 previously thought (Muir et al. 2019). In addition, depth range alone provides no information  
252 on important ecological factors such as changes in abundance, physiological performance,  
253 and genetic connectivity across depth that are essential for determining which species could  
254 use depth as a refuge (Roberts et al. 2019). Without knowledge of the abundance and  
255 physiological performance of species in deeper water, there is little justification for the use of  
256 estimates of depth range to inform conservation status.

257

258 Geographic range size is an important predictor of global extinction risk across a wide range  
259 of taxa (Purvis et al. 2000b, Payne and Finnegan 2007; Tietje and Rode 2018), and is  
260 therefore often used to assess species' conservation status. Based on traditional  
261 morphological taxonomy (e.g. Wallace 1999; Veron 2000), most coral species exhibit wide  
262 geographic ranges and would therefore be considered at low risk of global extinction (Hughes  
263 et al. 2014). Most small-ranged species are thought to occur in low-diversity systems, such as  
264 the Eastern Pacific or at high latitudes - a key difference from terrestrial systems where  
265 small-ranged endemics tend to occur in biodiversity hotspots (Hughes et al. 2002).  
266 Importantly, even those corals with relatively small geographic ranges (i.e. the species in the  
267 lowest quartile of range size) have much larger ranges than many terrestrial taxa. For  
268 example, species 'endemic' to the 'Coral Triangle' biodiversity hotspot have range sizes  
269 spanning 5.5 million km<sup>2</sup> or more - 30% of the world's coral reef habitat (Hughes et al.  
270 2014). The large ranges of the vast majority of recognised coral species suggests few species  
271 would be at particular risk of global extinction due to small population sizes, therefore the use  
272 of range size to inform extinction risk is questionable.

273

274 An additional problem with assessing species' extinction risk on the basis of geographic  
275 range size that is becoming increasingly apparent is recognition that traditional taxonomy is  
276 incongruent with species boundaries and evolutionary relationships revealed by phylogenetic  
277 analysis (e.g. Romano and Palumbi 1996; Fukami et al. 2004; Fukami et al. 2008; Schmidt-  
278 Roach et al. 2013; Keshavmurthy et al. 2013; Luck et al. 2013; Warner et al. 2015; Kitahara  
279 et al. 2016). An ever-increasing body of literature highlighting the significant limited  
280 knowledge of species taxonomy and therefore distributions within virtually every group of reef-

281 building corals suggests that extinction risk assessments are of little value until there is a  
282 better understanding of species boundaries and geographic ranges, many of which are likely  
283 to be far smaller than previously thought (e.g. Schmidt-Roach et al. 2013; Richards et al.  
284 2016; Arrigoni et al. 2016). For example, molecular and genetic evidence has demonstrated  
285 that high-latitude ‘morphs’ of widespread coral species such as *Pocillopora damicornis* are  
286 actually distinct species restricted to a few high-latitude reefs of eastern Australia (Schmidt-  
287 Roach et al. 2013), and there is increasing evidence of considerable but previously  
288 unrecognised endemism at neighbouring Lord Howe Island (e.g. Baird et al. 2017; Bridge  
289 and Baird unpublished data). The substantial incongruence between species’ identity and  
290 geographic ranges based on traditional morphological taxonomy compared to integrated  
291 taxonomic approaches incorporating molecular phylogenetics will clearly affect assessments  
292 of relative extinction risk among species (Agapow et al. 2004). Extensive ‘cryptic’  
293 speciation, particularly at peripheral locations such as high latitudes, suggests that global-  
294 scale estimates risk overlooking the ‘silent extinction’ of undescribed cryptic species  
295 (Curnick et al. 2015). Furthermore, peripheral locations with high proportions of small-  
296 ranged endemic species are of far greater conservation concern than currently appreciated,  
297 and will almost certainly be the first to see extinctions in reef corals.

298

299 The lack of data available to estimate the size and trajectories of coral populations across  
300 their geographic ranges clearly inhibits reliable assessments of relative extinction risk at  
301 global scales. Consequently, we suggest that the vast majority of corals should be considered  
302 Data Deficient, and that the vulnerability of corals to disturbances must be assessed by  
303 quantitative surveys at local to regional scales (e.g. Muir et al. 2017). More broadly, the  
304 issues associated with extinction risk assessments in corals are likely to apply to other marine  
305 flora and fauna, which often share similar life history traits such as a bipartite lifecycle with

306 high dispersal capacity, high fecundity, and large geographic ranges compared to terrestrial  
307 taxa. Consequently, processes threatening the persistence of corals and other marine  
308 invertebrates are likely to be different to those affecting terrestrial species. If conservation  
309 prioritisation and actions are to be based on relative extinction risk, assessments must account  
310 for lack of knowledge on species boundaries and distributions that are ubiquitous in corals  
311 and many other, lesser-known marine invertebrate taxa, and must be tailored to accommodate  
312 the life histories of and threats facing specific taxonomic groups.

313

314 Given the strong relationships identified between species traits and extinction vulnerability  
315 for better-known species groups (Purvis et al. 2000b, Cardillo et al. 2005), it is unlikely that  
316 traits associated with the key ecological and demographic factors of energy acquisition, stress  
317 tolerance, reproduction and habitat specialisation would be unrelated to population  
318 trajectories, and therefore extinction risk, in corals at the global scale. Consequently, our  
319 results suggest that the criteria used to assess extinction risk in corals are flawed, and that  
320 coarse estimates of coral cover across large geographical regions are of limited use for  
321 identifying species most at risk of extinction. Given the increasing evidence that many  
322 species ranges and population sizes are likely to be smaller than currently appreciated, we  
323 recommend that conservation actions aimed at conserving species diversity should be made  
324 following population assessments at the local scale.

325

326 The lack of data on fundamental aspects of coral species, such as species boundaries and  
327 geographic ranges, suggests global-scale lists of extinction risk among species are of limited  
328 value for conservation of coral reefs because they provide little capacity to identify which  
329 taxa are at greatest risk of extinction. Consequently, assessing reefs at local to regional scales  
330 may be more effective at conserving both taxonomic and functional diversity. For example,



331 the dramatic declines in the abundance of *Acropora cervicornis* and *A. palmata* on western  
332 Atlantic reefs since the 1970s have caused substantial changes to ecosystem function across  
333 the region despite neither species actually going extinct (Aronson et al. 2004; McWilliam et  
334 al. 2018). Similar declines in habitat-forming species have been observed across reefs  
335 worldwide in recent years (Hughes et al. 2018), leading some to suggest that management of  
336 Anthropocene reefs should prioritise preserving ecological functions rather than traditional  
337 metrics of taxonomic diversity (Bellwood et al. 2019). While there is strong evidence for a  
338 relationship between taxonomic diversity and ecosystem function and therefore a need to  
339 monitor and conserve multiple facets of biodiversity (Devictor et al. 2010; Villéger et al.  
340 2010; Huang & Roy 2015), such efforts are only effective when conducted at appropriate  
341 spatial scales to detect changes and implement appropriate responses. The spatial mismatch  
342 of developing local-scale conservation actions from global-scale assessments based on little  
343 quantitative support risks misidentifying causes of decline at local scales and consequently  
344 misdirecting limited conservation resources. Moreover, basing conservation decisions on data  
345 containing such clear biodiversity knowledge gaps increases the risk of ‘silent extinctions’,  
346 where species are lost due to inadequate biodiversity data. Management actions that facilitate  
347 the persistence of functional and taxonomically diverse reef ecosystems can therefore only be  
348 implemented based on assessments at local scales, conducted using appropriately rigorous  
349 and reliable biodiversity data.

350

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353

## 354 **Conflict of Interest Statement**

355 On behalf of all authors, the corresponding author states that there is no conflict of interest.

356

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518

## 519 **Figures**

520

521 Fig. 1: Stacked bar plot showing the distribution of IUCN Red List categories among coral  
522 families.

523

524 Fig. S1: Location of study sites along the Great Barrier Reef.

525

526 Fig. S2: Partial dependency plots for unweighted, weighted and binomial boosted regression  
527 tree models.