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REVIEW

Important ecosystem function, low redundancy and high vulnerability: The trifecta argument for protecting the Great Barrier Reef's tabular *Acropora*

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Abstract

Identifying organisms that play an important role in maintaining ecosystem function is a key aspect of resilience-based management. For Australia's Great Barrier Reef (GBR), we found that the recovery ability of shallow exposed fore-reefs is more than 14 times higher when tabular *Acropora* are present. The disproportionate role that tabular *Acropora* play appears to be driven by a combination of traits including high recruitment, high growth rate and, importantly, large maximum colony sizes. Despite this key role, tabular *Acropora* are highly sensitive to most pressures. We compile evidence suggesting that if tabular corals were to decline or disappear on the GBR, the potential for reef recovery on exposed fore-reefs would be considerably slowed. We then consider the merits of placing special emphasis on the protection of tabular *Acropora* within the management of the GBR. Importantly, we recognise that an analysis of costs and benefits of such recognition is vital before any change is implemented. Actions might include targeted crown-of-thorns starfish control, anchoring restrictions and protection for tabular corals on reefs identified as essential for their larval dispersal. In addition, targeted communications about the critical importance of these highly recognisable corals may boost community support and participation in their protection.

KEYWORDS

coral reef recovery rate, ecosystem functioning, ecosystem-based management, functional redundancy, functional role, Great Barrier Reef, resilience-based management, species prioritization, species protection, tabular *Acropora*

1 | INTRODUCTION

Resilience-based management has become a common tool for environmental managers (Anthony et al., 2015; Berkes, 2012; McLeod et al., 2019; McLeod & Leslie, 2009). Although preserving biodiversity continues to be a paramount goal of management agencies, maintaining the ecological functioning of the ecosystems being managed has become crucial given the predicted increase in the

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frequency and/or intensity of disturbances in most world ecosystems (Long et al., 2015).

One of the critical properties of an ecosystem's function is its ability to recover after disturbances (Cole et al., 2014; Veraart et al., 2012). Given that reductions in recovery rate have been recently documented for several terrestrial and marine ecosystems (Anderson-Teixeira et al., 2013; Ortiz et al., 2018; Turkalo et al., 2017), identifying processes and organisms that play a disproportionate role in the ability of the ecosystem to recover may enable managers to design more effective plans for environmental protection (Flynn et al., 2011; Grman et al., 2010; Oliver et al., 2015; Ortiz, González-Rivero, et al., 2014). Furthermore, as the frequency and intensity of disturbances are expected to increase in the near future, safeguarding the ability of ecosystems to recover in periods between disturbances may become the most effective way to maintain critical ecosystem services.

Autogenic engineers such as corals and trees are the main drivers of physical complexity for the most biodiverse ecosystems (rainforests and coral reefs) and the main providers of habitat for the multitude of organisms inhabiting them (Jones et al., 1994; Nadrowski et al., 2010; Wild et al., 2011). Differences in species characteristics affect the provision and dynamic maintenance of this complexity (Flynn et al., 2011). Although the idea of using a functional approach to explain ecological patterns in coral reefs has been explored in the past (Steneck & Dethier, 1994), only recently has it started to prevail over traditional taxonomic or phylogenetic classifications (Darling et al., 2017; Denis et al., 2017; Madin et al., 2016; Mouillot et al., 2013). In relation to habitat provision in coral reef environments, colony growth form is particularly important. Among coral growth forms, tabular corals provide several ecosystem benefits including tridimensional structure, shelter for fish at different life stages, shelter from wave energy, protection against extreme irradiance for fish and food provision (Graham & Nash, 2013; Hongo & Kayanne, 2011; Johns et al., 2014; Kerry & Bellwood, 2012, 2015; Ortiz, Bozec, et al., 2014; Pratchett, 2007b).

Here, we combine a revision of published information and new analysis from monitoring data to characterise the role tabular corals play on the Great Barrier Reef (GBR). We then evaluate the potential consequences of losing tabular corals on the GBR and propose management that emphasises the protection of critical organisms for maintaining a coral reef's ability to recover from disturbances.

2 | ECOSYSTEM SERVICES PROVIDED BY TABULAR *Acropora*

Tabular *Acropora* provide multiple ecosystem services in coral reefs (Kerry & Bellwood, 2015). Their fast growth rate facilitates a competitive advantage over macroalgae and many other corals, leading to dominance in shallow forereefs (Halford et al., 2004; Roelfsema et al., 2018). Although it could be argued that tabular *Acropora* affect most of the ecosystem services provided by coral reefs, including indirectly through complex ecological interactions, here we will focus on those services more directly influenced by tabular *Acropora*.

2.1 | As ecosystem engineers

Tabular corals play a significant role in the provision of structural complexity on coral reefs (Denis et al., 2017; Graham & Nash, 2013; Kerry & Bellwood, 2012). Their morphology leads to the creation of a variety of microhabitats of different heights and sizes that can be exploited by a variety of organisms from small epifauna (Vytopil & Willis, 2001) through to small corallivorous fish (Pratchett et al., 2008) to mesopredatory fish (Kerry & Bellwood, 2015). In addition, due to their fast recovery rate, they are one of the few GBR coral type that can provide relatively fast recovery of complexity after structure-altering disturbances such as cyclones (Johns et al., 2014).

2.2 | As habitat for fish

Many reef fish species are highly dependent on tabular *Acropora*, from small corallivores to midsize and large predators (Kerry & Bellwood, 2015; Pratchett et al., 2008). Several corallivorous fish species show a strong preference for feeding on tabular corals over other coral morphologies (Pratchett, 2005a, 2007b). In some cases, this preference makes them almost entirely dependent on the presence of tabular *Acropora* (Kerry & Bellwood, 2015). Many midsize and large predators spend significant amount of time under plates of tabular *Acropora*, leading to different levels of habitat dependency (Kerry & Bellwood, 2012; Khan et al., 2017). Although the ultimate reason for this dependency is not clear, recent evidence suggests it may be driven by the need for protection from solar irradiance (Kerry & Bellwood, 2015). Perhaps due to this dependency, studies have shown that large reductions in coral cover (in reefs often dominated by tabular corals) lead to reductions in fish diversity and biomass (Bonin, 2012; Cheal et al., 2017; Graham et al., 2007; Munday, 2004).

2.3 | As substrate for coral recruitment

Dead tabular corals provide one of the preferred substrates for coral larval settlement (Yadav et al., 2016). There are two main mechanisms that are likely to drive this pattern. Coral larvae have a strong preference for settling on crustose coralline algae (CCA) (Babcock & Mundy, 1996; Harrington et al., 2004) and dead tabular coral is often dominated by CCA (Yadav et al., 2016). Secondly, because coral settlement is maximised in shaded areas of shallow coral reefs (Kuffner, 2001; Maida et al., 1994), the underside of dead tabular coral plates provides ideal substrate for coral settlement.

2.4 | As regulators of macroalgal abundance

A less well–studied ecosystem benefit provided by tabular *Acropora* is their impact on grazing intensity. Grazing intensity is controlled by the abundance of herbivores, their individual feeding behaviour and the amount of grazable space (Mumby, 2006; Mumby & Steneck, 2008; Williams et al., 2001). When large disturbances reduce live coral cover, grazing occurs over a significantly larger area (the original substrate covered by turf algae and macroalgae plus the new bare substrate provided by the dead coral skeleton) (Bozec et al., 2019; Mumby et al., 2007; Steneck et al., 2018). As a result, if herbivore biomass is not high enough to compensate for increased grazable space, grazing intensity per unit area may decline, and subsequent coral recovery can be compromised by macroalgal abundance (Cheal et al., 2010; Done, 1992; Hughes, 1994; Mumby, 2009). Within this context, tabular corals likely play an important role in maintaining grazing intensity because they recover space relatively rapidly after disturbance. In other words, recovery of tabular corals may shorten the time grazing intensity remains diluted after disturbances (Johns et al., 2014). Such mechanism influencing grazing intensity may have contributed to the macroalgal bloom observed around Havannah Island on the inshore GBR (Cheal et al., 2010).

2.5 | As facilitators of reef recovery

Empirical evidence from the GBR suggests that reefs dominated by tabular *Acropora* tend to recover rapidly (Johns et al., 2014; Linares et al., 2011; Osborne et al., 2011). However, these studies do not focus on the ecological mechanisms of recovery, nor do they explicitly test for differences in recovery as a function of the dominance of specific coral types. Similarly, simulation modelling suggests that tabular *Acropora* are important for coral recovery in the GBR (Ortiz, Bozec, et al., 2014), but no formal evaluation of the effect size of the enhancement of recovery rate when tabular *Acropora* are present has been carried out. We therefore undertake such an analysis here.

3 | TABULAR *Acropora* AS CATALYSTS FOR REEF RECOVERY IN EXPOSED FORE-REEFS SLOPES

As part of this study, we analysed monitoring data from the GBR to evaluate if the early colonization and growth of remaining tabular corals influence reef recovery rate, and if other coral types have a similar impact on reef recovery.

3.1 | Recovery periods

We used the Australian Institute of Marine Science Long Term Monitoring Program data (Sweatman et al., 2008). The data set contains information for 97 reefs with three sites per reef and five permanent 50-m-long transects per site between 6 and 9 m of depth. The reefs were sampled annually or biannually from 1992 to 2018. All sites in each reef are placed in the northeast flank of the reef. Therefore, this analysis is confined to the upper reef slopes of systems with intermediate wave exposure. These environments have been identified as naturally dominated by tabular acroporids (Madin et al., 2006; Roelfsema et al., 2018; Shimokawa et al., 2014), thus this analysis focuses on whether the recovery of these environments is hindered when tabular corals are not able to fulfil their natural ecological role. However, it is important to highlight that oceanographic and geomorphic properties of reefs or regions may naturally affect the ability of tabular acroporids to dominate some of the study reefs. For this reason, we explored two different data sets (see Supporting Information and Figure S1) to establish that the majority of GBR reefs that have been historically monitored have had at least one flank dominated by tabular *Acropora* in the past.

We identified 57 periods of recovery defined by the following criteria:

- Recovery period must start after a significant reduction in total coral cover or at the beginning of the data set.
- Recovery periods must start with an initial coral cover lower than 10% as we focused on early recovery. Ten per cent was chosen to ensure that enough recovery trajectories were available.
- The recovery period must have a minimum duration of at least 5 years.
- The recovery periods must end with the next statistically significant reduction of total coral cover or at the end of the data set.

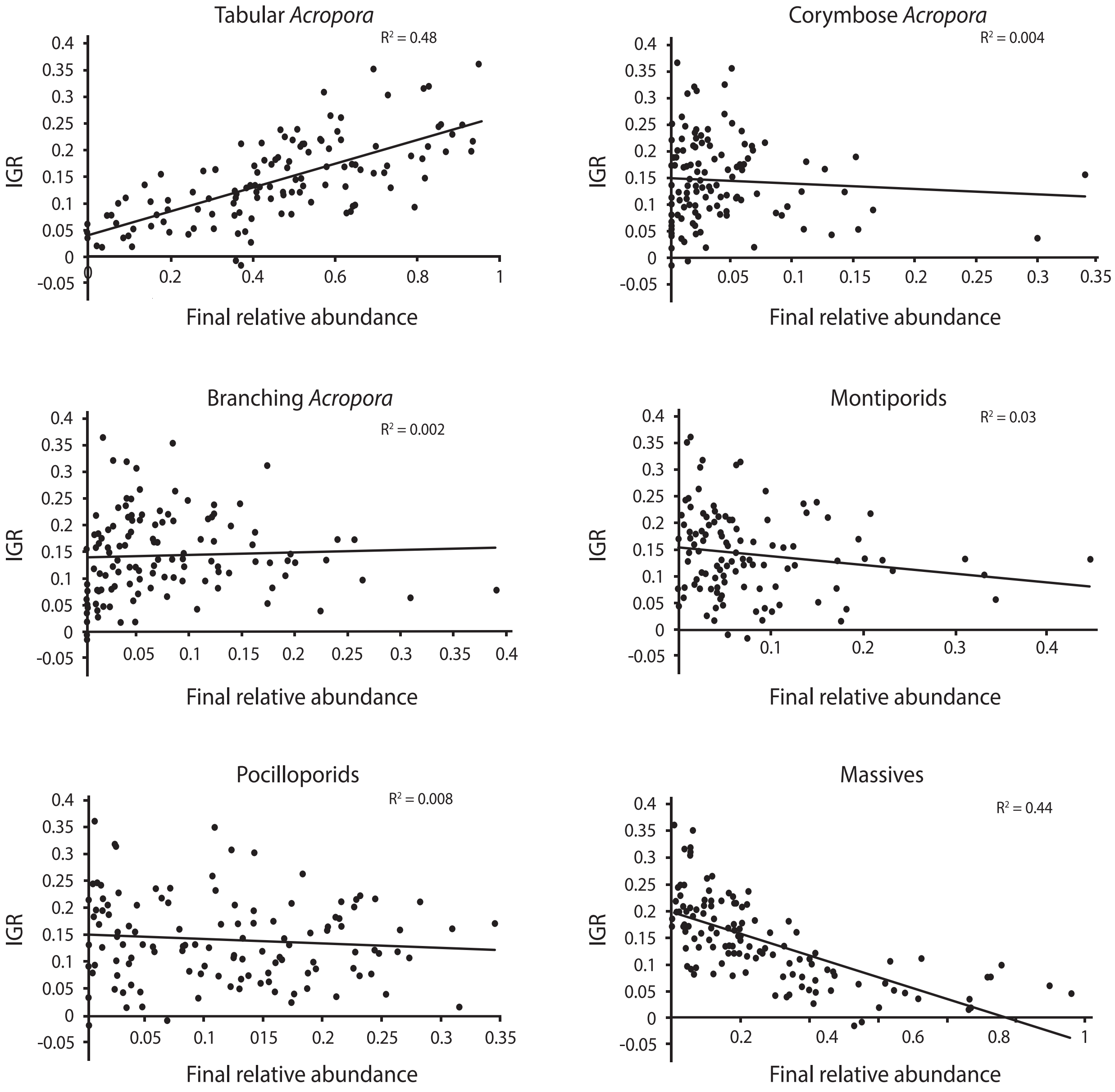

FIGURE 1 Relative contribution of different coral types to the recovery of exposed fore-reef environments on the GBR. Reef recovery is expressed as instantaneous growth rate (IGR). *X*-axis represents the relative abundance of each coral type at the end of each recovery period (before the next disturbance)

3.2 | Reef level recovery rate

For each recovery period, the instantaneous growth rate (IGR) based on total coral cover was calculated assuming exponential growth. Exponential growth was selected to avoid making assumptions about the reef-specific carrying capacity, or the reef-specific inflection point required for models with logistic behaviour. As the initial coral cover is low for all the recovery periods, and most periods were short (less than 10 years), most recovery periods were within the exponential phase of a logistic curve.

3.3 | Influence of different coral types on reef-level recovery rate

To evaluate the contribution of six different coral types to the overall reef recovery rate, we explored the relationship between the relative abundance of each coral type at the end of the recovery period and the overall community reef recovery rate (IGR) calculated based on total coral cover (Figure 1). As the explanatory variable is intrinsically linked to the duration of the recovery period, we explored the potential confounding effect of the differences in the duration of the recovery period on the patterns observed in

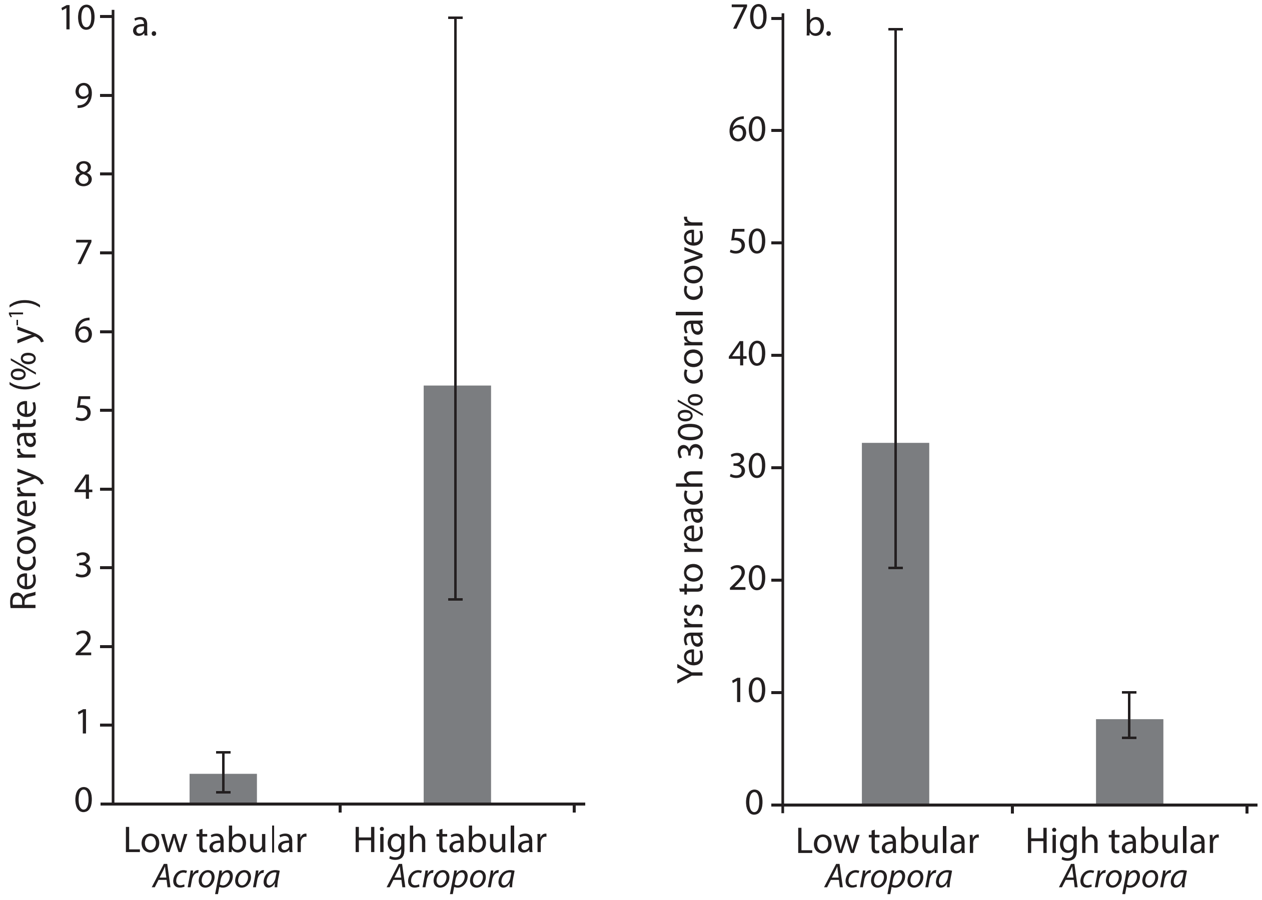

FIGURE 2 Differences in annual recovery rate depending on whether tabular corals dominated the recovery period (top 10 percentile from the tabular *Acropora* panel in Figure 1) or not (bottom 10 percentile from the tabular *Acropora* panel in Figure 1). (a) Annual site-level recovery rate. (b) Number of years to reach 30% coral cover, assuming a post-disturbance starting coral cover of 5%

Figure 1. We found that the duration of the recovery period did not correlate with either the IGR or the final relative abundance of any of the six coral types (Figures S3 and S4). We found a strong positive relationship between reef recovery rate (IGR) and the final relative abundance of tabular *Acropora*. There was no significant relationship between the abundance of any other coral type on the IGR, except for a negative one for massive corals (Figure 1). In reefs where the final relative abundance of tabular corals was in the top 10 percentile, recovery was 14 times faster than in reefs where the final abundance of tabular corals was in the bottom 10 percentile (Figure 2a). Although limitation in the number of recovery periods prevented us from formally testing the effect of time in this pattern, it appears tabular *Acropora*'s final relative abundance after disturbances has not changed over time in the GBR (Figure S2).

These results suggest that the presence of tabular *Acropora* after disturbances (through new recruitment and/or growth of remaining colonies) serves as a catalyst for boosting recovery of shallow fore-reefs. Importantly, the recovery rates observed on reef areas where tabular *Acropora* did not boost reef recovery were so low (0.0.38% a year) that it would take these areas an average of 32 years to recover from 5% to 30% coral cover. In contrast, areas where tabular *Acropora* boosted recovery achieved 30% coral cover in 7.5 years (Figure 2b). Given the observed and predicted increases in the frequency and intensity of disturbances on the GBR (GBRMPA, 2019), even under the most optimistic climate change scenarios, this low recovery rate in the absence of tabular *Acropora* would not be enough to keep up with the disturbance regime. Therefore, taking action directed at protecting and conserving populations of tabular *Acropora* could become a key tool to maintain resilience in this physical environment.

4 | WHAT IS SPECIAL ABOUT TABULAR CORALS?

Based on the life trait information of different coral types, we explored particularities in tabular *Acropora* that could explain the disproportionate role they play in coral recovery rates. The traits that might most intuitively explain tabular *Acropora* influence on reef recovery are colony

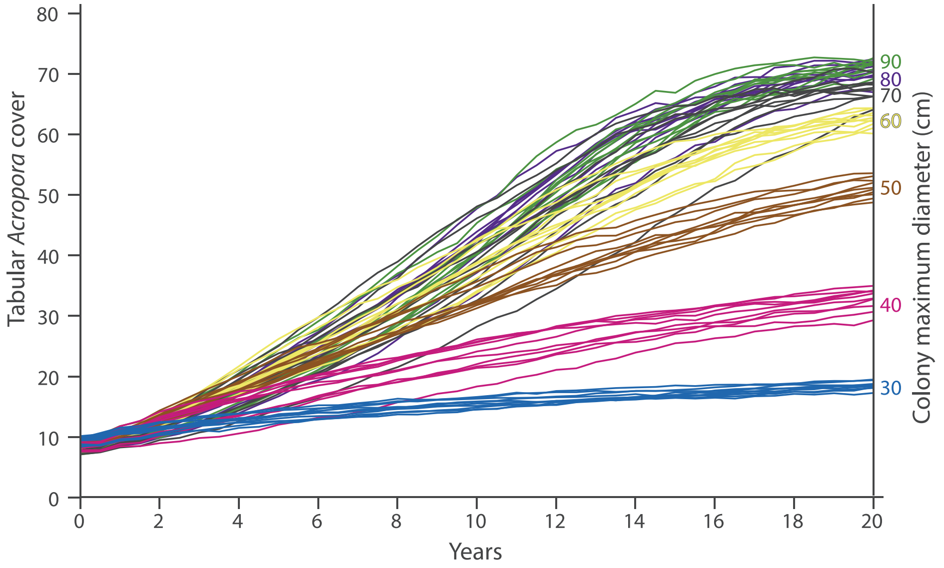

FIGURE 3 Modelled recovery of tabular coral populations as a function of different maximum diameters. Each colour represents simulations of tabular *Acropora* cover trajectories (left *y*-axis) for a particular maximum diameter (specified in right *y*-axis). Each line represents a simulation

somatic growth and recruitment rate. Tabular *Acropora* are among the fastest growing corals on exposed reef slopes in the GBR (Gold & Palumbi, 2018), but other coral growth forms such as corymbose or branching *Acropora* have comparable growth rates (Ortiz, Bozec, et al., 2014) and did not show the same ability to enhance reef recovery. Similarly, although species-specific data on recruitment within *Acropora* are scarce, the available information suggests that although tabular *Acropora* are good recruiters, other growth forms and taxa, such as corymbose *Acropora* and pocilloporids, have similar recruitment rates (Ortiz, Bozec, et al., 2014; Wallace, 1985). In contrast, one particularly unique characteristic of tabular *Acropora* is their large maximum diameter compared with other GBR coral with similar growth and recruitment rates.

4.1 | Effect of maximum diameter on the ability of tabular corals to enhance reef recovery

To explore the potential effect that the maximum diameter of tabular corals may have on its ability to enhance coral recovery rate, we use a previously published and validated spatially explicit simulation model of GBR reefs (Ortiz, Bozec, et al., 2014; Ortiz et al., 2018).

The individual-based model simulates the population dynamics of coral colonies distributed across a regular square lattice of 20 × 20 cells. Each cell contains a mixture of living substrata comprising multiple coral colonies and patches of algae. The model captures rates of recruitment, growth, reproduction and mortality of corals and algae as well as their competitive interactions. The model was implemented in MATLAB as a sequence of vectorised instructions so that all the cells of the lattice grid were processed simultaneously for a given matrix. The model was validated using a large independent data set from the GBR; this validation included long-term trajectories of 19 different reefs across a 1200-km section spanning the south and central GBR. We fixed the number of recruits and initial coral cover in all simulations. We simulated different maximum diameters tabular *Acropora* could grow to. We then plotted tabular coral cover trajectories for each maximum diameter (Figure 3).

As the maximum diameter of tabular *Acropora* is reduced in the model runs (while maintaining all other parameters unchanged), the simulated recovery trajectories are similar for the initial 5 years (Figure 3). However, a strong divergence is observed after 5 years with much faster recoveries as the maximum diameter increases. After 10 years, the yearly average recovery rate when maximum diameter is 40 cm (such as the one observed in corymbose corals) is 1.1% per year. In contrast, when the maximum diameter is 90 cm (the standard parametrization for tabular *Acropora*) the average recovery rate is 4.2% per year. The observed differences in recovery rate at different maximum diameters are likely to be the consequence of coral colonies with a planar circular shape increasing in surface area (cover) quadratically with diameter. This analysis suggests that the observed increase in reef recovery rate when tabular *Acropora* dominates during the recovery period may be a consequence of the combination of somatic growth rate, high recruitment rate and large maximum diameter.

5 | SENSITIVITY OF TABULAR *Acropora* TO DIFFERENT DISTURBANCES

Tabular *Acropora* are among the most sensitive coral morphologies to both natural and anthropogenic pressures. When considering the leading forces driving the degradation of GBR reefs, it becomes clear that the ecosystem services provided by tabular corals are at risk.

5.1 | Coral bleaching

Tabular *Acropor*a have been consistently ranked among the most sensitive corals to the effects of extreme thermal events (Hughes et al., 2018; Loya et al., 2001; Marshall & Baird, 2000). During the three best documented mass bleaching events in the GBR (1998, 2002 and 2016/17), tabular *Acropora* showed some of the highest levels of bleaching susceptibility and bleaching-related mortality of all coral types (Baird & Marshall, 2002; Berkelmans et al., 2004; Hughes et al., 2018; Marshall & Baird, 2000). This pattern was also observed across the Pacific and Indian oceans (DeCarlo et al., 2017; Loya et al., 2001; McClanahan et al., 2004; Pisapia et al., 2016; Pratchett et al., 2013). Tabular corals naturally inhabit relatively shallow waters, and their morphology maximises the harvesting of light. Therefore, they are particularly sensitive to photo damage and the concomitant effect of high irradiance and high temperature during extreme thermal stress events (Barshis et al., 2013; Gold & Palumbi, 2018). In some areas of the world, tabular corals have suffered dramatic reduction in abundance due to bleaching and subsequent recovery failure (Pisapia et al., 2016; Pratchett et al., 2013).

5.2 | Ocean acidification

The effect of ocean acidification (OA) on corals and particularly on calcification rates has been the focus of intense debate (Bove et al., 2020; Mollica et al., 2018). Although some studies have identified internal upregulation of pH as an acclimatory mechanism for coral to overcome the effect of OA (McCulloch et al., 2012), recent laboratory studies have challenged the magnitude of resistance that this mechanism may provide (Comeau et al., 2019). Reductions in calcification rates in response to natural and controlled reductions in pH have been documented in several coral species (Fabricius et al., 2011; Guo et al., 2020; Mollica et al., 2018), including tabular acroporids (Anderson et al., 2019). If these effects are realised, tabular corals may be particularly threatened by OA due to its morphology. Because these corals are attached to the substrate through a thin (albeit strong) stalk, if the skeletal density of tabular corals is reduced due to the effects of OA, the incidence of colony dislodgement could increase significantly (Fabricius et al., 2011; Hennige et al., 2015; Madin et al., 2008, 2012; Mollica et al., 2018). In contrast to many other coral types, the consequence of colony dislodgement for tabular *Acropora* is usually whole colony mortality (Madin & Connolly, 2006). Therefore, the reduction in the ability of tabular corals to provide the discussed ecosystem benefits may be exacerbated by the effects of OA.

5.3 | Cyclones

Tabular *Acropora* require high water flow to thrive, showing maximum dominance in areas with intermediate to high wave exposure (Roelfsema et al., 2018). However, due to their morphology, tabular *Acropora* have been shown to be among the growth forms most sensitive to extreme wave exposure, mechanistically (Madin, 2005; Madin et al., 2006; Madin & Connolly, 2006) as well as empirically (Roelfsema et al., 2018). There are a number of examples of significant reductions in the abundance of tabular corals in the GBR after cyclones (Beeden et al., 2014; Cheal et al., 2010; Johns et al., 2014; Madin et al., 2008). Even though fast recovery has been observed repeatedly (Osborne et al., 2011), future reductions in larval supply if adjacent coral stocks are simultaneously depleted could jeopardise the ability of tabular *Acropora* to recolonize after intense storms.

5.4 | Crown-of-thorns starfish outbreaks

Early studies observed that crown-of-thorns starfish (CoTS) do not prey on all coral types equally and actively favour corals of the genus *Acropora* (De'ath & Moran, 1998). Subsequent analysis demonstrated that within *Acropora*, tabular forms are preferred over all other forms by a factor of between 5 and 35 times (Pratchett, 2007a). Consequentially, even relatively modest CoTS outbreaks could have devastating effects on tabular corals (Pratchett, 2005b). In some cases, recovery after a CoTS outbreak has been poor, even years after the initial event (Lourey et al., 2000; Seymour & Bradbury, 1999).

5.5 | Coral diseases

Tabular corals have also been shown to be highly susceptible to coral diseases (Haapkylä et al., 2013; Hobbs et al., 2015; Montano et al., 2016; Roff et al., 2006). The main group of diseases affecting tabular *Acropora* to date is White Syndromes (WS) (Bourne et al., 2015). Disease outbreaks have had significant impacts on populations of tabular corals in the Pacific (Brodnicke et al., 2019; Hobbs et al., 2015; Roff et al., 2011). During a single WS outbreak, 36% of all tabular *Acropora* were killed in Christmas Island, with some sites losing up to 96% of tabular colonies (Hobbs et al., 2015). Similarly, a single outbreak of WS affected more than 50% of all large tabular corals in the Capricorn Bunker Group (southern GBR). Due to the fast progression of the disease, many of these colonies died, reducing the overall cover of tabular corals in the area (Roff et al., 2011). Although the population recovered over time, potentially as a consequence of the high connectivity of the GBR, this example demonstrates how sensitive this growth form is to disease outbreaks.

5.6 | Water quality

Tabular corals are relatively rare in inshore environments characterised by low irradiance, high nutrients and sedimentation (Done, 1982; Fabricius et al., 2005; Shimokawa et al., 2014). Tabular corals have limited ability to supplement energetic needs through particle feeding at least in comparison to other coral types such as massive corals (Ferrier-Pages et al., 2011; Palardy et al., 2005; Porter, 1976). Furthermore, their morphology makes the removal of sediment through mucus secretion difficult (Stafford-Smith & Ormond, 1992). As the growth rates of fast growing corals such as tabular *Acropora* are linked to light availability (Marubini et al., 2001; Roth et al., 1982), reductions in light such as the ones observed in the mid-shelf of the central GBR (Fabricius et al., 2014, 2016; Logan et al., 2013) have the potential to significantly reduce the growth rate of tabular corals. If light-driven reductions in growth rate are prolonged and coincide with reduced abundance of tabular *Acropora* because of other disturbances, together these circumstances could prevent tabular corals from providing the rapid recovery rates observed in the previous analysis.

5.7 | Anchor damage

Although specific information on the relative susceptibility of different coral growth forms to anchor damage is scarce, the morphology of tabular corals makes them particularly sensitive (Riegl, & Riegl, 1996). While other coral types, such as branching thickets, may suffer partial colony mortality from anchor damage, this can actually favour reproduction by fragmentation (Riegl & Velimirov, 1991). However, tabular corals will more likely experience whole colony mortality (Liddle, 1991; Riegl, & Riegl, 1996). As discussed previously, the stalk of tabular *Acropora* is important for whole colony survival (Madin, 2005) and can be broken either by the anchor hitting the colony when deployed, through warp movement while a vessel is at anchor, or as a consequence of retrieving an anchor lodged underneath a tabular coral. As tabular *Acropora* grow to large sizes, the per capita likelihood of the tabular population to be affected by anchor damage is larger than for other coral types.

6 | FUNCTIONAL REDUNDANCY OF TABULAR *Acropora* ON THE GBR

It has been argued that the GBR has a low risk of losing functional roles due to the amount of redundancy in the system (Bellwood et al., 2003; Flynn et al., 2011; Hoey & Bellwood, 2009; Pillar et al., 2013). There are more than 100 species of *Acropora* on the GBR (Wallace, 1999) suggesting a high level of redundancy which should minimise the likelihood of function loss. However, there are only 10 species of tabular *Acropora* on the GBR, and of those, only three are abundant and widespread (*Acropora hyacinthus*, *Acropora cytherea* and *Acropora clathrata*) (Veron, 1986, 2000; Wallace, 1999). This low level of functional redundancy increases the risk of losing their functional role. There are documented examples where the reliance of ecosystem function on a low number of species has led to erosion of ecosystem recovery rate. One such example is the loss of acroporids in the Caribbean.

Although there is no growth form in the Caribbean that is morphologically equivalent to tabular corals in the Pacific, the two species of *Acropora* previously abundant on Caribbean reefs (*Acropora cervicornis* and *Acropora palmata*) used to play an important role in reef recovery (Aronson & Precht, 2001; Bak, 1983). Previous studies have pointed out that Pacific reefs appear to recover more frequently after disturbances than Caribbean reefs over the last 30 years (Baker et al., 2008; Roff & Mumby, 2012). Furthermore, in a comparison of the ecosystem benefits expected for Caribbean and Pacific reefs under different climate change scenarios, Ortiz, Bozec, et al. (2014) demonstrated that the fast recovery observed in Pacific reefs would be diminished if tabular corals were absent (Figure 4).

Despite the vast ecological differences between the Pacific and the Caribbean, the Caribbean case provides an example of how low functional redundancy represents a high risk of losing ecosystem function. Even though there is considerable uncertainty when predicting the consequences of losing tabular Acropora on the GBR, taking early action to prevent steep declines in the populations of these corals could be crucial to reduce the risk of compromising the resilience of the GBR ecosystem.

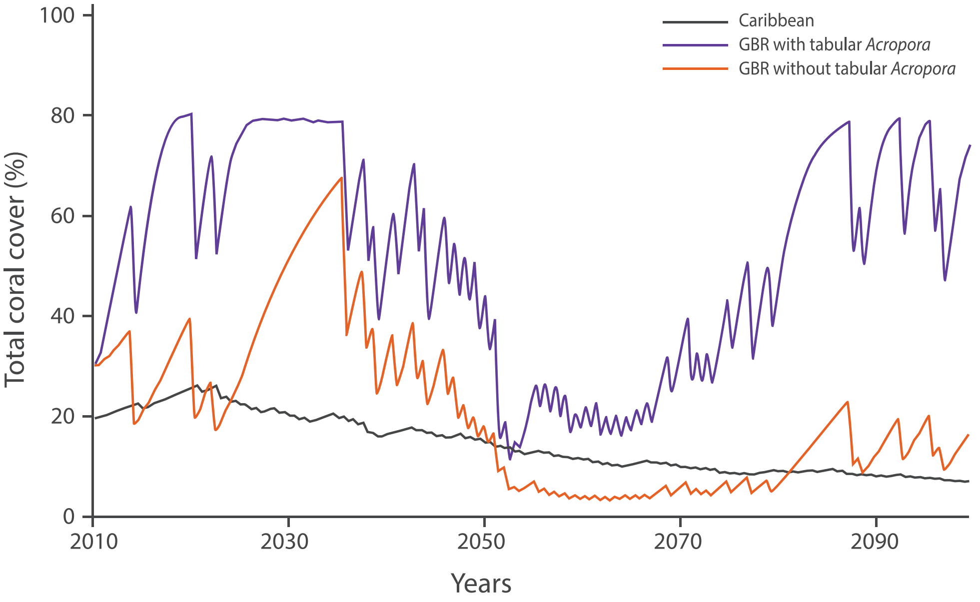

FIGURE 4 Predicted coral cover trajectory of Caribbean reefs, Pacific reefs with tabular *Acropora* and Pacific reefs without tabular *Acropora*. Modified from Ortiz, Bozec, et al. (2014)

7 | A FUNCTIONAL APPROACH FOR RESILIENCE-BASED MANAGEMENT

7.1 | A shift in focus from maintaining biodiversity to enhancing key ecosystem functions

Coral reef management around the world has traditionally been driven by principles of maintaining biodiversity and ecosystem functioning (Flynn et al., 2011; Le Saout et al., 2013; Oliver et al., 2015; Pimm et al., 2014; Precht et al., 2004; Selig et al., 2014). The majority of species-specific management actions are focussed on preventing species extinction or protecting and managing species of particular social, economic or cultural interest. Examples include Dugongs (Butler et al., 2012; Preen, 1998), sea turtles (Butler et al., 2012; Mrosovsky, 2003) and Caribbean *Acropora* (Precht et al., 2004) among others. There are some examples of species being protected due to their role in the ecosystem. Perhaps the best known and oldest examples involve the protection of top predators both in terrestrial and marine environments (Ritchie et al., 2012; Sergio et al., 2006; Terborgh & Estes, 2013). In the past 30 years, a significant body of work has illustrated the cascading effects, including ecosystem collapse, of losing top predators (Terborgh & Estes, 2013). Terrestrial examples include the loss of wolves in U.S. forests, leading to an unprecedented population expansion of herbivores, and subsequent habitat degradation due to intense grazing (McLaren & Peterson, 1994; Ripple & Beschta, 2007). Similarly, the loss of top predators in tropical rainforest has been the cause of ecosystem collapse within a few decades (Terborgh et al., 2001). In marine ecosystems, some examples include the decline of the cod and seal populations in the northern Atlantic leading to loss of ecosystems' complexity and function (Springer et al., 2003; Steneck et al., 2013). Recently, the functional role of species important for maintaining resilience of coral reef ecosystems has started to be considered under a resilience-based management framework. Herbivorous fish have been given legal protection in some Caribbean reefs based on the role they play in ecosystem function (Kaplan et al., 2015). Empirical and theoretical evidence demonstrated that the loss of herbivore populations could lead coral reef ecosystems to become entrapped in a macroalgal-dominated basin of attraction, making it almost impossible for corals to recover (Hongo, 2012; Mumby et al., 2006, 2007, 2013; Mumby & Steneck, 2008). Although some coral species have been granted legal protection based on their threatened status (NOAA, 2014), and *Acropora hyacinthus* (a tabular coral) has been designated as 'Near Threatened' by the IUCN Red List (Aeby et al., 2008), there are no examples to date where coral species have been conferred legal protection based on their role in maintaining coral reef ecosystem resilience.

7.2 | How can targeted management actions protect tabular corals?

The 10-fold enhancement of coral recovery highlighted in this study, combined with susceptibility to multiple disturbances (Aeby et al., 2008), and the low functional

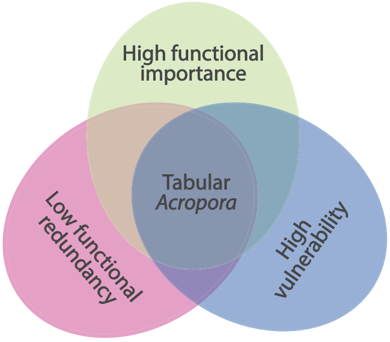

FIGURE 5 Diagram showing tabular *Acropora* in the intercept of high functional importance, high sensitivity and low natural redundancy

redundancy of the GBR (Figure 5) suggest that special attention should be given to the maintenance of populations of tabular *Acropora* in (wave) exposed reef environments (GBRMPA, 2017). Reducing risks associated with current and predicted pressures to species that make key contributions to reef resilience through recovery as well as enhancing populations of these species are key elements of effective resilience-based coral reef management (Anthony et al., 2015; GBRMPA, 2017; McLeod et al., 2019).

We examined potential management options for tabular corals and identified three main types of management actions: protect, restore and adapt. We provide examples for each of these three types of management, how they would benefit tabular corals and the degree of anticipated ecological benefit (Table 1). The relative ecological benefit was ranked from low to high based on the current scale of implementation and the expected feasibility and scalability of established and proposed actions in the future. Table 1 does not represent an exhaustive list of every management action that could help protect tabular corals; rather, it includes examples that have already been implemented (but not targeted to a specific coral taxa) or are considered possible future options. Furthermore, this is not a list of specific recommendations that should be prioritised over new or existing management actions, as a cost–benefit analysis would be required to inform such a prioritization which is outside the scope of this article.

By specifically targeting tabular corals, 'protective' management actions would provide direct benefits to coral populations, exposed habitats and individual colonies (Table 1). Some of these protective actions, such as in-water CoTS culling, have demonstrated direct benefits to tabular corals on target reefs of the GBR, with the magnitude of the benefit dependent on the scale of implementation. These culling programs typically target only a limited number of reefs owing to logistic constraints (Babcock et al., 2016; Pratchett et al., 2019). However, prioritizing reefs and reef habitats that are particularly important for the dispersal and growth of tabular Acropora (Hock et al., 2016) could rapidly enhance the ecological and economic effectiveness of CoTS control and enhance overall coral recovery in wave-exposed environments of the GBR. Recent technological innovations have identified other potential protective measures such as shading and cooling. For example, reducing thermal stress by marine cloud brightening could provide low to moderate ecological benefits (Latham et al., 2013; Stjern et al., 2018), particularly if logistical details and scalability are resolved. Other protective actions are based on behavioural change, by regulation or voluntary uptake (e.g. stewardship and stakeholder engagement), for example the reduction of anchor damage associated with recreational and commercial boating activities in tabular coral habitats. At present, such protective measures are focused on high-use areas rather than specific habitats. A proactive approach to reduce anchor damage in preferred tabular *Acropora* habitats, guided by new GBR habitat maps (Roelfsema et al., 2018) and using available management tools with a coordinated education and stewardship campaign (such as that deployed in the Southern GBR; Beeden et al., 2014), could significantly increase protection effectiveness.

Restorative actions are mainly focused on promoting reef recovery (Ceccarelli et al., 2018) such as improving physical conditions for recruitment (e.g. rubble consolidation). At present, these actions would have relatively low to medium ecological benefit due to limitations of large-scale implementation. Recent advances in large-scale techniques to increase coral recruitment (e.g. artificially enhancing larval supply – Dela Cruz & Harrison, 2017) could deliver medium levels of ecological benefit (Table 1). Although this approach has proven to be effective in other corals species, albeit at a small scale, perfecting these techniques for tabular *Acropora* would be a logical next step towards resilience-based management.

Regardless of the effectiveness of protective and restorative measures, corals will still be vulnerable to the ongoing impacts of climate change, such as coral bleaching, increasing storm intensity and OA. Novel interventions (e.g. holobiont enhancement through assisted evolution) are emerging that focus on limiting the effect of stressors on corals and some could potentially be implemented at ecologically relevant scales (Chan et al., 2018; McLeod et al., 2019; Richards, 2018; van Oppen et al., 2018). Adaptation actions could provide low to medium ecological benefits depending on the scale of the implementation and the level of enhancement achieved (Table 1). Among these interventions, using assisted evolution to artificially enhance coral's capacity to tolerate further ocean warming shows promise for reducing reef degradation (van Oppen et al., 2018). Species of tabular *Acropora* should be among the first targeted for assisted evolution to maximise

TABLE 1 Example management actions that may help protect tabular *Acropora* in the GBR

Management type	Example measures	Target	Type of benefits to tabular corals	Anticipated ecological benefit at present	Anticipated ecological benefit after further research and development
Protect	Prioritise crown-of-thorns starfish culling in preferred tabular coral habitat and in areas that are crucial for the dispersion of larvae by tabular *Acropora*	Colony habitat population	Maintaining population state by reducing predation, increasing population recovery rate	Medium	Medium to high depending on spatial scale
	Marine cloud brightening in areas identified as essential for the protection or recovery of tabular corals	Habitat population	Maintain population state or increase recovery rate by reducing intensity of disturbance (extreme temperature)	Not ready for implementation	Low to medium depending on scale of implementation Limited empirical information on feasibility
	Reduce Marine Park user anchor damage (e.g. through reef protection markers, no anchoring areas, moorings, maps and education) in tabular coral habitats	Colony habitat	Maintaining population state by reducing colony mortality	Low due to current limitations for broad implementation	Medium. Level of benefit could increase when GIS layers of preferred habitat for tabular corals are available
Restore	Target tabular corals in programs focusing on active larval re-seeding of corals	Population	Increasing recovery rate by enhancing larval supply	Low only tested at very small spatial scales	Medium. Recent innovations suggest potential for increased benefit in the near future
	Rubble consolidation to promote recovery after disturbances	Habitat	Increasing recovery rate by facilitating recruitment	Minimal	Low to medium due to logistical limitations in implementation Could increase benefit in the future with new innovations
Adapt	Target tabular corals in programs using innovative actions aimed at enhancing coral holobiont tolerance to multiple stressors	Colony population	Maintaining population state by reducing sensitivity to disturbances	Not ready for implementation	Low to medium depending on level of enhancement and scale of implementation Recent innovations suggest potential for increased benefit in the future
	Include tabular *Acropora*'s key life traits (fast growth rate, high recruitment ability and large maximum colony size) as key targets in assisted evolution approaches	Colony population	Maintaining population state by reducing sensitivity to disturbances	Not ready for implementation	Low to medium depending on level of enhancement and scale of implementation Recent innovations suggest potential for increased benefit in the future

ecosystem benefit (Voolstra et al., 2015). Furthermore, the traits identified in this study that are important for the provision of fast recovery (i.e. high growth rate and large maximum diameter) should be explored along with tolerance to disturbance traits in the targets of assisted evolution programs.

7.3 | Special management status of tabular corals as a catalyst for effective resilience-based management

As the anticipated ecological benefits from individual management actions were generally low to medium and given that some of the actions considered are still in the development phase, a package of measures may be needed for tabular *Acropora*. This will help to ensure tabular corals are not subject to unsustainable pressures and their abundance is maintained or enhanced to support reef recovery. Species (or ecosystem) protection by legislation under one or more jurisdictions (Miller et al., 2007; Rodriguez et al., 2015) represents an additional action, which would confer special status at regional to international levels to protect and promote the recovery and enhancement of designated tabular coral species (Aeby et al., 2008). Whether such actions would galvanise effort to improve the efficacy of management actions is not yet clear but would warrant exploration. As has been the case in the Caribbean, regulatory protection could also serve to influence research priorities to advance understanding of tabular corals (e.g. taxa-specific 'omics' approaches – Voolstra et al., 2015). Furthermore, stakeholder engagement, community support and participation in resilience-based actions could be enhanced by targeted communications and stewardship campaigns about the critical role that tabular *Acropora* play in the resilience of coral reef ecosystems.

It is important to note, however, that providing any taxa with special management status has additional consequences including the need for continual monitoring and reporting, as well as the actual cost of providing protection. Consequently, a cost–benefit analysis and other regulatory evaluations would need to be performed before adoption.

8 | THE RISK OF SELECTING LOW-DIVERSITY, TABULAR-DOMINATED REEFS AND POTENTIAL ASSOCIATED LOSS OF OTHER ECOSYSTEM FUNCTIONS

If special attention is given to tabular *Acropora*, there might be a perceived risk that actively increasing the relative abundance of this group could potentially lead to a reduction of overall coral diversity. This perceived risk arises because many GBR reef areas that are highly dominated by tabular corals have lower coral diversity in comparison to areas where tabular *Acropora* is less dominant (Done, 1982; Johns et al., 2014). However, the following factors suggest that the risk of reducing GBR diversity by protecting tabular corals is low.

8.1 | Natural distribution of tabular *Acropora*

In general, tabular corals only dominate reef areas where the natural wave exposure is favourable for them (Madin et al., 2006; Roelfsema et al., 2018; Shimokawa et al., 2014). In the absence of a large, recent disturbance, tabular corals often dominate the flanks of mid-shelf and offshore reefs of the GBR with intermediate wave exposure (Done, 1982; Linares et al., 2011; Roelfsema et al., 2018). Furthermore, historical records suggest that tabular corals have been highly abundant in the GBR over geological time (Montaggioni, 2005). However, areas of the reef protected from wave exposure are less commonly dominated by tabular corals (Roelfsema et al., 2018). The most likely explanation for this spatial distribution is that tabular corals require relatively high flow and high-light environments (Shimokawa et al., 2014). Similarly, in areas with extreme wave exposure tabular corals are rare, as they tend to be dislodged by hydrodynamic forces (Madin, 2005; Madin et al., 2006; Madin & Connolly, 2006; Shimokawa et al., 2014; Stafford-Smith & Ormond, 1992). Therefore, even if the management actions to protect tabular corals are successful, it would only lead to ensuring their abundance remains high in the areas that are naturally favourable for them, as opposed to increasing their abundance in habitats where they are less successful.

8.2 | Benefit to other coral types

Whilst the actions considered here are centred on tabular *Acropora*, none are likely to have negative effects on other coral species. In fact, the protection of tabular *Acropora* is likely to have positive effects on other growth forms. As explained earlier, tabular *Acropora* provide many ecosystems services, some of which are crucial for the success of other coral types. In particular, there is some evidence that coral larvae tend to prefer recruiting on dead tabular coral (Yadav et al., 2016). Although recruiting on tabular corals in an area with high dominance of live tabular *Acropora* may lead to a low survivorship due to competition. in transition areas between habitats that are favourable to tabular *Acropora* and habitats that are not, this preferential recruitment on tabular corals can serve as a catalyst for recovery resulting in highly diverse communities. Additionally, the high dominance of tabular corals in their preferred habitat can increase grazing intensity in adjacent non-preferred habitats as it reduces the overall grazeable space (Bozec et al., 2019).

9 | CONCLUDING REMARKS

In this article, we have demonstrated the critical importance of tabular *Acropora* to the function of a widespread coral reef habitat on the GBR. Indeed, approximately, 30% of GBR fore-reef habitat has the requisite wave exposure for tabular *Acropora*. Yet, this functional group does not always form a key part of reef recovery even when the environment is appropriate (Figure 1). The causes of periodic 'failures' of tabular coral recovery are unclear but the high sensitivity of these corals to most stressors implies that considerable scope exists for management to improve reef recovery and ensure that tabular corals lead recovery more often. More detailed studies are needed to explore the specific opportunities that management provides to facilitate recovery in these habitats. Assuming such scope exists, then actions prioritised to manage threats in this habitat should serve to deliver a relatively high 'bang for buck' in terms of facilitating recovery after disturbance. In short, the case to consider the importance of tabular corals as part of a reef-wide resilience strategy seems clear. Further studies are needed to examine the scope for management efficacy and evaluate the cost and benefits of a suite of interventions across multiple coral community types.

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AUTHOR CONTRIBUTIONS

JCO and PJM conceived the study. JCO, RJP, RB and JD conceptualised management section. JCO and NHW ran the analysis. JCO and MdCGC designed and edited the images. All authors contributed to writing and editing the manuscript.

DATA ACCESSIBILITY STATEMENT

All data will be made accessible from the authors on request.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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