1	Cumulative effects of c	vclones and bleaching	g on coral cover and s	pecies richness at Lizard
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Abstract: Coral reefs are being subjected to an increase in the frequency and intensity of 16 disturbance, such as bleaching and cyclones, and it is important to document the effects of such 17 18 disturbance on reef coral assemblages. Between March 2014 and May 2017, the reefs of Lizard 19 Island in the northern section of the Great Barrier Reef were affected by four consecutive, disturbances: severe tropical cyclones Ita and Nathan in 2014 and 2015, and mass bleaching in 2016 20 21 and 2017. Loss of coral cover following the cyclones was patchy and dependent on the direction of the waves generated. In contrast, loss of cover following bleaching was much more uniform. 22 Overall, coral cover declined five-fold from 36% pre-cyclone Ita to 7% post-bleaching in 2017, 23 while mean species richness dropped from 10 to four species per transect. The spatial scale and 24 magnitude of the loss of coral cover in the region suggests that it will be many years before these 25 26 reefs recover.

28 Key words: community ecology, coral reefs, climate change, disturbance, diversity,

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30 Introduction

Coral reefs are under threat, with the general consensus that these ecosystems are degrading globally (Hughes et al. 2003, Hughes et al. 2018a). Reef-building corals provide the habitat structure that allows associated coral reef fauna to thrive. Therefore, declines in coral cover lead to loss of fish abundance and species richness (e.g. Jones et al. 2004, Graham et al. 2006). In the context of global change, the intensity and frequency of climate-associated disturbances on coral reefs are increasing (Bender et al. 2010). To predict the fate of coral reefs, we need to document and understand the effects of different types of disturbance on reef coral abundance and diversity.

38 In the Indo-Pacific region, coral cover has declined on average by 0.7% per year since the 39 late 1960s (Bruno & Selig 2007). Coral cover change is not monotonic: typically, declines are episodic and driven by disturbance events such as crown-of-thorn starfish outbreaks, cyclones and, 40 41 more recently, mass bleaching events. Disturbance-led declines are typically interspersed with 42 periods when, under the right conditions, coral cover increases (Gilmour et al. 2013). Coral reefs are naturally mosaics of communities at different successional stages of recovery from a myriad of 43 44 disturbances. However, rapid sequences of intense disturbances can result in phase-shifts in coral ecosystems (Hughes 1994, Hughes & Connell 1999) from which recovery is much less likely. Some 45 reefs can recover from large losses of cover, with the abundance of herbivores, topographic 46 complexity, and depth being important predictors of the probability of recovery (Graham et al. 47 2015). 48

Sections of the northern Great Barrier Reef (GBR) centred around Lizard Island were
recently affected by a sequence of extreme disturbances—the first disturbances on record to affect
these reefs in 20 years (Wakeford et al. 2008, Pratchett 2010, Death et al. 2012). In April 2014,
Severe Tropical Cyclone (STC) Ita (Category 4) crossed the island from the north. In March 2015,

STC Nathan (Category 4) affected the island through waves generated from the south. The largest 53 mass bleaching event on record affected the island in April 2016, with estimates of bleaching and 54 loss of coral cover in the area of between 50-100% (Hughes et al. 2017), and close to 90% for 55 56 Lizard Island (Hughes et al. 2018b). We documented a subsequent bleaching event in early 2017. 57 This sequence of disturbance has drastically changed the assemblage structure of reefs around the island when compared to data from 2011 and the mid-1990s. Here, we quantified the cumulative 58 59 effects of the two cyclones and two bleaching events on the cover, richness and composition of 60 coral assemblages at 19 sites around Lizard Island.

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62 Materials and methods

We used line intercept transects (Lova 1972) to estimate coral cover and species diversity at two to 63 19 sites around Lizard Island, in the northern Great Barrier Reef (14.6688° S, 145.4594° E) in 1995. 64 1996, 1997, 2011, 2014, 2015, 2016 and 2017 (see map in Fig. 3). North Reef and South Island 65 were surveyed in 1995; Lizard Head and Washing Machine were added in 1996; North Reef, Lizard 66 Head, Trimodal, Lagoon 1 and 2 and Horseshoe reef sites were sampled on every sampling 67 occasion since 2011, the remaining 13 sites were sampled since 2015. At each site, five or six 10m 68 transects were haphazardly deployed parallel to the reef margin at 1 to 2 m depth and no less than 69 70 10m apart. All colonies with a maximum diameter greater than 5 cm were identified to genus 71 between 1995 and 1997 and to species between 2011 and 2017 following Veron (1986). We did not transform cover or richness data, and used Welch's t-tests for unequal variances for reporting 72 73 comparisons with an alpha of 0.05. Analyses were run using the function "t.test" in the statistical 74 software R (R Core Team 2018).

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76 Results and Discussion

Coral cover, taxonomic richness and assemblage structure at the start of surveys in 2011, and prior
to the sequence of severe disturbances, were very similar to those in the historical surveys in the

79 1990s (Figs. 1 and 2). The series of disturbances corresponded with in a five-fold loss of coral cover between 2011 and 2017 at the six sites that were surveyed consistently during this time (from 36% 80 to 7% average cover; Fig. 1). At the island scale, the decline in cover was particularly high 81 82 following cyclone Nathan in 2015, after which cover approximately halved, followed by the 2016 bleaching, after which cover halved again. However, the spatial pattern of loss varied among the 83 different disturbances (Fig. 3). Following cyclones, coral loss was greatest at sites facing the 84 direction from which the cyclone approached. For example, following STC Ita, cover declined 85 86 proportionally by 85% at North Reef (t=5.33, df=7.47, p<0.001), whereas there was no statistically significant change in cover at sites on the south side of the island (e.g., Trimodal, Lagoon 1 and 2, 87 88 Lizard Head and Horseshoe). Similarly, south-facing sites suffered major declines following cyclone Nathan. Coral cover declined proportionally by 90% and 66% at Trimodal and Lagoon 2, 89 respectively (t=9.7, df=8.57, p<0.001; t=2.98, df=6.62, p=0.02), whereas there was no further 90 91 change in cover at North Reef (t=0.40, df=2.82, p=0.72). In contrast, loss of cover following 92 bleaching was more uniform across the six main sites following both bleaching events, with all sites with greater than 10% cover remaining showing significant declines in cover. Nonetheless, coral 93 94 cover at some of the 19 sites surveyed since 2014 has remained relatively constant or even increased, particularly Resort, Cooks Path and Turtle Beach (Fig. 3), which were dominated by taxa 95 such as *Montipora* and *Porites* that are less susceptible to bleaching. Overall, these patterns are 96 97 consistent with previous research suggesting that cyclone-driven declines in cover are patchy and mediated by exposure to prevailing winds (Connell et al. 2004, Wakeford et al. 2008, Fabricius et 98 99 al. 2008), whereas bleaching-driven declines tend to be more uniform and contingent on the 100 structure of the coral assemblage at the time of bleaching (Marshall & Baird 2000, McClanahan et al. 2005). 101

The cumulative results of these four major disturbances are drastically altered coral
assemblages. Loss of cover was accompanied by declines in genus and species richness (Fig. 4).
The total number of species across the six consistently surveyed sites decreased from 76 in 2011 to

49 in 2017. Furthermore, only 28 of the species recorded in 2011 were recorded again in 2017.

Many of the additional 21 species recorded in 2017 were likely hidden within the living structure of the reef, such as underneath tabular-*Acropora* spp. colonies (Baird & Hughes 2000). Therefore, the loss of species richness is likely to be more extensive than the observed net difference before and after the disturbances (i.e., 76 vs. 28 species). The spatial patterns across sites for average species richness per transect (and genus richness, which could be included for 1995-97) were consistent with the patterns of change in cover, but far less pronounced (Fig. 1 and 3).

112 In the historical surveys, and prior to STC Ita, most reefs around Lizard Island were dominated by Acropora spp. (Fig. 2). For instance, on Trimodal Reef in 2005 there were 43 113 114 Acropora spp, including the third and fourth most abundant species at the site (Dornelas & Connolly 2008). Only one of these species, A. hvacinthus, occurred on the transects in 2017 and 115 was represented by only a few, very small colonies. Acropora cover declined by over 95% (Fig. 2. 116 117 dark blue), more than any other genus. Currently, the dominant benthic taxa at Lizard Island are soft corals and members of the hard coral genus Porites, and family Faviidae. Here, Porites, 118 Pocillopora, Faviidae and Stylophora were the only common taxa that lost less than half their cover 119 across the sequence of disturbances (Fig. 2). 120

The two cyclones and two bleaching events have changed Lizard Island coral assemblages 121 profoundly. The high mortalities resulting from these events have reduced coral cover to below 4% 122 at ten out of the 19 sites. Only two sites have cover above 40% in 2017, which was the norm for 123 Lizard Island's reefs prior to these disturbances (Fig. 1; Wakeford et al. 2008, Pratchett et al. 2010). 124 Moreover, the species most affected were those that created much of the structural complexity of 125 these reefs. The current most common taxa have much simpler morphologies (e.g., massive Porites 126 and Faviidae) and account for very little coral over on the reef of Lizard Island. These changes are 127 128 likely to have severe knock-on effects on the abundance and diversity of fishes that rely on structural complexity for habitat (Pratchett et al. 2006, Wilson et al. 2006). 129

130	Whether the reefs around Lizard will recover from this degraded state remains to be seen.			
131	Estimates of recovery time following major disturbances range from 5-20 years (Done et al. 2010,			
132	Johns et al. 2014). While the effects of the cyclones were dramatic, the spatially clustered nature of			
133	their effects mean that multiple source populations remained in the region to potentially supply			
134	recruits for recovery. However, the cumulative effects of the cyclones and mass bleaching means			
135	that far fewer reproductively active adults remain in the region. In fact, recruitment rates in the area			
136	have dropped by two orders of magnitude following the mass bleaching (Woods et al. in prep) and			
137	are likely to increase the expected recovery period. In contrast, the abundance of juveniles (i.e.,			
138	colonies < 5 cm maximum diameter) has been much more stable, and the juveniles of most taxa			
139	were less affected by bleaching than the adults (Alvarez-Noriega et al. 2018) offering some promise			
140	of a recovery, but only if the region does not experience another severe disturbance event in the			
141	next decade.			
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237	Figure captions			
238	Figure 1. Change in average (A) coral cover, (B) genus richness and (C) species richness per			
239	transect (±SE) for the six consistently surveyed reefs at Lizard Island. Black arrows: tropical			
240	cyclones; red arrows: bleaching events.			
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242	Figure 2. Compositional change in cover of the ten most dominant taxa: nine coral genera and a			
243	single category for soft corals. Arrows correspond with tropical cyclones (black) and bleaching			
244	events (red). Soft coral was not surveyed in the 1990s. Due to low densities, Seriatopora was not			
245	recorded in some years. Sample sizes reported refer to number of sites surveyed (see Methods for			
246	details of within-site replication).			
247				
248	Figure 3. Change in coral cover (grey bars \pm SE) and per transect species richness (white bars \pm SE)			
249	across the 19 Lizard Island sites (6 surveyed since 2011, 13 since 2015). Grey shading land and			
250	light grey shading is coral reef.			
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252	Figure 4. Temporal trajectories of changes in coral cover and species richness per transect for the			
253	six consistently surveyed sites. Grey background points show data for all sites and years.			
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