Vulnerability to collapse of coral reef ecosystems in the Western Indian Ocean

Obura, David; Gudka, Mishal; Samoilys, Melita; Osuka, Kennedy; Mbugua, James; Keith, David A.; Porter, Sean; Roche, Ronan; van Hooidonk, Ruben; Ahamada, Said; Araman, Armindo; Karisa, Juliet; Komakoma, John; Madi, Mouchtadi; Ravinia, Isabelle; Razafindrainibe, Haja; Yahya, Saleh; Zivane, Francisco

Nature Sustainability

DOI:
10.1038/s41893-021-00817-0

Published: 01/02/2022

Peer reviewed version

TITLE: Coral reef ecosystems are vulnerable to critically endangered across a biogeographic province

Authors, affiliations and email addresses:

1. Obura, David. CORDIO East Africa, Mombasa, Kenya. dobura@cordioea.net; IUCN Coral Specialist Group.
2. Gudka, Mishal. CORDIO East Africa, Mombasa, Kenya. mgudka@cordioea.net
3. Samoilys, Melita. CORDIO East Africa, Mombasa, Kenya. melita.samoilys@gmail.com; IUCN Grouper and Wrasse Specialist Group
4. Osuka, Kennedy. CORDIO East Africa, Mombasa, Kenya. kosuka@cordioea.net;
5. Mbugua, James. CORDIO East Africa, Mombasa, Kenya. jmbugua@cordioea.net
6. Keith, David A. University of New South Wales, Sydney, Australia. David.Keith@unsw.edu.au
7. Porter, Sean. Oceanographic Research Institute, Durban, South Africa. sporter@ori.org.za
8. Roche, Ronan. Bangor University, Bangor, Gwynedd, United Kingdom. r.roche@bangor.ac.uk
9. van Hooidonk, Ruben. Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School of Marine and Atmospheric Science, University of Miami; ruben.van.hooidonk@noaa.gov
10. Ahamada, Said. AIDE, Comoros. ahamadas@yahoo.com
11. Araman, Armindo. Administração Nacional das Áreas de Conservação (ANAC), Mozambique. aaraman@anac.gov.mz
12. Karisa, Juliet. Kenya Marine and Fisheries Research Institute, Mombasa, Kenya. jfuraha@gmail.com
13. Komakoma, John. Marine Parks and Reserves Unit (MPRU), Tanzania. jkomakoma@gmail.com
14. Madi, Mouchtadi. Moheli Marine Park, Comoros. mouchtadimadi@yahoo.fr
15. Ravinia, Isabelle. Seychelles National Parks Authority, Seychelles. i.ravinia@gov.sc
16. Razafindrainibe, Haja. Centre National de Recherches Océanographiques (CNRO), Madagascar. hajaniry@gmail.com

17. Yahya, Saleh. Institute of Marine Science (IMS), Zanzibar, Tanzania.
saleh_y@yahoo.com
18. Zivane, Francisco. National Institute of Fisheries Research, Mozambique.
franciscozivane@hotmail.com

Running title: Coral reef ecosystem collapse

Keywords: climate change, coral reefs, ecosystem collapse, ecosystem integrity, policy, Red List of Ecosystems, resilience, risk assessment, Western Indian Ocean.

Correspondence: David Obura, CORDIO East Africa, P.O. BOX 10135, Mombasa, Kenya; Tel: +254 715 067417; Email: dobura@cordioea.net

Ecosystems worldwide are under increasing threat. We applied a standardized method for assessing the risk of ecosystem collapse, the IUCN Red List of Ecosystems, to coral reefs in the Western Indian Ocean (WIO), covering 11,919 km^2 of reef (about 5% of the global total). Our approach combined indicators of change in historic ecosystem extent, ecosystem functioning (hard corals, fleshy algae, herbivores and piscivores), and projected sea temperature warming. We show that WIO coral reefs are Vulnerable to collapse at the regional level, while in eleven nested ecoregions they range from Critically Endangered (islands, driven by future warming) to Vulnerable (continental coast and northern Seychelles, driven by fishing pressure). Responses to avoid coral reef collapse must include ecosystem-based management of reefs and adjacent systems combined with mitigating and adapting to climate change. Our approach can be replicated across coral reefs globally to help countries and other actors meet conservation and sustainability targets set under multiple global conventions – including the Convention on Biological Diversity's post-2020 global biodiversity framework and the United Nations' Sustainable Development Goals.

The collapse of an ecosystem signifies its 'extinction' in functional terms, when the characteristics and functions that define it are transformed [1,2]. The risk of collapse in multiple ecosystems has increased in the Anthropocene, as human impacts have changed fundamental aspects of biosphere functioning [3]. Of particular concern is where ecosystem collapse results in permanent loss of evolutionary history through raising the risk of species extinction, loss of ecological functions critical for ecosystem recovery and avoiding collapse, and loss of ecosystem services vital for peoples' livelihoods, income and wellbeing. Coral reef ecosystems are among the most biodiverse and societally important ecosystems globally, but up to 50% of the world's coral reefs are already degraded [4], and the weight of evidence suggests that increasing local (fishing, pollution, coral diseases, cyclones) and global (warming, acidification) stressors, and their cumulative and synergistic interactions [5], give a window of only several decades [6–8] before collapse of these flagship ecosystems.

The global status of reefs is well known because one key indicator, live coral cover, is both conceptually straightforward and accessible to measure, thus becoming a leading indicator of ecosystem health in the ocean [9]. However, while live coral cover provides a basic measure of the presence and status of a coral reef ecosystem, it lacks information on composition of the coral community, algae, other invertebrates and fish [10,11]. All these groups contribute to a reef's properties, ecological functioning and potential services to people, and these attributes may vary across all scales from local to regional and global. Transition of coral reefs to alternative ecological states, and possible ultimate collapse, depends on the status and trends in many of these components and functions [2,12,13]. Many regional and global studies have assessed coral reef trends at these scales, shedding light on drivers of decline, status of reefs and management options. However differences in their methods and datasets, and in interpretation of results, limit their direct application in supporting regional and global policy, as well as application within individual countries.

The Red List of Ecosystems (RLE) was designed to provide a uniform, easily-understood classification of the risk of ecosystem collapse across all ecosystems and across multiple scales [14,15]. Defining ecosystem collapse is operationalized for the RLE by setting thresholds for key variables describing the ecosystem (Table 1, SI2.6). The RLE enables integration of multiple variables of varying coverage and quality across different ecosystem components, and has direct application to policy [16]. Building on the Red List of Threatened Species [17], the RLE integrates multiple variables into five broad criteria, and a standard output comprising an ordered set of unthreatened to threatened categories, from Least Concern to Collapsed (fig. 1). This study assesses the current status of coral reefs in the Western Indian Ocean using the global Millennium coral reef layer, an extensive regional dataset on coral reefs recently compiled from multiple data contributors that includes hard coral, fleshy algae and fish abundance data [18], as well as projected sea surface temperatures [19].

WIO coral reefs are at risk of collapse

Western Indian Ocean coral reefs, covering 11,919 km^2 and comprising about 5% of the global total (fig. 1, Table S1), are Vulnerable (VU) to ecosystem collapse. We assessed four of five criteria of the RLE, based on available data to parametrize a coral reef ecosystem model (fig. 2a) over a 50-year time span: decline in ecosystem extent (Criterion A), vulnerability due to restricted geographic distribution (B), and ecosystem disruption resulting from decline in the quality of abiotic (C) and biotic factors (D) (Table 1). Two criteria (C, D) returned a result of VU (Table 2) based on future warming using a likely pathway for global greenhouse gas emissions (Criterion C, RCP 6.0), and biotic disruption based on reduction in piscivorous fishes linked to fishing (D). The other two criteria (A, B) returned a result of Least Concern (LC). The RLE assigns the most threatened result (VU) as the final status [15].

At a finer geographic scale, there was considerable variation in risk of ecosystem collapse among coral reef ecoregions within the WIO (Table 2). The highest levels of risk were scored for seven ecoregions (four Critically Endangered (CR) and three Endangered (EN)) due to future warming, in the island ecoregions spread across Madagascar, the Comoros, the outer Seychelles and the Mascarene Islands (Mauritius and Reunion) (fig. 1). The remaining four ecoregions were assessed as VU. Of these, reefs in the large continental ecoregions (N. Tanzania-Kenya and N. Mozambique-S. Tanzania) were vulnerable based on declining populations of piscivorous fishes, whereas reefs in Seychelles North and Delagoa (southern Mozambique - northern South Africa) were vulnerable due to decline in reef areal extent, and in Delagoa due to limited geographic distribution of reefs (Table 2, SI3-6).

Climate vulnerability

The dominant threat to coral reef ecosystems in the WIO is future increase in thermal stress, as indicated in the 7 island ecoregions rated CR and EN, over the next 50 years. Earlier onset of catastrophic heat stress in island than mainland locations is largely consistent with prior studies [6,19,20]. We selected emissions scenario RCP 6.0 as the basis for our analysis as current trends in carbon emissions are more consistent with RCP 6.0 than higher or lower emissions pathways [21], and the results for RCP 6.0 provided a closer fit to observed bleaching among ecoregions in recent years (SI5.2). However, interpreting thermal stress to corals from projected temperatures must be done with caution as variance of temperature within the large grid cells in climate models is very attenuated compared to variance of empirical observations, affecting calculations of exceedance of thermal thresholds [19,22]. A possible illustration of this is that our analysis showed a result of Least Concern (LC) for RCP 2.6 over the next 50 years (Table S6) despite empirical records of up to 30% coral declines in the 1998, and substantial mortality in the 2016, mass coral bleaching events [18,23]. In the section on policy and management options we focus our interpretation on the comparative risk among ecoregions to warming temperatures.

Ecological integrity and biotic collapse

Ecological integrity is complex and includes functional, compositional, structural and spatial components [24]. Developing a conceptual ecosystem model as required for the RLE (SI2.5) provides an explicit hypothesis of ecological integrity, and by extension, collapse. Arguably, as one of the most diverse, complex and variable ecosystems in the world, coral reefs present challenges to specifying a realistic model. Percentage coral cover is a primary measure for coral reef health [11], but is insufficient for describing integrity [10]. Our data did not include taxonomic or functional sub-classes of corals, thus this analysis could not distinguish shifting composition of coral [10], which might show a decline in coral functional diversity and thus greater risk of collapse within the coral compartment and thus initial step in our algorithm, than we found using just total hard coral cover alone (Tables S2, S18).

Our dataset did, however, include fleshy algae cover and two trophic groups of fishes (herbivores and piscivores, fig. 2e,f) as additional components of integrity (SI2.5). Standard RLE practice has been to assign the maximum threat level across alternative indicators within each criterion [15,25]. However, in complex ecosystems with multiple biotic compartments, interactions between them of different strengths, and functional redundancies [26,27], it is not clear that in all cases where any one compartment is at high risk, the whole ecosystem should be at that risk level (SI2.6). In this study, coral cover was assessed LC in three ecoregions

(North Tanzania-Kenya, North Mozambique-South Tanzania, Comoros; Table S15) where piscivores were EN-CR; we judged that it was not credible that the entire reef systems across the four countries within these ecoregions be rated EN-CR on the basis of one fish group.

To resolve this issue we developed a structured algorithm for assessing ecological integrity and risk of collapse based on hierarchical interactions between ecosystem compartments (SI2.6, Table S2), and tested it against two alternatives with less structure (SI6.1.4, 6.3.1). The algorithm started with assigning the coral risk level, then the risk level was increased incrementally if risk was higher in the algae, then herbivore (parrotfish), then piscivore (grouper) compartments. In the examples in the prior paragraph, this resulted in final risk levels in all three ecoregions of VU, in each case stepped up twice by higher risk levels in any two of the algae, herbivore and piscivore compartments (Table S15). This final status reflects the importance of piscivores in the top-down control of prey populations with direct and indirect impacts on reef ecology (SI6.1), but avoids undue inflation of overall risk where other compartments may be in a good state. Applying this algorithm would result in the findings for both Meso-American [25] and Colombian [28] coral reef RLEs being the same as reported in those studies, because in both cases the coral compartments were at the highest levels of risk, either equal to, or higher than, other ecosystem compartments they assessed. The value of this algorithm will emerge with increasing application of the RLE where data to parametrize the model and the importance of different compartments may vary, effecting greater standardization and consistency among studies. This algorithm may be also appropriate to other ecosystems which have a defining biogenic architectural compartment such as forests on land [29], and other marine ecosystems such as oyster reefs, mangroves, seagrasses, and kelp forests.

The dominant biotic signal of ecosystem collapse, decline in piscivore populations, was assessed as EN-CR in four of the seven ecoregions with sufficient data (fig. 3). Grouper are vulnerable to the loss of coral structure [30] and their life histories make them especially vulnerable to fishing [31]. The lower risk level of parrotfish, our indicator of herbivore populations, concurs with studies where parrotfish responded positively to coral degradation in Tanzania [32,33], the Chagos Archipelago [34], and in Seychelles, masking fishing effects [35]. The RLE thus distinguishes signals from multiple ecological components – among biotic compartments in Criterion D, and across area and integrity components among the criteria –

in assessing collapse or loss of ecological integrity, and whether they are responding to global or local threats.

Regional and global comparisons

The RLE has previously been applied to coral reefs in three studies. The first assessed Caribbean reefs [14], comprising 6.7% of the world's coral reefs, as EN-CR. This higher risk level than WIO reefs is consistent with broad evidence that Caribbean reefs have experienced greater decline than those in the Indo-Pacific, due to a variety of intrinsic (e.g. coral and algal dynamics) and extrinsic (land-based impacts, connectivity) factors [18,36–38]. The second assessed the Meso-American Barrier Reef [25], also an ecoregion in the same classification used in this study [39] and one of the healthiest coral reef regions in the Caribbean [38], as CR on the basis of both coral and piscivore compartments in a quantitative model. This compares with corals being LC to VU and piscivores NT (Near Threatened) to EN-CR in the WIO (Table S15). A recent assessment of Colombian Caribbean coral reefs [28] used a similar spatially hierarchical approach as used here, though extending from a scale comparable to our ecoregions (national and 'ecoregional' in their study) down to individual reef areas. Its two ecoregions, 'continental' and 'oceanic', were VU and EN respectively, while at the larger national level reefs were VU.

The RLE method provides a consistent result across the above studies and the present one, however differences in selection of variables, thresholds and how they are parametrized introduces uncertainties in comparisons among them, even within the same ecosystem type. More broadly, the RLE has been critiqued on consistency in identification and definition of ecosystem units, the meaning of 'collapse' for an ecosystem, and specifics of the categories and criteria used [40]. Many of these critiques have been addressed over time [2,41], and growing acceptance of the RLE is shown by its application globally [42], exploration of its use in multiple policy domains [16,42] and its acceptance as an indicator in the monitoring frameworks of the Convention on Biological Diversity and the Sustainable Development Goals [41,43]. To further strengthen applicability of the RLE to coral reefs globally and to support national commitments under these conventions, we developed an approach that strengthens standardization of application of the RLE to coral reefs regions, in five ways: a) we used a consistent biogeographic and ecosystem framework, based on the Marine Ecoregions of the World [39], a global ecosystem typology developed for the RLE [44] and the established Global

Coral Reef Monitoring Network (GCRMN) regional structure [11], all based on the Millennium coral reef layer maintained by the World Conservation Monitoring Centre (UNEP-WCMC); b) we used globally-consistent real-time datasets from: i. collaborative networks on reef health compiled through the GCRMN as the global aggregator of Essential Ocean Variables for coral reefs [9,11], and ii. on projected thermal stress [19]; c) we formulated a basic ecosystem model applicable to a) and b) with scope for additional variables if relevant and if data availability allows (SI 2.5, fig. 2a); d) we developed a structured algorithm for assessing risk of biotic disruption based on dominant interactions affecting coral reef ecosystem integrity (SI2.6, 6.1.4, 6.3) that allows for data gaps that are inevitable given the resources and capacities available in most coral reef countries [11]; and e) we generated a Git-based repository and R code for all steps of the analysis (SI3-6) to facilitate tailored application in other regions.

Management and policy implications

Uncertainty in the climate trajectory that will eventuate, and variance at many scales in how corals and reefs may respond to warming [45] and other threats, mean that varied policy and management responses (Table 3) need to be considered [46]. This includes a spectrum of actions addressing climate mitigation and adaptation to those addressing local threats. The multiple criteria and broad evidence-base of the RLE enable structured consideration among these [16]. In those ecoregions on the mainland coast less threatened by future warming, local management actions will have greater scope to maintain or improve reef health, particularly those targeting alleviating fishing pressure and promoting coral recovery after thermal stress events. Some of these ecoregions (North Mozambique-South Tanzania and to a lesser extent Seychelles North) show strong levels of larval supply to more vulnerable ecoregions [47], and may play a key role in the recovery of corals from mass mortalities through larval connectivity, so managing them as central nodes in a connectivity network will be an important element of resilience-based management across the entire region. In addition, protecting climate refugia – reefs demonstrating lesser impact from thermal stress events, whether on scales from 100s of meters to 100s of kilometres – must be a key platform for extending protection [6] through marine protected areas or other effective conservation measures.

However, even for the ecoregions threatened by warming, it will be important to reduce local reef threats and reef vulnerability to address three 'no regrets' objectives: a) to maintain ecosystem function and resilience to buy time for coral populations to potentially adapt to warmer conditions through compositional shifts and/or genetic changes, b) to sustain the valuable economic and livelihood benefits coral reefs provide on a daily basis for as long as possible into the future [46], and c) as part of broader integrated and ecosystem-based management of coastal and marine ecosystems that can facilitate positive biotic transitions with a changing climate (IPCC/IPBES, in review).

Reporting on international and national policies addressing biodiversity [48], climate [8,49] and people's dependence on nature [4], have relied solely on mean percentage hard coral cover as a primary indicator of coral reef status. Current consultations on new ecosystem targets for the Convention on Biological Diversity (CBD) strongly recommend separate measures of area and integrity for quantifying ecosystem health [24], to guide actions to protect or restore ecosystems effectively. The RLE is well suited for this purpose, as ecosystem area is addressed in Criteria A and B, and ecosystem integrity in Criteria C and D, incorporating multiple variables in addition to coral cover. As an indicator in the proposed monitoring framework for the post-2020 Global Biodiversity Framework (GBF), the RLE can support a broader assessment of the ecosystem component of biodiversity, and thereby also benefits supplied to people [4,50,51]. Extending coverage of the RLE for coral reefs to global levels can strengthen application of global policies for coral reef conservation and sustainability [52].

While coral reefs are distributed globally, the regional scale provides a spatial unit where reef function and connectivity match scales of ocean governance processes [53]. Applying the RLE at this scale supports both intra- and inter-regional comparisons, informing policy and action across scales. The Western Indian Ocean region corresponds to the scope of the Nairobi Convention, one of the ten UNEP Regional Seas that contain coral reefs. At this scale, and with nested ecoregional analyses, the RLE can support coherent intra-regional policy processes among countries. However, to inform management at national and smaller scales, the ecoregional scale applied here is too broad. Including more localized data to address more aspects of the reef model (fig. 2a), and setting analysis within national policy frameworks, can guide management down to local scales [16] adding to the wide variety of detailed studies already contributing to reef management at these scales.

Methods

We assessed the risk of ecosystem collapse of coral reefs at a regional level for the Western Indian Ocean (WIO) as well as in 11 ecoregions within it (Table S1, fig. 1), applying the IUCN Red List of Ecosystems methodology[15,54]. The coral reef ecosystems assessed correspond to distinctive reef areas based on global [39,55] and regional [56] analyses, and level 4 in the IUCN Global Ecosystem Typology [44] (SI2.1) (Table 1). We developed a conceptual ecosystem model to structure the assessment based on recent syntheses of coral reef status and resilience (SI2.5), focused on the primary interactions between hard corals, fleshy algae and two trophic groups of fish, herbivores and piscivores (fig. 2a). Based on the literature, we identified fishing (extraction) and climate change (increasing thermal stress) as the two dominant pressures on coral reefs of the WIO (SI2.4). Following the RLE guidelines we evaluated all criteria, focussing on these two pressures, although there were insufficient data to evaluate criterion E. The SI contains full details of the methods, including a synthesis of data limitations (SI7.1).

Coral reef ecosystem model. The RLE requires a cause-effect conceptual model to be developed for an ecosystem [54]. The coral reef ecosystem model we developed (fig. 2a) is based on key interactions on coral reefs and builds on earlier coral reef applications of the RLE (SI2.5,6.1). It involves corals, fleshy algae and functional interactions of herbivorous and piscivorous fish, and the influence of external pressures[14,25]. The model incorporates understanding of coral reef community dynamics and transitions between states [13,57–59] and reef resilience dynamics [59–61]. Corals are recognized as the ecosystem engineers, affected by competitive interactions with fleshy algae and cascading effects of top-down consumers through the trophic ecology of multiple taxonomic groups. The algae community is the primary ‘alternate’ space occupier on coral reefs competing with corals [62], here represented by turf, macro and calcareous algae summed together. Herbivorous fishes (here represented by parrotfish) have strong mediating effects on algae and corals [63–65], while piscivorous fishes (represented by groupers) play a key functional role in nutrient cycling, biomass production [27,66], transfer of energy and material [67]. These comprise the four main compartments in our coral reef ecosystem model, and correspond to available and consistent data across the whole region for parametrizing the model (SI6.1) [18].

Aspects of the ecosystem model that we could not include in the assessment included: direct data on fishing pressure on coral reefs – data were not available among countries and at regional levels, and we determined that direct abundance data for groupers, which are sensitive to fishing pressure (see Criterion D below), provided a more reliable metric than indirect measures based on human population or market proximity [68]. Sedimentation and eutrophication pressure were not assessed; though indices and proxies can be derived for these from remotely sensed water-leaving radiances [69,70], it is difficult to parametrize thresholds at local scales for reef collapse for WIO reefs [71], and data were not available for the required 50 years (see SI2.4). However, these variables may be more appropriate at finer scales within countries where datasets may be available to enable filling such gaps.

RLE Criteria. The RLE evaluates risk in five broad criteria: reduction in geographic distribution of an ecosystem (Criterion A), risks associated with small size or restricted geographic distribution (B), risks from environmental degradation or abiotic factors (C), risks from biotic disruption or changes among ecosystem compartments (D), and quantitative ecosystem dynamics modelling (E). All criteria must be evaluated, returning a result of Not Evaluated (NE) if analysis is not possible (fig. 1), or a threatened or unthreatened status from the highest risk identified among the criteria evaluated.

Criterion A – Reduction in geographic distribution of coral reefs. Decline in the extent of an ecosystem is a direct measure of its disruption and collapse (SI3). Coral reefs combine two features – the geomorphological biogenic substratum, and dominance of hard corals that build the reef and provide habitat for diverse ecological interactions. Given the lack of data on change in the geographic extent of coral-dominated habitat over time, we developed a proxy indicator representing the extent of functioning coral reef. The literature on coral reefs is converging on a value of 10% coral cover as a threshold below which insufficient calcification and carbonate deposition occurs for the maintenance of a coral reef ecosystem [72]. Site-based coral cover data used in Criterion D were used to identify the proportion of sites within an ecoregion currently below the critical coral cover threshold for reef accretion. In this criterion, 10% coral cover relates to reef accretion in terms of the maintenance of the substratum for potential coral colonisation, whereas in Criterion D, a lower threshold of 5% coral cover is used as a limit for collapse in relation to recovery of the coral population (Table 1, SI3.1). We evaluated recent decline over 50 years (Criterion A1), but could not evaluate future (A2a, A2b) or longer term historical (A3) declines.

Criterion B – Restricted geographic distribution. Limited geographic distribution is a key determinant of ecosystem vulnerability, as any given major threat may affect a large proportion of the overall ecosystem extent. We used the Millennium coral reef layer [73] maintained by the World Conservation Monitoring Centre (UNEP-WCMC) to derive the Extent of Occurrence (EOO, the minimum convex polygon within which all ecosystem units in the ecoregion are located) and Area of Occupancy (AOO, the number of 10x10-km grid cells of which at least 1% of their area was coral reef) of coral reefs, and compare these to the standard RLE thresholds, to assess Criteria B1 and B2 respectively (Table 1, SI4.1). We were able to apply two of the three possible sub-criteria for B1 and B2: a(iii) "a measure of disruption to biotic interactions appropriate to the characteristic biota of the ecosystem" and b "observed or inferred threatening processes that are likely to cause continuing declines in geographic distribution, environmental quality or biotic interactions within the next 20 years" (SI2.2-2.4).

Criterion C – Environmental Degradation. Abiotic degradation reduces the capacity of an ecosystem to sustain its characteristic biota. Sea surface temperature (SST), supporting calculation of an index of thermal stress, was the only abiotic variable with adequate temporal and spatial coverage to assess Criterion C, and is the dominant environmental stress affecting coral reefs in the WIO (SI2.4) [74,75]. Sedimentation and eutrophication (using chlorophyll-*a* as a proxy) were investigated but had insufficient historical timeseries and no clear thresholds for collapse to enable their analysis (SI5.1). Historical SST timeseries did not span the required 50 years, thus, we assessed Criterion C2a, using SST projections 50 years into the future [19]. We did not assess hindcasted SST from the same climate models because historical changes in coral cover provide a more direct measure of risk.

Future thermal stress was assessed using two critical thresholds for bleaching, 8 and 12 Degree Heating Weeks (DHW) per annum, [76], across four greenhouse gas emission scenarios (RCPs 2.6, 4.5, 6.0 and 8.5) (SI5.1). A threshold of two major bleaching events per decade (i.e. two annual exceedances of the DHW threshold) was used as the threshold for ecosystem collapse [25], calculated using decades spanning the fifty-year period from 2020 (2015–2024) to 2070 (2065–2074). Final analysis was based on the following critical thresholds (see SI5.2 for more detail, as well as the discussion):

DHW 12 is associated with more severe warming impacts to corals, and less likely to be within the adaptative capacity of corals to thermal stress, and

RCP 6.0 presents a more plausible scenario, provides greater differentiation among ecoregions and matches conditions observed to date of coral bleaching (see SI5.2 and section 'Climate vulnerability').

Criterion D – Biotic disruption. Disruption of biotic processes and interactions leads to loss of function in an ecosystem and its potential collapse, particularly for important processes and/or organisms playing key functional roles. We assessed four main compartments in the ecosystem model (SI6.1, fig. 2a) with the following indicators: hard coral cover, fleshy algae:coral cover ratio, parrotfish abundance and grouper abundance. Data were obtained from a regional dataset [18,23] generated through a collaborative process and globally consistent methods established by the Global Coral Reef Monitoring Network [11,77,78] and applying best practices established for global biodiversity and ocean observing systems [9,79,80].

Monitoring sites were spread unevenly across ten ecoregions (fig. S3), with varying sample sizes for different variables due to characteristics of each contributing monitoring programme (Tables S7, S8, S9). Given the consistency in survey sites in shallow fore reef and lagoon patch reefs across the WIO [18], we grouped all sites to represent coral reef habitats as a whole (SI6.1). Data were sufficient to assess coral cover and algae-coral ratio for 10 of the 11 ecoregions, but for parrotfish and grouper abundance, only for 6 and 7 ecoregions, respectively (SI6.1.1). Variables used included:

- percent hard coral cover;
- percent fleshy algae cover, as the sum of turf algae, macroalgae and articulated calcareous algae (e.g. *Halimeda*), when available. Note that some programmes use 'fleshy' and 'macro' as synonyms, but here, 'fleshy' algae is a broader group than macroalgae, in agreement with emerging usage in the GCRMN and for consistency with EOV definitions for coral reefs [11,81];
- abundance of parrotfish and abundance of groupers, as representatives of herbivorous and piscivorous fish, respectively. Although biomass data are often considered a more sensitive indicator [35], much of the regional GCRMN survey data [18] do not include fish size, therefore biomass could not be calculated. Several studies support abundance as an important fish metric in ecological function (e.g. [82,83]) .

We evaluated Criterion D1, for change over the last 50 years, using data from 2013–2019 to estimate current conditions. Data were not available from 50 years ago, so we extrapolated initial values from available historical data (SI6.1.1): for coral and algae cover, based on sites known to be in healthy condition prior to the 1998 mass coral bleaching event, and for fish abundance, based on reference sites that are remote, well protected for at least 10 years and/or uninhabited. This gave mean and variance estimates for initial values (SI6.1.1) based on which we randomly sampled initial values to calculate relative severity of decline for all sites, and repeated this 750 times to derive an aggregate result (SI6.1.3). Collapse thresholds for each indicator were set at 5% for hard coral cover, 0.83 for algae-coral ratio, and 10% and 20% of initial population values for parrotfish and grouper abundance, respectively (Table 1). These collapse thresholds were based on different factors for each variable (SI6.1.2); for corals and algae, on expectations of potential recovery of corals from low levels, and relative proportions of algae to coral cover that might affect coral recovery. For the fish indicators the thresholds represent severe biotic disruption to the reef ecosystem, based on reef fish productivity – biomass relationships [84] and stock productivity modelling in tropical fisheries [85], though for longer lived species such as groupers, 30% is generally recommended [31].

Given there are multiple compartments to the model, whether all of them need to have crossed collapse thresholds for the system to be collapsed, or just one, or several, needs to be considered. Current RLE practice assigns the highest risk category across indicators within and across criteria to the overall ecosystem risk, however in complex ecosystems with multiple compartments and interactions of different hierarchy and strength, this may not provide the most effective representation of risk. Further, with variation in data availability being a real constraint, both within an assessment as here, or between assessments, the inclusion or exclusion of compartments would influence results too strongly to allow comparisons if the highest risk category across compartments is applied (SI6.1.4).

Based on our ecosystem model and the compartments used (fig. 2a), we constructed an algorithm that considers each compartment in sequence, and relative risk levels from LC to CR. In this algorithm, percentage coral cover is the 'root variable' for setting the base state of the ecosystem, then the following interactions are considered in sequence – first competition with algae, then top-down control of algae by parrotfish, and finally apex predator interactions by groupers. For each step in this sequence, the initial risk status may be raised a single step in the sequence VU-NT-VU-EN-CR, based on the following logic:

1. If the risk status of the next compartment is the same as, or less than, that of the prior compartment(s), the current risk status is conserved;
2. If the risk status of the next compartment is higher than that of the prior compartment(s), the current risk status is increased by one step, irrespective of the gap in status between the two.

Thus, the coral risk status sets the initial risk level, then first algae:coral ratio, then parrotfish then grouper status might increase the aggregate level of risk by a single category at each step (Table S2). We tested this algorithm of biotic collapse (SI2.6) against two alternatives, each incorporating less biological structure, to evaluate potential uncertainties and their implications (SI6.1.4, SI6.3.1). Based on these findings we selected the structured model as most appropriately reflecting ecological interactions and stages in biotic collapse.

Criterion E – Quantitative model. Criterion E was Not Evaluated (NE) due to lack of a quantitative model for WIO coral reef ecosystems.

Overall risk of collapse. Following standard RLE guidance [15,54], overall risk of collapse for each ecoregion was determined by selecting the highest risk level among criteria A–D. We also assessed risk of collapse for the WIO region as a whole, for each criterion, by weighting each ecoregion's score by its area of coral reefs (SI2.7,3.2,5.2,6.2).

Strengths and weaknesses. Data gaps for some threatening processes, spatial coverage of data, lack of disaggregation by reef zone, the length and robustness of time series, and actual thresholds for collapse, influence confidence in some inferences about risk of collapse (SI7.1). Nonetheless, the RLE assessment protocol requires a comprehensive and critical review of the key processes and available data to diagnose those processes most important to ecosystem viability, using multiple approaches. As a result, despite the limitations, this RLE assessment of WIO coral reefs has produced five important advances: i) an up-to-date regional-scale analysis of reefs most at risk; ii) a diagnosis of the dominant threats among these; iii) increased robustness and relevance of decision-support for coral reef management and policy; iv) an updated coral reef database compiled by the Global Coral Reef Network's (GCRMN) regional network under the Coral Reef Task Force (CRTF) of the Nairobi Convention, with an improved understanding of data gaps, and v) introduced a novel assessment approach that can be adapted to other coral reef regions globally, as well as other critical ecosystems, such as mangroves and seagrass beds.

Corresponding author

All correspondence and requests for materials should be addressed to David O. Obura

Data availability

The study utilised existing and available data and did not involve any primary data collection. Data on hard coral and algae cover as well as fish abundance was compiled from multiple contributors (coral reef monitoring data collected using standard methods defined by the Global Coral Reef Monitoring Network) as described in Obura et al. (2017). These data are owned by the various data contributors (full list in SI8.1), and permissions to access data would need to be sought from individual contributors, which can be facilitated by the corresponding author. SST projection data were obtained from van Hooidonk et al. 2016, open access (https://www.nature.com/articles/srep39666), and coral reef extent data was from Millennium coral reef layer as described in Andrefouet, S. et al. 2006 (http://www.imars.usf.edu/MC/).

Code availability:

Data processing, aggregation and analysis was undertaken in R with code saved in GitHub. Each Criterion was calculated using individual analytical flows developed using R Markdown. Each code file had its own specific input data, and utilised standard R functions like tidyr, dplyr, plyr and ggplot for the various steps. For Criterion B, calculations of the Area Of Occupancy (AOO) and Extent Of Occurrence (EOO) were done using a tool specifically developed for the RLE, redlistr (https://cran.r-project.org/web/packages/redlistr/index.html). These analytical workflows could be made available from the corresponding author upon request.

References

Acknowledgements

We thank contributors in the Western Indian Ocean Global Coral Reef Monitoring Network for access to data for this study, and the IUCN Red List of Ecosystems Unit for initial training and scoping. This study was supported by the Norwegian Agency for Development Cooperation (NORAD) for the project "Innovating and sharing knowledge for coastal resilience in Eastern Africa" at CORDIO East Africa. The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect the views of NOAA or the Department of Commerce.

Author contributions

All authors contributed materials and/or analysis tools through the analysis workshops, and participated in writing the paper. DO, MG, MS, KO, JM, DK, SP and RR conceived and designed the analysis, DO, MG, MS, KO, SP, SA, JK, MM and SY contributed primary monitoring data, and DO, MG, MS, KO, JM, SP, RR and RvH ran the analyses of the RLE criteria.

Competing interests

The authors declare no competing interests.

Table 1. Criteria and thresholds of collapse applied to the Western Indian Ocean coral reef ecosystem Red List of Ecosystems (RLE) assessment. Standard thresholds are set by the RLE protocol, with coral reef-specific ones derived from the literature (citations in the table). See the Supplementary Information for details (SI6.1.2). VU, Vulnerable; EN, Endangered; CR, Critically Endangered; NE, Not evaluated; DHW, Degree Heating Weeks; RCP, Representative Concentration Pathways.

Criterion	**Criterion details and standard RLE thresholds**	**Coral reef indicators & collapse threshold**
A – decline in ecosystem extent	A1 – historical decline, past 50 years Decline: VU > 30%; EN > 50%; CR > 80	Percent coral cover ≤ 10% (Perry and Alvarez-Filip 2019)
B – restricted geographic distribution	B1 – area of ecosystem (km^2); VU ≤ 50,000; EN ≤ 20,000; CR ≤ 2,000	Area (km^2)
	B2 – area of ecosystem (number of 10x10 km grid cells) ; VU ≤ 50 ; EN ≤ 20 ; CR ≤ 2	# grid cells
C – abiotic disruption	C2a – future decline, 50 years Combination of relative severity of disruption over extent of ecosystem. Thermal stress (Degree Heating Weeks, DHW) calculated from sea surface temperature in global climate projections (Van Hooidonk et al. 2016)	Exceedance of DHW 12 > 2 years per decade using RCP 6.0.
D – biotic disruption	D1 – historical decline, past 50 years Recent coral reef monitoring data (mean values, 2013-2019) compared to baseline estimates 50 years ago.	Percent hard coral cover - 5% Algae:coral ratio - 0.83 Parrotfish abundance - 10% initial (Morais et al. 2020) Grouper abundance - 20% initial (Harford et al. 2019, Sadovy de Mitcheson et al. 2020)
E – quantitative model	Not evaluated (NE), due to absence of an applicable quantitative model	

Table 2. Risk of collapse of Western Indian Ocean coral reef ecosystems in 11 ecoregions, across Criteria A–D of the Red List of Ecosystems. The overall result lists the final risk level and in parenthesis the criteria and subcriteria on which it is based. DD, Data Deficient; LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered. For details behind these results and the sub-criteria coding see SI3-6).

Region		**A**	**B**	**C**	**D**	**Overall**
WIO region		LC	LC	VU	VU	VU(C2a,D1a)
Ecoregions						
1	N.Tanzania-Kenya	LC	LC	LC	VU	VU(D1a)
2	N.Mozambique-S.Tanzania	LC	LC	LC	VU	VU(D1a)
3	Comoros	LC	LC	CR	VU	CR(C2a)
4	West Madagascar	LC	LC	EN	VU	EN(C2a)
5	North Madagascar	LC	LC	EN	LC	EN(C2a)
6	Seychelles.Outer	VU	LC	EN	VU	EN(C2a)
7	Seychelles North	VU	LC	LC	VU	VU(A1,D1a)
8	Mascarene Islands	LC	VU	CR	NT	CR(C2a)
9	East Madagascar	LC	VU	CR	LC	CR(C2a)
10	South Madagascar	DD	EN	CR	DD	CR(C2a)
11	Delagoa	VU	VU	LC	VU	VU(A1,B1a(iii)b,B2,D1a)

Table 3. Portfolio of policy and management responses to address the main drivers of risk of collapse of Western Indian Ocean coral reefs. Given the broad scale of this assessment at ecoregional levels, multiple responses across climate and ecosystem-focused actions will likely be required within any country. VU, Vulnerable; EN, Endangered; CR, Critically Endangered; MPA, Marine Protected Areas; NDC, Nationally Determined Contribution; OECM, Other Effective Conservation Measures. Based on [16]

<table>
<tr><th>Risk level and critical factor</th><th>Ecoregions and specific indicators of risk</th><th colspan="2">Range of policy and management responses to alleviate critical risk factors</th></tr>
<tr><td>Climate, EN-CR (C2a, SST warming)</td><td>• Comoros, Mascarene Islands, East Madagascar & South Madagascar (CR)
• North Madagascar (EN)</td><td rowspan="3">• Commit to strong climate change mitigation, through Paris Agreement/NDCs and national implementation of emission reductions and adaptation plans relevant to coral reefs.
• Use scenarios in policy and management planning, to consider higher and lower risk levels to maintain future options.
• Establish climate adaptation plans, to e.g.:
o optimize benefit flows (on 20–30 yr. time frames) until coral reefs transition to an alternative state;
o develop ecosystem and resource use policies anticipating potential alternative states of reefs, to maximize biodiversity and benefits after a transition;
o identify and develop ‘climate smart’ fisheries with reduced ecosystem impacts and more secure livelihood benefits;
o identify alternative livelihood options and diversified income streams in coral reef landscapes;
• Identify and protect climate refugia and connectivity nodes through MPAs and OECMs.
• Invest in local (co)management (OECMs) to reduce synergistic threats, to maximize climate resilience and buy time for adaptation.
• Improve management of species and pressures that disrupt ecosystem processes, such as fisheries, land-based impacts to coral reefs, direct damage from tourism, etc.
• Develop guidance and best practices on enhancing recovery of reefs through alleviating pressures, understanding of role of herbivory, assisted restoration efforts, etc.</td><td rowspan="3">**Climate and change-focus <<- - - - - - - - - ->> Ecosystem resilience focus**</td></tr>
<tr><td>Climate with biotic disruption, EN-VU</td><td>• Seychelles Outer (climate, EN ; coral, VU)
• West Madagascar (climate, EN; herbivores & piscivores, VU)</td></tr>
<tr><td>Biotic disruption, VU (D1a)</td><td>• N.Tanzania-Kenya, N.Mozambique-S.Tanzania (piscivores, VU)
• Seychelles North (coral & piscivores, VU)
• Delagoa (coral, algae & herbivores, A & B1/B2, VU)
• Algae not a significant driver of higher threat alone, but in synergy with other factors (N. Tanzania-Kenya, Delagoa)</td></tr>
</table>

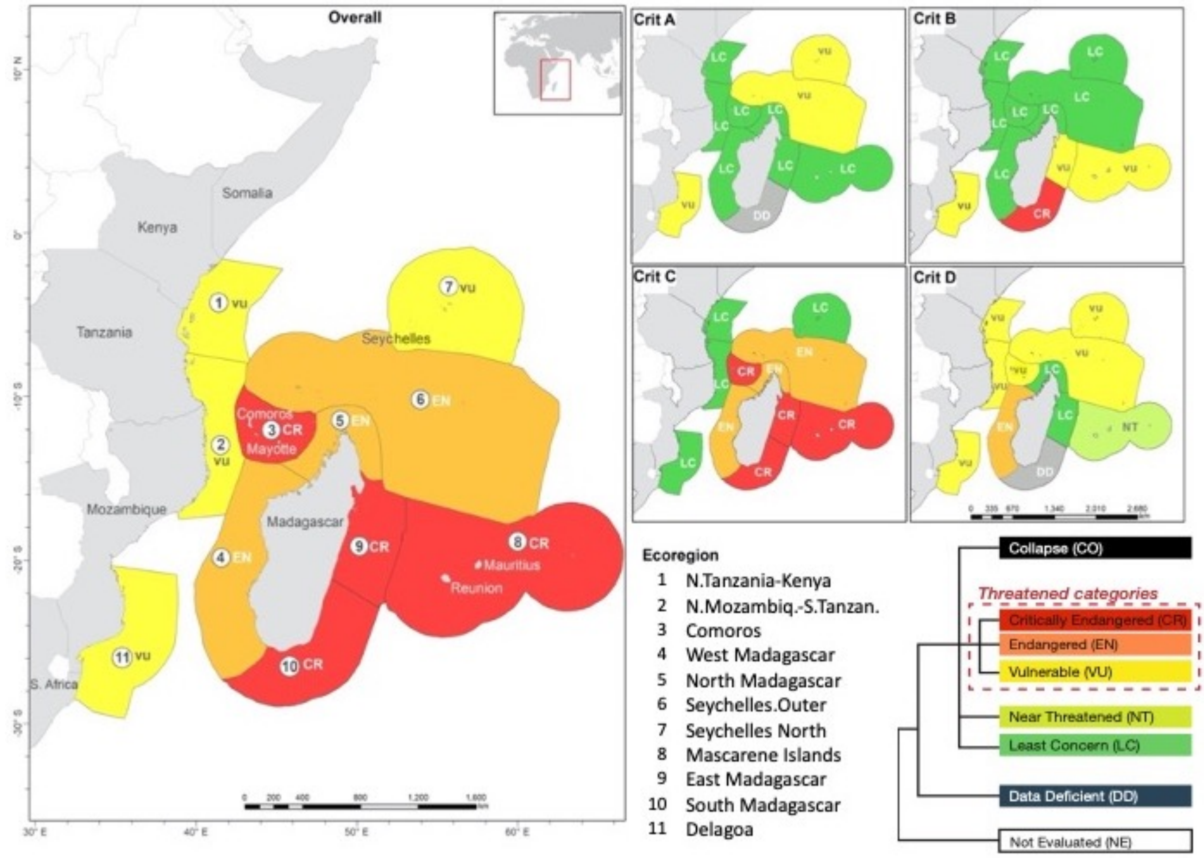

Fig. 1. Coral reefs in the Western Indian Ocean and 11 of its ecoregions were evaluated using the Red List of Ecosystems (RLE). The overall risk level for each ecoregion is shown (left) and for each of Criteria A, B, C and D (panels in upper right, see also Table 2). Coral reefs in the Somali ecoregion were Not Evaluated (NE). The ecoregion names and RLE categories hierarchy and colour codes used throughout the study are shown in the lower right.

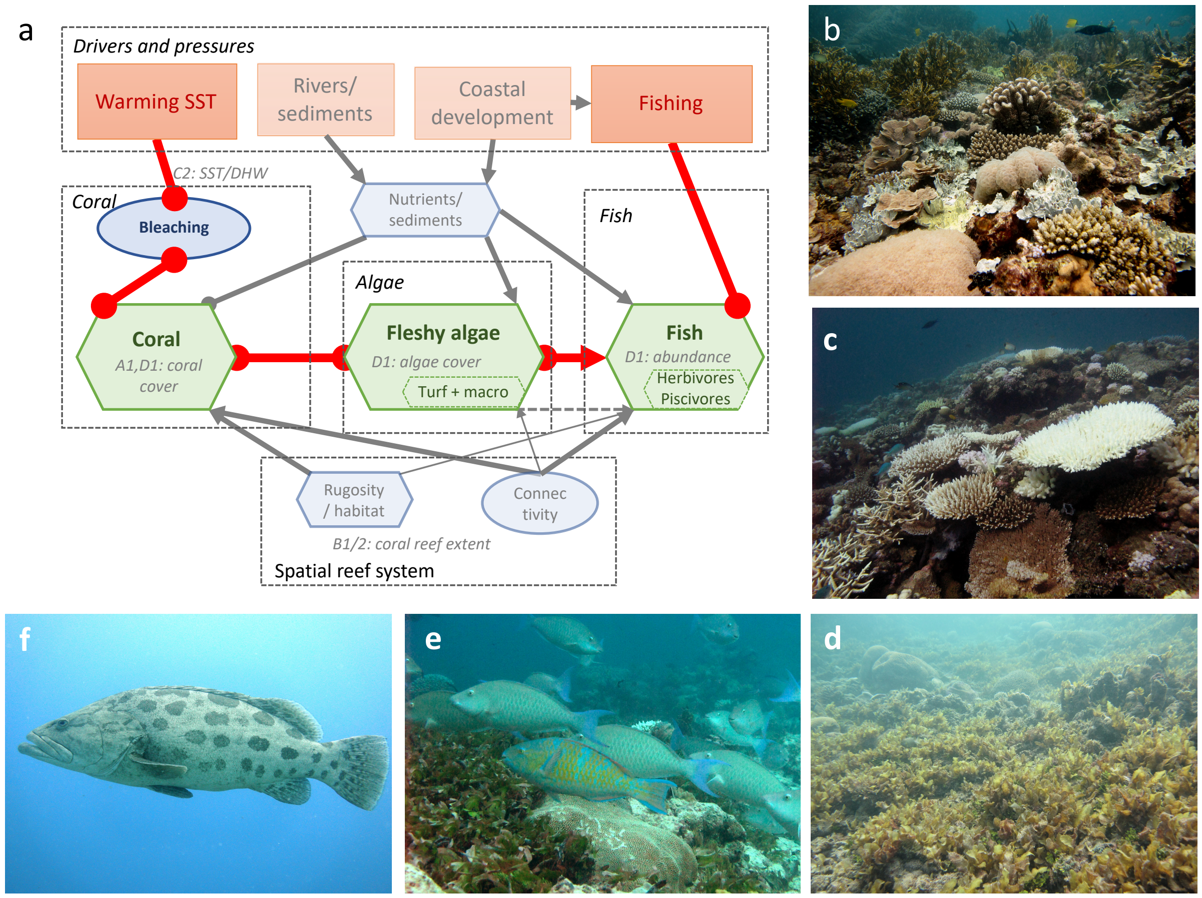

Fig. 2. Coral reef ecosystem model applied in assessing the risk of collapse for Western Indian Ocean coral reefs. a) the coral reef model, further details are provided in SI2.5; b) a healthy coral community in 5 m depth in Mafia Island, Tanzania, with diverse and abundant coral; c) bleaching and mortality among coral genera due to thermal stress in 2016, Mayotte, Comoro Archipelago; d) a reef surface dominated by *Sargassum* macroalgae, Songosongo, Tanzania; e) a school of the parrotfish *Hipposcarus harid,* St. Brandons Island, Mauritius; and f) the grouper *Epinephelus tukula*, a dominant piscivore and highly vulnerable to fishing, Northern Mozambique. Image credits: b-e, David Obura; f, Melita Samoilys.

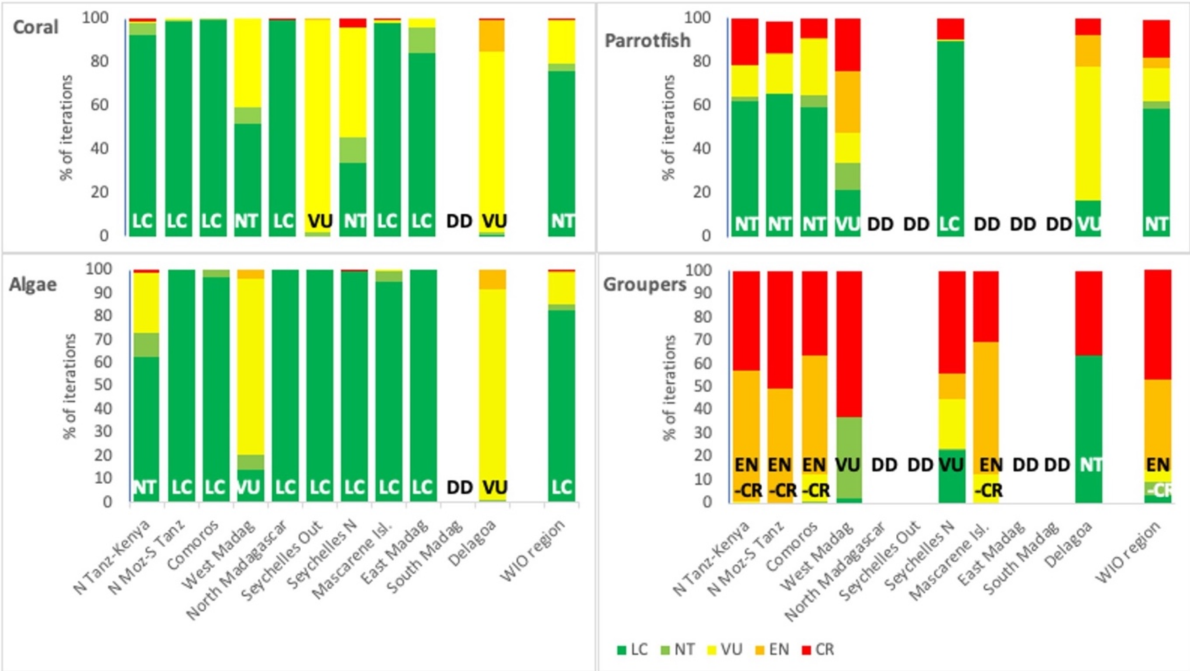

Fig. 3. Risk levels of biotic disruption for each compartment in the reef model for Criterion D of the Red List of Ecosystems. a) coral cover, b) algae-coral ratio, c) herbivorous fish (parrotfish) abundance and d) piscivorous fish (grouper) abundance for each ecoregion and the WIO as a whole (see Tables S12-S14). The y axis shows the percentage of iterations returning each risk level of 750 iterations randomly selected initial values from a defined range for each compartment (Table S7, S8, S10). The letters at the base of each column show the risk level assigned to each ecoregion, by compartment. The final risk level determined for each ecoregion is shown in Table 3. DD, Data Deficient; LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered.