Received: 19 April 2023 | Revised: 28 September 2023 | Accepted: 6 October 2023

DOI: 10.1111/ele.14332

ECOLOGY LETTERS cnrs WILEY

LETTER

Natural recovery of corals after severe disturbance

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Funding information
Australian Museum Lizard Island Research Station; Australian Research Council, Grant/Award Number: FL190100062; Ian Potter Foundation; International Coral Reef Society

Editor: Adrian Stier

Abstract

Ecosystem recovery from human-induced disturbances, whether through natural processes or restoration, is occurring worldwide. Yet, recovery dynamics, and their implications for broader ecosystem management, remain unclear. We explored recovery dynamics using coral reefs as a case study. We tracked the fate of 809 individual coral recruits that settled after a severe bleaching event at Lizard Island, Great Barrier Reef. Recruited *Acropora* corals, first detected in 2020, grew to coral cover levels that were equivalent to global average coral cover within just 2 years. Furthermore, we found that just 11.5 *Acropora* recruits per square meter were sufficient to reach this cover within 2 years. However, wave exposure, growth form and colony density had a marked effect on recovery rates. Our results underscore the importance of considering natural recovery in management and restoration and highlight how lessons learnt from reef recovery can inform our understanding of recovery dynamics in high-diversity climate-disturbed ecosystems.

KEYWORDS
Acropora, coral cover recovery, coral growth, coral recruitment, demography: Coral bleaching, Great Barrier Reef

INTRODUCTION

Human-induced ecosystem stressors, such as climate change, are intensifying and reconfiguring ecosystems globally (Arrigo et al., 2020; Betts et al., 2017; Pecl et al., 2017). These stressors have affected almost all ecosystems, including those in terrestrial (Field et al., 2007; Mason et al., 2022), freshwater (O'Reilly et al., 2003) and marine realms (Hoegh-Guldberg & Bruno, 2010), via their impacts on plant, faunal and microbial biodiversity and abundance, across all trophic levels (van Moorsel et al., 2023). In turn, these stressors are compromising the capacity of ecosystems to sustain functions and services and to resist future global changes (Dakos et al., 2015). However, ecosystems are inherently self-regulating systems that have developed mechanisms for self-repair (Holling, 1973; Jones & Schmitz, 2009). After a disturbance, or upon the removal of human-induced pressures, natural processes often bring the system back to a near-equilibrium state, if given enough time (Arnoldi et al., 2018; O'Neill, 1998). However, as the temporal (shortening) and spatial (growing) scales of climate change-induced stress changes rapidly, the capacity of ecosystems to recover is becoming increasingly limited (Trisos et al., 2020; Vercelloni et al., 2020). Therefore, a better understanding of ecosystem recovery processes in the context of climate change is increasingly important for implementing relevant management strategies to enhance natural recovery and establishing priorities for ecosystem restoration efforts (Clewell & McDonald, 2009; Jones et al., 2018; Montoya, 2021).

Of all the world's ecosystems being impacted by climate change, coral reefs provide one of the most iconic examples (Graham et al., 2015; Hughes, Barnes, et al., 2017; Sully et al., 2019). Indeed, bleaching-induced coral mortality has resulted in widespread concerns, with changes in coral reef structure, biodiversity, functioning and productivity (Graham et al., 2015; Hughes et al., 2019; Morais et al., 2022). In turn, this rapidly unfolding situation has raised questions about our approach to ecosystem management on coral reefs (Bruno et al., 2019; Hughes, Barnes, et al., 2017; Morrison et al., 2020). Traditionally, interventions aimed at mitigating climate impacts on coral reefs have focused on reducing chronic pressures, to preserve ecosystem resilience and to enhance coral survival (Graham et al., 2013; Harvey et al., 2018; Mcleod et al., 2019). However, given the recent shortening of recovery periods (Sully et al., 2019; Vercelloni et al., 2020), active management interventions such as coral restoration have grown in popularity among politicians and coral reef managers (Anthony et al., 2017; McLeod et al., 2022; Quigley et al., 2022).

Coral reef restoration is increasingly viewed as a promising tool to enhance coral reef resilience (McLeod et al., 2022). However, coral restoration can be expensive (Hughes et al., 2023), with the median cost per hectare for coral gardening estimated to be over 60 times higher than intertidal mangrove restoration and over 90 times greater than for sea grasses (Bayraktarov et al., 2016). Interestingly, in the last 2 years since the last major coral mortality event, some regions of the Great Barrier Reef are showing signs of extensive, natural recovery of coral cover, driven primarily by *Acropora* spp. (AIMS report 2022). This increase in coral cover is likely driven by two processes: (a) growth of remnant (surviving) colonies and/or (b) coral recruitment with subsequent survival and growth (Graham et al., 2011; Linares et al., 2011; Pearson, 1981).

Coral colony growth can drive rapid increases in coral cover (Diaz-Pulido et al., 2009; Kayal et al., 2018), yet this process depends on colony survival. Unfortunately, survivors are often scarce following coral bleaching mass-mortality events (Gilmour et al., 2013; Hughes et al., 2019; Morais et al., 2021). In these cases, recruitment, survival and growth of new corals are the main processes underpinning coral cover recovery (Edmunds, 2023; Evans et al., 2020; Gilmour et al., 2013; Gouezo et al., 2019). In Moorea, for example, multiple studies have shown that fast coral cover recovery after disturbances largely depends on the successful growth and survival of new recruits, with recruitment in this location being predominantly driven by *Pocillopora* spp. (Bramanti & Edmunds, 2016; Holbrook et al., 2018; Kayal et al., 2018). Similarly, in Palau, dormant recruits from before a typhoon disturbance that killed almost 100% of adult corals have been identified as the drivers of subsequent fast recovery to pre-disturbance coral cover levels (Doropoulos et al., 2022). Thus, the rapid increase in coral cover, from 13% in 2017 to 36% in 2022, in the northern region of the GBR (AIMS report 2022), seems to be at odds with the reported failure of coral recruitment (Hughes et al., 2019) following the regional collapse of coral cover (Hughes, Kerry, et al., 2017). Given this apparent mismatch, the challenge now is to understand the capacity of local reefs to support natural short-term coral recovery following widespread thermal disturbances. Against the backdrop of continued global coral demise, with contemporary global average coral cover sitting at just 25% (Tebbett et al., 2023), it is important to understand, and to quantify, the potential for natural recovery processes in order to inform ecosystem management and to place multimillion dollar restoration projects in context.

In this study, we take advantage of a unique opportunity in a GBR location where there was local extirpation of fast-growing *Acropora* corals after the back-to-back bleaching events in 2016 and 2017 (i.e. a 95% decline in *Acropora* cover at the scale of the whole island (Madin et al., 2018) and 100% mortality of branching and tabular *Acropora* colonies in our study area (Morais et al., 2021)). Following this extirpation, we were able to closely track the natural recovery of the reef system, which appears to have been tightly linked to recruitment in 2018/2019 (Tebbett et al., 2022). Specifically, by using an extensive spatial design of fixed photo-quadrats, we were able to record and track the growth of 809 individual *Acropora* recruits over 2 years across the 16 km^2 wide Lizard Island reef complex on the GBR (Figure 1; Figure S1). Our goal was to evaluate the potential for natural coral recovery driven by fast-growing *Acropora* spp. and to examine how the physical setting (wave exposure), traits (growth form) and colony density affected the growth of recently settled recruits. In quantifying this process our study provides insights into the potential of *Acropora* to increase coral cover after bleaching events.

MATERIALS AND METHODS

Study area and sampling

Tracking of individual coral recruits was based on a widespread photo-quadrat census at Lizard Island (14°40′ S, 145°28′ E), a mid-shelf island in the northern region of the GBR. In recent years this region was impacted by two prolonged thermal events. First from February to April 2016, leading to the most severe coral bleaching recorded on the GBR, and second from January to March 2017, leading to additional bleaching-induced coral mortality (Madin et al., 2018; Richards et al., 2021; Tebbett et al., 2022). In February 2016, immediately before the onset of major bleaching, a series of 19 permanent transects (between 50 and 210 m in length, as constrained by reef morphology) along the reef crest/edge (at 0–4 m below chart-datum) were established around Lizard Island (Figure S1). Along each transect, between 12 and 38 quadrats (1 m^2 area), approximately 5 m apart, were photographed. For the present study, these transects were photographed: in January 2018 (24 months after the 2016 bleaching event); January 2020 (after 48 months), January/February 2021 (after 60 months) and January/February 2022 (after 72 months). Photo-quadrat methods follow (Wismer et al., 2019) (see Text S1 for a full description).

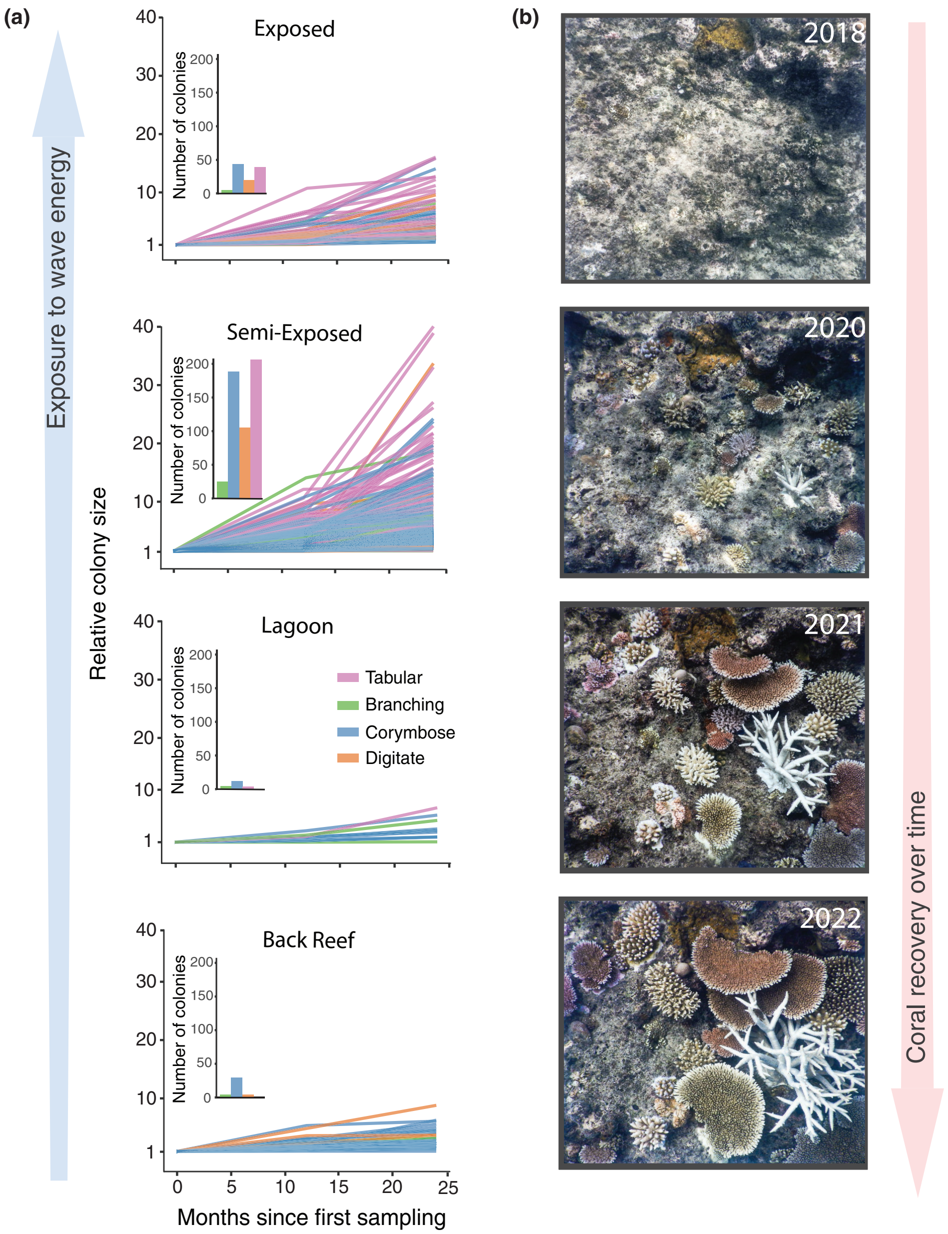

FIGURE 1 (a) Relative colony size of *Acropora* spp. coral recruits across the 24-month sampling period (2020–22). Each line represents a single colony, with colours representing the different growth forms. Relative size (cm^2) is the planar area of each colony relative to the size at first detection. The small bar graph inset in each panel represents the number of colonies from each growth form in each exposure level. (b) Example of a sequence of photo-quadrats from 2018 (before recruits were detected) to 2022 showing the growth of individual colonies and the increase of coral cover over time.

In the photo-quadrats, we considered recruits to be all *Acropora* colonies that were first seen in photographs from the 2020 sampling campaign (i.e. they were not visually detectable in the photographs from the previous sampling in 2018). Recruits were defined as new colonies in our photographs that were larger than 3 cm^2 (~2 cm in diameter). The mean size of *Acropora* recruits at the first detection in our study was ~70 cm^2. The growth form of larger recruits was apparent at first detection; however, when this was unclear, growth form was readily identified in the subsequent photographs of the same recruits in 2021 and 2022 (see Text S2 for full details of coral recruits).

Following the identification of new *Acropora* spp. recruits in the photo-quadrats, we measured the planar surface area of each colony. To do this, planar colony live tissue area was measured (in cm^2) by tracing around the live coral tissue of each colony using the software ImageJ and the quadrat as a scale (Schneider et al., 2012). This process was repeated for each colony in each sampling period. When colonies were partially covered, we estimated their size by tracing the natural shape of the colony based on the previous sampling photograph. Coral cover of each quadrat was considered to be the sum of individual *Acropora* colony areas relative to the 1 m^2 area of the quadrat. However, we classified colonies as 'partially covered' if they had a major part (50% or more) of their area covered by a neighbouring colony. These colonies (6% of all colonies) were excluded from our estimates of coral cover to reduce colony overlap effects. Our comparison of coral cover was solely focused on the cover of the recruits tracked within our sampling area. To contextualise our findings with recruitment levels observed across the Indo-Pacific, we utilised a large-scale dataset available from the supplementary material of Koester et al. (2021). This dataset comprises estimates of coral recruitment (i.e. counts of recently settled coral colonies) on natural reef substrata across 106 reefs in 11 different locations throughout the Indo-Pacific realm.

Data analyses

Initially, we examined the relationship between *Acropora* coral cover change and recruit density to determine the minimum number of recruits needed to reach global average coral cover (i.e. 25%; cf. Tebbett et al., 2023) within 24 months (note all mentions of 'global average coral cover' refer to this level of 25% hereafter). To do this, we utilised a Bayesian generalised linear mixed effects model (GLMM) with a gaussian distribution. In this model the change in *Acropora* cover (i.e. final—initial planar surface area per quadrat) during the 24 month period was treated as the response variable, while recruit density (individuals m^{-2}) was fitted as a continuous fixed effect. Transect identity was also incorporated as a random effect in the model to account for any lack of spatial independence in the data. In addition to this model, we also wanted to examine how a range of factors were related to the growth rates of individual colonies. To do this, we used a second Bayesian GLMM. In this second model, we considered the growth rate of individual *Acropora* colonies as the difference in live tissue area between the first time each colony (recruit) was seen (2020) and subsequent observations (i.e. in 2021 and 2022). Note, data were only derived from recruits first detected in 2020 and all growth data were based on repeated measures of the exact same individual colonies. We then divided this difference by the sampling period (years) to obtain individual coral colony growth rate in $cm^2 year^{-1}$. We then tested if the density of recruits (number of recruits m^{-2}), level of wave exposure (see Figure S1), coral growth form and initial colony size (recruit size when first recorded in our sampling) influenced the subsequent growth rates of coral recruits at Lizard Island. This second GLMM was based on a Gamma distribution with a log-link function. Growth rate of individual coral colonies was the response variable, while recruit density, wave exposure and the interaction between growth form and initial colony size were fitted as fixed effects. We also fitted quadrat identity, nested in transect identity, as a random effect to account for any lack of spatial independence. In both cases, the models were based on three MCMC chains with 5000 iterations, including 1000 iterations to warm-up and a thinning interval of 5, to avoid within-chain auto-correlation, with weakly informative priors. Model fit and assumptions were evaluated using residual and auto-correlation plots, supplemented by metrics of sampling efficiency (rhat) and effective sample size (neff) scores, all of which were satisfactory and suggested that the MCMC chains were well mixed and converged in both models. All Bayesian models were performed in Stan (Stan Development Team, 2021) via the *brms* package (Bürkner, 2017) in the software R (R Core Team, 2020).

RESULTS

By tracking the growth of 809 *Acropora* colonies that settled after severe back-to-back bleaching events in 2016 and 2017, we were able to examine the capacity of these corals to lead ecosystem recovery as they quickly drive coral cover increases (Figure 1). Remarkably, *Acropora* corals have the potential to increase coral cover to levels that reach, or even exceed, the global average coral cover in coral reef habitats (25%) in just 2 years. However, this ability was strongly dependent on the number of recruits that had successfully settled, and survived, on the benthos. In this respect, we observed very low mortality rates. Only 18 of the 809 (2.2%) initial colonies died, while 114 (14.1%) were completely covered by neighbouring colonies. We found a strong positive relationship between recruit density and changes in coral cover over the subsequent 2-year period (Figure 2; Figure S2; Table S1). Based on this relationship, our model suggests that, on average, a density of just 11.5 *Acropora* recruits m^{-2} will yield 25% coral cover after 2 years (Figure 2a; Table S1). However, in areas with recruit densities lower than 11.5 individuals m^{-2} coral cover increase was slow and is likely to remain low (<10%) even after 2 years (Figure 2b).

The recovery of coral cover in areas with high *Acropora* recruitment appears to be strongly location dependent. In our study area, semi-exposed sites not only supported most of the recruits (78%; Figure 1), but also recruits that grew approximately twice as fast as on lagoonal and back reefs and about 30% faster than exposed sites (Figure 3a,b; Table S2). This was mediated by species traits (Figure 3c) since our model detected an interaction between coral growth form and initial colony size (Figure 3c; Table S2). In general, tabular corals had the highest growth rates, followed by branching forms, while digitate forms had the slowest growth rates (Figure 3c; Figure S3). However, only exposed, and semi-exposed sites had *Acropora* recruits from all four growth forms: back reefs lacked tabular forms; lagoonal sites lacked digitate corals. Finally, our model also revealed a location-independent negative effect of recruit density on the growth rate of individual colonies (Figure 3d;

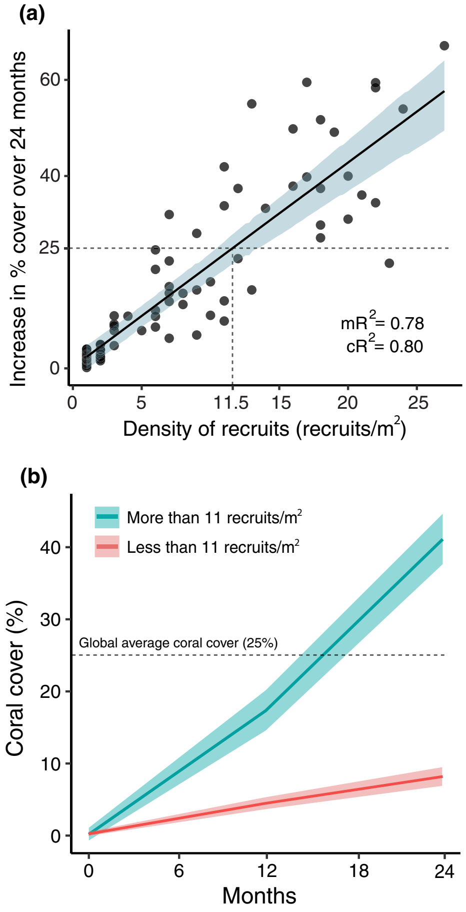

FIGURE 2 (a) The relationship between *Acropora* recruit density (individuals m^{-2}) and the change in *Acropora* coral cover (%) in each quadrat over the 24-month study period. The black line and coloured ribbon denote the mean predicted fit and 95% credibility intervals of a Bayesian GLMM, while the dots show raw data points. The dashed lines represent the global average coral cover of 25% on coral reefs (cf. Tebbett et al., 2023) and the recruit density of 11.5m^{-2} that is the minimum density required, on average, to reach average global coral cover within two years. mR^2=marginal R^2 and cR^2=conditional R^2. (b) Differences in recovery of coral cover between areas with more than 11 recruits m^{-2} and areas with less than 11 recruits m^{-2}. Note that initial cover was subtracted from both lines to ensure they started from the same point, facilitating comparisons between the two.

Table S2). Specifically, within localities with relatively high recruitment, coral colonies grew less, on average, than colonies in less occupied areas (Figure 3d; Table S2).

Throughout our study area, only 7.2% of the 428 quadrats (including those that did not have any coral recruits) had more recruits than the identified threshold for rapid coral cover recovery (i.e. 11 recruits m^{-2}) (Figure 4a). Indeed, average recruit density across all quadrats was just 1.5 recruits m^{-2}. The proportion of quadrats with high recovery capacity herein (>11 recruits m^{-2}) was virtually identical to values in an Indo-Pacific wide dataset of post-bleached reefs (Figure 4b), showing that high post-bleaching coral recruitment is relatively rare. This observation contrasts starkly with recruitment rates in the same Indo-Pacific dataset for pre-bleached reefs, where 27% of transects had at least 11 recruits m^{-2}. The average recruit density for pre-bleached reefs was 9.96 recruits m^{-2}. This represents a more than three-fold decline, from 27% to 7.4%, in the proportion of samples featuring recruitment rates sufficient for rapid short-term coral recovery following bleaching events (Figure 4b).

DISCUSSION

Rapid recovery driven by early-successional species

Globally, disturbed ecosystems show inherent self-repair mechanisms, often with a recovery trajectory driven by early-successional species (Arnoldi et al., 2018; Connell & Slatyer, 1977; O'Neill, 1998). While these abundant species with high growth and colonisation rates typically drive short-term recovery, such early-successional species are generally less prominent over longer-term recovery trajectories (Arnoldi et al., 2018; Connell, 1978; Jentsch & White, 2019). Thus, species-specific traits, combined with location contexts, significantly influence temporal and spatial recovery scales (Hewitt et al., 2022). In the Amazon rainforest, for example, early-successional species play a pivotal role in early recovery due to their fast growth and ability to establish in direct sunlight. Later, 'intermediate' species grow underneath early-successional species and eventually pave the way for 'climax' species in the final recovery stages (Mausel et al., 1993; Uhl et al., 1981). In the context of coral reefs, we quantified and highlighted the capacity of the early-successional *Acropora* to generate coral cover in a high-diversity tropical system (i.e. coral reefs around Lizard Island, Great Barrier Reef), following their local extirpation after back-to-back bleaching events in 2016 and 2017 (Madin et al., 2018; Morais et al., 2021). This marked recovery capacity was clearly dependent on the density of *Acropora* colonies that successfully settled to, and survived on, the benthos. These densities correlated strongly with coral cover in subsequent years. Indeed, we found that, on average, 11.5 recruits per m^2 were sufficient to recover coral cover to levels that are equivalent to the global average for coral reefs, in just 2 years. Importantly, our results from Lizard Island strongly align with those from a recent long-term monitoring report from the Australian Institute of Marine Science (AIMS), which showed that for the entire northern GBR coral cover rapidly rose from a record low level (following the 2016 bleaching event) to its highest level (>75% coral cover on some reefs) since the beginning of the monitoring program (AIMS report 2022). This rapid recovery aligns with past research, which has suggested that recovery in marine benthic systems can outpace recovery rates of other ecosystems (Jones & Schmitz, 2009), although as recovery was heavily driven by one group of corals (*Acropora*) it also has implications for our understanding of ecosystem restoration and recovery debts (e.g. Moreno-Mateos et al., 2017).

The capacity for marine benthic systems to recovery rapidly is underpinned by the demographic processes

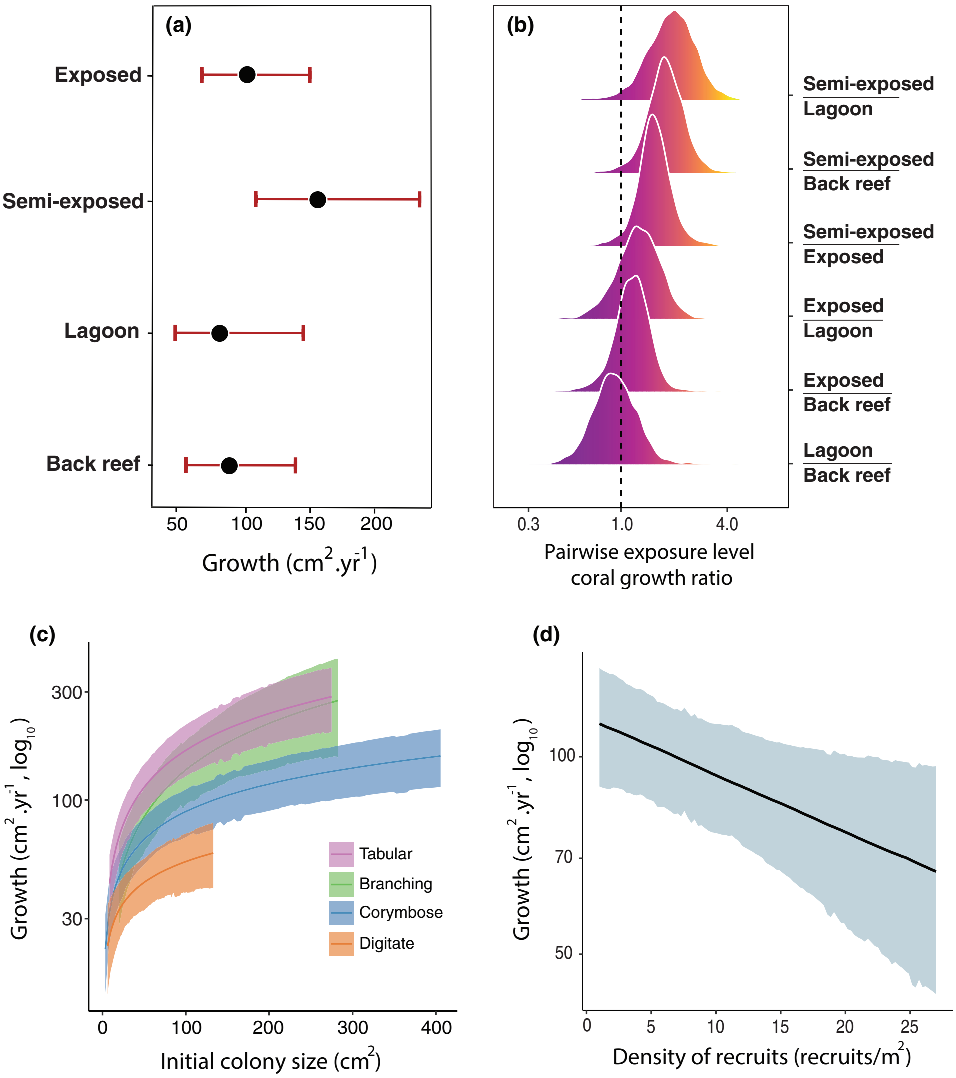

FIGURE 3 Effect plots of the relationship between growth rates of individual *Acropora* colonies and the response variables based on a Bayesian generalised linear mixed effects model: (a) model predicted colony growth rates for the different exposure levels; (b) pairwise comparisons (ratio) of coral growth rates between the different exposure levels. Ratios were obtained using the draw values from our Bayesian generalised linear mixed effects model. Distributions with values predominantly exceeding 1 indicate that the exposure level in the numerator had higher colony growth rates, while distributions with values predominantly lower than 1 indicate that the exposure level in the numerator had lower colony growth rates; (c) the interaction between initial colony size and coral growth form in determining colony growth rate (average initial sizes: branching=91.8 cm^2; corymbose=84 cm^2; digitate=43 cm^2; tabular=64 cm^2); (d) the relationship between colony growth rate and recruit density. The black points in (a), and lines in (c) and (d) represent model estimated marginal means, the red lines in (a) and ribbons in (c) and (d) denote the 95% high posterior density intervals.

regulating the organisms that comprise these ecosystems (Carpenter & Turner, 2000; Thrush & Whitlatch, 2001). In this respect, the capacity for rapid coral cover recovery described in our study aligns with the results of a number of previous studies, which have examined the links between demographic processes (i.e. recruitment, growth and survival) of corals and the rapid recovery of coral cover (e.g. Bramanti & Edmunds, 2016; Edmunds, 2021; Holbrook et al., 2018; Kayal et al., 2018). For example, on reefs around Moorea, Holbrook et al. (2018) highlighted substantial variation in the rate and extent of recovery across different sites following disturbances, with some locations not only regaining their pre-disturbance coral cover but even surpassing it within 5 years. However, it should be noted that in this case, coral cover recovery was driven by *Pocillopora* spp. recruitment (i.e. brooding corals) rather than *Acropora* spp. (i.e. broadcast spawners) (Holbrook et al., 2018). In addition, another study in the same region examining coral demographic rates revealed that rapid recovery of coral cover is not solely dependent on recruitment, but also on the growth and survival of these recruits (Kayal et al., 2018). Such processes also appear to be important in our study system, as mortality rate of the colonies we tracked was very low (just 2.2% of colonies died during the study period). While this apparent coral recovery on the GBR appears to be positive, and contrary to some previous predictions, it raises a number of concerns.

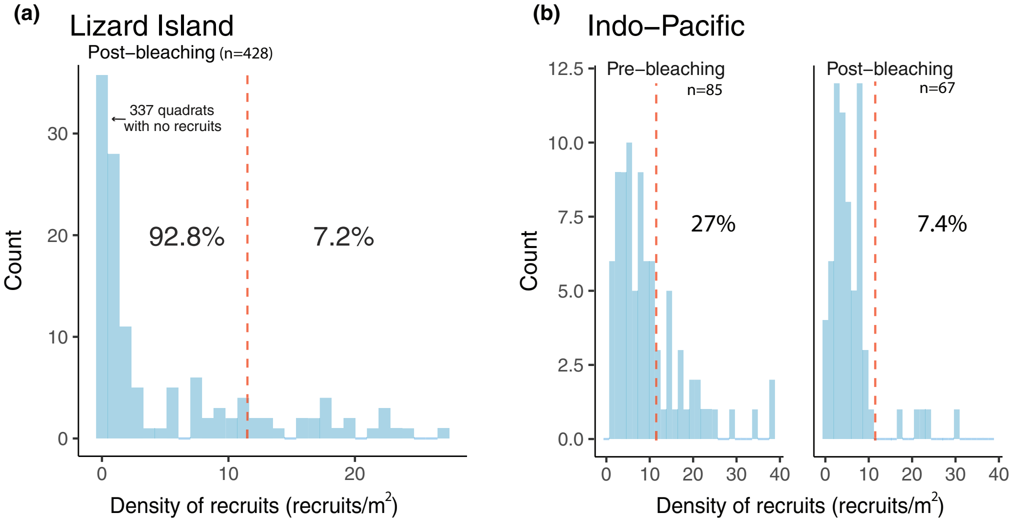

FIGURE 4 Histograms showing frequency distributions of recruit density and the proportion of locations with more than 11 recruits per m^2 (percent values and the red dashed lines). (a) Histogram with data from our study, which includes all quadrats from our sampling area, including those without colonies ($n=428$). Note that to enhance visibility, given the zero-inflated nature of the data, we limited the y-axis. (b) Histograms with data from 106 reefs at 11 Indo-Pacific locations, before and after local bleaching events (locations in which there was no mention of bleaching events were assumed to represent pre-bleaching conditions). For panel (b) we used data compiled in Koester et al. (2021).

One of the primary concerns has to do with the use of 'coral cover' as the metric of interest. This metric, analogous to commonly used forest metrics such as 'canopy cover', is broadly used to quantify coral reef declines (e.g. Bellwood et al., 2004; Gardner et al., 2003), yet it provides limited information concerning key aspects of ecosystem recovery (Connell, 1973; Edmunds & Riegl, 2020; Hughes, 1984) and can mask recovery debts (see below). This information includes recruitment, size structure and community composition, all of which are critical if one wishes to determine the demographic drivers underpinning coral cover changes and, most importantly, their functional implications (Dietzel et al., 2021; Edmunds & Riegl, 2020; González-Barrios et al., 2021; McWilliam et al., 2020). For example, it is well known that most of the early recovery of hard coral cover reported on Indo-Pacific reefs is mainly driven by one group of corals, fast-growing *Acropora* (Emslie et al., 2008; Gilmour et al., 2013; Johns et al., 2014; Roff, 2020; Tanner et al., 1996). Here, we specifically focused on this group of corals to quantify the extent to which this group alone can increase coral cover. In doing so, we revealed that *Acropora* has the capacity to rapidly drive marked increases in coral cover in just 2 years, potentially underpinning the apparent 'recovery' in coral cover on the northern GBR.

Instability and potential for boom-and-bust dynamics

It is important to note that the 'recovery window' between disturbances is expected to shrink in the near future because of the intensification of human-induced impacts (Trisos et al., 2020; Vercelloni et al., 2020). Consequently, only short-term recovery will be possible in the new Anthropocene configuration. Thus, our results, in terms of coral reefs, are key to understanding how these short-term recovery dynamics may play out. Furthermore, it is also critical to place our findings of rapid coral cover recovery in a broader spatial context. Notably, only 7.2% of investigated quadrats in our study, including those with no recruits, had over 11 *Acropora* recruits per m^2 and thus the potential to reach 25% coral cover within 2 years. Indeed, the mean recruit density herein, across all quadrats, was just 1.5 recruits per m^2, meaning it would take at least a decade to achieve the same 25% coral cover. This situation is very similar to data derived from 106 post-bleached reefs at 11 reef locations across the Indo-Pacific (see tab. S5 in Koester et al., 2021), where only 7.4% of surveyed transects had the potential for rapid recovery (i.e. >11 recruits m^{-2}) (Figure 4). Thus, nearly 93% of the impacted sites will take more—and often much more—than 2 years to display the same degree of coral cover recovery after bleaching-induced mortality. A period of time that these coral reefs may not have as the median return time between severe bleaching events is already only 6 years, with this time forecast to become increasingly shorter (Hughes, Anderson, et al., 2018; Vercelloni et al., 2020). Consequently, only a limited number of locations may have the opportunity for effective recovery, and these areas that do undergo recovery are expected to be subject to a cycle of rapid growth followed by disturbance-induced declines (Morais et al., 2021; Pratchett et al., 2020; Wilson et al., 2019). As such, these increases in coral cover may be the beginning of regional-scale boom-and-bust coral dynamics.

Importantly, the potential for boom-and-bust dynamics of *Acropora* colonies is also likely to be embedded in a distinct spatial context that is delineated by environmental variation; the recovery process was not evenly spread across coral growth forms nor exposure. Indeed, as for recruitment rates (cf. Tebbett et al., 2022), there was distinct spatial patchiness in the growth rates of individual colonies across exposure regimes, with the rapid growth of tabular *Acropora* in semi-exposed locations being particularly notable. In this respect, our results support previous studies which suggest that tabular corals have one of the highest coral growth rates (Gold & Palumbi, 2018; Pratchett et al., 2015) and, when combined with their shape and large size, can disproportionately enhance recovery rates of coral cover (Ortiz et al., 2021; Tanner et al., 1996). Hence, reefs dominated by tabular *Acropora* tend to recover rapidly in terms of coral cover (Johns et al., 2014; Linares et al., 2011; Osborne et al., 2011). However, the sensitivity of these corals to heat-induced bleaching means that these reefs also experience some of the most severe declines during marine heatwaves (Burn et al., 2023; Hughes, Kerry, et al., 2018). The spatially patchy boom-and-bust coral dynamics may, therefore, typify Anthropocene reefs, or habitats, that are dominated by tabular *Acropora* (Pratchett et al., 2020).

Restoration initiatives and recovery debt

The findings presented herein, in terms of coral recovery, also have important implications for reef restoration initiatives. Since restoration of reefs is a nascent practice, it is essential to transfer knowledge amassed in terrestrial ecosystems from decades of experience (Quigley et al., 2022). For example, facilitation of natural recovery is widely recognised as a key factor determining the success, or failure, of forest restoration initiatives (Clewell & McDonald, 2009; Higgs et al., 2018; Shono et al., 2007). Thus, careful consideration of the appropriate scales of the interventions, as well as their location, has been identified as crucial for effective restoration efforts on coral reefs (Hughes et al., 2023; Madin et al., 2023; Quigley et al., 2022; Vardi et al., 2021). Indeed, in many cases, a spatial–temporal mismatch exists between the stressors acting on coral reef ecosystems that reduce coral cover (e.g. marine heatwaves, crown of thorns starfish outbreaks, cyclones) and restoration actions (Bellwood et al., 2019). It is often not logistically or economically feasible to restore corals at large scales, although restoration could make a contribution at small scales, especially on high-value reefs (Hughes et al., 2023). In this endeavour, quantitative criteria may be important in determining the suitability of restoration interventions in different areas. This may include factors such as the likelihood of coral colony survival under future climate change conditions (Beyer et al., 2018), target coral density and the growth rates of the selected coral species (Edmunds & Putnam, 2020; Ladd et al., 2018; Madin et al., 2023).

As in forest restoration initiatives (Stanturf et al., 2014), coral restoration often prioritises fast-growing coral species, which may enhance the rapid recovery of coral cover and re-establish some reef functions and structures (Bramanti & Edmunds, 2016; Kayal et al., 2015; Ortiz et al., 2021). In this respect, our results provide invaluable guidance, as they suggest that if densities of just 11–12 *Acropora* recruits are established m^{-2} this can yield 25% coral cover after 2 years. A coral colony target that appears to also represent a good middle-ground when density dependent effects are fully considered (see Text S3 for a full discussion). Nevertheless, any intervention needs to be placed in the context of natural recovery phenomena and the existing cover of corals (Clewell & McDonald, 2009). Indeed, when considering the extent and speed of natural recovery the question may shift from 'how to restore' to 'if to restore', especially as the primary cause of declines (i.e. climate change), has yet to be addressed. In this respect, it is valuable to consider what prioritising fast-growing early-successional species can mean for the recovery debts that ecosystems experience during disturbance.

Species that are rare and exhibit slow growth and low colonisation rates tend to face a greater risk of local or even global extirpation after disturbance due to insufficient time for recovery (Leão et al., 2014; Morais et al., 2021). For example, while marine ecosystems have one of the quickest recovery rates among six major ecosystem categories (i.e. forests, grasslands, wetlands, rivers, lakes and marine), they also incur a substantial recovery debt in terms of reduced biodiversity and functions during the recovery process (Moreno-Mateos et al., 2017). Coral reefs may be at the forefront in facing this issue, with most of the short-term recovery driven by fast-growing early-successional *Acropora* corals, which are also the primary corals replanted in coral restoration (Boström-Einarsson et al., 2020). Meanwhile, species with slower growth and lower colonisation rates are experiencing protracted population declines (Morais et al., 2021; Pratchett et al., 2020) and are rarely prioritised in restoration initiatives (Boström-Einarsson et al., 2020). Therefore, the combined influence of rapid natural recovery in fast-growing species and the enhanced recovery of such species via restoration, may accentuate recovery debts as slower-growing rare species are increasingly overlooked. This could indicate the future trajectory for numerous other ecosystems, aligning with a broad new framework of high turnover recovery dynamics in climate-disturbed systems (e.g. Donohue et al., 2010; Jones & Schmitz, 2009; Wilcox et al., 2020; Yim et al., 2020). Therefore, the fast, yet potentially unstable, recovery reported herein, driven by abundant and fast-growing species, may become progressively more common among climate-disturbed ecosystems, making coral reefs a perfect case study for the understanding of recovery dynamics in high-diversity systems.

CONCLUSION

Overall, our data revealed the marked capacity of *Acropora* corals to recolonise reefs following severe mortality, with reefs regaining high coral cover within a few years. While such a result may offer grounds for optimism, we must be cautious when interpreting reef recovery based solely on coral cover. Furthermore, it is critical to note that *Acropora* are highly vulnerable to disturbances, which may lead to boom-and-bust dynamics; an emerging phenomenon in disturbed ecosystems globally. Coral reefs have remarkable natural recovery potential, drawing a strong parallel with forests that quickly recover canopy cover as a result of fast-growing trees. However, there are concerns pertaining to recovery debts and the logistics of restoration in both systems, especially as restoration projects often focus on species that already exhibit a high potential for natural recovery. Going forward, reef management, like management in terrestrial systems, may need to operate within an increasingly dynamic framework. Rapid recovery on coral reefs may not be a cause for optimism; it may simply reflect high-speed boom-and-bust dynamics.

AUTHOR CONTRIBUTIONS

Juliano Morais, Sterling B. Tebbett, Renato A. Morais and David R. Bellwood conceived the ideas and designed methodology; Juliano Morais and Sterling B. Tebbett collected the data; Juliano Morais, Sterling B. Tebbett and Renato A. Morais analysed the data; Juliano Morais and David R. Bellwood led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank R.P. Streit, J.A Schlaefer, M. Mihalitsis, C. Bowden, W. Collins, C.R. Hemingson, J. Grimm, P. O'Brien, C.H.R. Goatley and the Lizard Island Research Station staff for field support; and the anonymous reviewers for insightful and constructive comments. We also thank the Australian Research Council (DRB: FL190100062), the Ian Potter Foundation (JM, SBT), the Australian Museum's Lizard Island Research Station (JM, SBT) and the International Coral Reef Society (SBT) for financial support. Open access publishing facilitated by James Cook University, as part of the Wiley—James Cook University agreement via the Council of Australian University Librarians.

FUNDING INFORMATION

Australian Museum Lizard Island Research Station; Australian Research Council, Grant/Award Number: FL190100062; Ian Potter Foundation; International Coral Reef Society

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14332.

DATA AVAILABILITY STATEMENT

The data and scripts that support the findings of this study are openly available in the Zenodo repository at https://doi.org/10.5281/zenodo.8384830.

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SUPPORTING INFORMATION

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

How to cite this article: Morais, J., Tebbett, S.B., Morais, R.A. & Bellwood, D.R. (2024) Natural recovery of corals after severe disturbance. *Ecology Letters*, 27, e14332. Available from: https://doi.org/10.1111/ele.14332