Evaluating the precariousness of coral recovery when coral and macroalgae are alternative basins of attraction

Russell J. Schmitt,1,2* Sally J. Holbrook,1,2 Andrew J. Brooks,1 Thomas C. Adam1

1Coastal Research Center, Marine Science Institute, UC Santa Barbara, Santa Barbara, California
2Department of Ecology, Evolution & Marine Biology, UC Santa Barbara, Santa Barbara, California

Abstract

When coral and macroalgae are alternative attractors, the trajectory of the benthic community following a major disturbance is shaped in part by whether herbivores keep macroalgae suppressed, leaving reef surfaces in a state suitable for coral colonization. Because macroalgae tend to colonize much faster than coral, an important issue is how close ambient herbivory is to the level where control of macroalgae is lost, that is, the precariousness of the coral-invasible state relative to the switch-point to macroalgae. In Moorea, French Polynesia, reefs dominated by the macroalga Turbinaria ornata remained so for multiple population turnovers, whereas reefs where Turbinaria was removed by a simulated pulse disturbance remained free of macroalgae throughout the 5-yr study. A field experiment revealed that macroalgae was unable to proliferate on disturbed reefs until ambient herbivory was reduced by more than 50%. Low precariousness of the coral-invasible state facilitated a gradual transition to a coral community because it allowed sufficient time for coral to repopulate. Accumulation of coral on disturbed reefs was 3.5 times greater than on undisturbed, Turbinaria-dominated reefs. Long-term persistence of the coral-invasible state was facilitated by high abundances of grazing herbivores that prevent the establishment of macroalgae, whereas persistence of the Turbinaria-dominated state reflected the scarcity of browsing herbivores that consume mature macroalgae. By revealing processes that foster bistability of coral and macroalgae states, our work helps explain the rich dynamical behavior exhibited by coral reef communities in Moorea and elsewhere.

Nonlinear dynamics in ecosystems are of great interest because they can result in large, abrupt, and unanticipated shifts in state (Scheffer et al. 2001; Scheffer and Carpenter 2003), which often lead to diminished ecosystem services (Suding and Hobbs 2009). Furthermore, the nature of the nonlinearity influences the reversibility of the state shift (Scheffer and Carpenter 2003; Bestelmeyer et al. 2011; Petraitis 2013), as well as the qualitative response of the system to a major disturbance (Scheffer et al. 2001; Beisner et al. 2003). A dynamically complex situation arises when hysteresis in the relationship between a major driver (e.g., herbivory) and system response (e.g., algal abundance) creates a region of state space where, theoretically, bistability of alternative states is possible (Scheffer et al. 2001; Scheffer and Carpenter 2003; Petraitis 2013). When the system is close to a threshold in a nonlinear driver–response relationship (i.e., high “precariousness”), a small change in the driver can cause an abrupt shift to the alternative state. When hysteresis exists in the relationship, reversibility of the shift is impeded because a much greater relaxation of the driver, well past the original tipping point, is required to restore the system to the original state (Scheffer et al. 2001; Briggs et al. 2018). Additionally, when a system with hysteresis lies within the region of state space where bistability is possible (i.e., when each state is maintained by a different set of feedbacks under the same environmental conditions), a sufficiently large disturbance alone can, in theory, flip the system to an alternative stable state without any change in the driver (Scheffer et al. 2001; Beisner et al. 2003). These dynamical attributes have profound societal consequences, and represent fundamental challenges to conservation, restoration, and resource management (Suding and Hobbs 2009).

Among the ecosystems where state shifts are a major concern are coral reefs (Bellwood et al. 2004; Hughes et al. 2010, 2017), which support vast biodiversity and provide ecosystem services of enormous value. Coral reefs are being degraded by both local and global stressors, resulting in...
worldwide declines in coral and a myriad of other coral-dependent organisms (Holbrook et al. 2008, 2015; Hughes et al. 2010). Loss of coral can be accompanied by a significant increase in macroalgae (Hughes et al. 2007; Ceccarelli et al. 2020), which can occur when herbivores fail to keep algae under control. These coral-to-macroalgae shifts can be highly persistent. In some cases, a chronic change in an underlying driver (e.g., altered herbivory or nutrient loading) is the mechanism that maintains the macroalgae state (Dudgeon et al. 2010; Mumby et al. 2013). However, there is a growing body of evidence that the macroalgae state can represent an alternative basin of attraction to coral under the same environmental conditions. The evidence includes patterns of community trajectories from time series measurements (Bestelmeyer et al. 2011; Mumby et al. 2013), parameterized, mechanistic models (Mumby et al. 2007; Muthukrishnan et al. 2016; Briggs et al. 2018), and field experiments (Steneck et al. 2014; Schmitt et al. 2019). Definitive experimental tests of multiple attractors are rare (Petratis and Dudgeon 2004; Collins et al. 2021; Northrop et al. 2021), although recent field experiments support the idea that a macroalgae state can, on at least some coral reefs, be an alternative attractor (Schmitt et al. 2019).

Coral reefs frequently experience large disturbances from cyclones, mass bleaching events, and outbreaks of coral predators (Graham et al. 2011). When a reef is subjected to a major coral and/or macroalgae-killing disturbance, the benthic community does not immediately transition between coral and macroalgae (Cheal et al. 2010). Rather, the denuded reef surface is first colonized by a thin layer of epilithic turf algae that can be colonized by both coral larvae and spores of macroalgae (Birrell et al. 2005; Cheal et al. 2010; O’Brien and Scheibling 2018). If herbivores do not keep turf algae closely cropped, and by doing so remove early life stages of macroalgae, the benthic community can transition fairly rapidly to one where macroalgae are a major space holder (Cheal et al. 2010; Adam et al. 2011), a state that cannot be readily colonized by coral (Birrell et al. 2005; Kuffner et al. 2006; Bulleri et al. 2018). Because macroalgae on coral reefs have much faster dynamics than corals, herbivores play a crucial role in the resilience of the coral state by maintaining the surface of a disturbed reef in a condition that is suitable for coral replenishment (Cheal et al. 2010; Wakwella et al. 2020).

In addition to herbivory maintaining a coral-invasible benthic state (i.e., closely cropped turf), the return of coral following a landscape-scale disturbance depends on the input rate of coral propagules (Graham et al. 2011; Holbrook et al. 2018; Cowles et al. 2021), together with their subsequent growth and survivorship (Connell et al. 1997; Kayal et al. 2018; Kopecky et al. 2021). Observed return rates to high cover of coral following a sudden, mass mortality event range from under 5 yr (Tomascik et al. 1996; Diaz-Pulido et al. 2009; Holbrook et al. 2018) to one or more decades (Connell et al. 1997; Helford et al. 2004; Van Woesik et al. 2011). This indicates that depending on the input rate of coral and their subsequent growth and survivorship, resilience of the coral state may require herbivores to control macroalgae for many years after a large disturbance. Thus, a critical but poorly resolved issue regarding the resilience of the coral state concerns the precariousness of the transitional, coral-invasible state that initially forms on highly disturbed reef surfaces—that is, how close the ambient level of herbivory on turf algae is to the tipping point to domination of space by macroalgae?

In this study, we explore three related issues that influence the resilience of coral following disturbance. The first involved analysis of a 5-yr-long dataset to explore the persistence of alternative states at our study site, together with a repeat of an earlier field experiment (Schmitt et al. 2019) to determine whether a persistent switch from a macroalgae (Turbinaria-dominated) to a nonmacroalgae state triggered by a disturbance was dependent on either the year of the event or the particular set of patch reefs perturbed. Second, we experimentally quantified the degree to which herbivory on coral-invasible turf algae needed to be reduced below ambient before the system reverted to a macroalgae-dominated state (i.e., the precariousness of the transitional turf state relative to the tipping point to macroalgae). Finally, we explored the pattern of coral replenishment as a function of the benthic community, specifically the rate of coral replenishment to the macroalgae (undisturbed) and nonmacroalgae (disturbed) states and the broad mechanisms that caused them to differ. Our findings provide insight into why the coral-invasible and the macroalgae states were each highly resilient under the same environmental conditions.

**Methods**

**The study location and system**

All field work was conducted at a mid-lagoon location on the north shore of Moorea (5°17.54′S 149°83′W), French Polynesia (Fig. S1a), that we have used for previous resilience field experiments (Schmitt et al. 2019). The site consists of several hundred coral bommies (skeletons of dead or partially dead massive Porites corals) 1 to 3 m² in surface area. These small patch reefs are spaced ~0.5–5 m apart on sand at ~2 m depth within a ~1400 m² area of bottom (Fig. S1b). Dead portions of Porites skeletons are used as substrate by other scleractinian corals, particularly branching corals in the genera Pocillopora and Acropora, encrusting Montipora spp., and other mounding and massive corals in the genus Porites. Macroalgae also can be major space holders on the bommies. The dominant species, Turbinaria ornata (hereafter Turbinaria) is a brown, fucoid alga whose adult stage (Fig. S1c) is morphologically and chemically defended from herbivores, and who produce short-dispersing germings year round (Stewart 2008). It is relatively short-lived; based on the measured longevity of Turbinaria plants at this site and elsewhere on Moorea, there are at least two complete population turnovers each year (Davis 2018; Schmitt et al. 2019). Turbinaria in Moorea can provide an associational
refuge for other taxa of macroalgae that are more vulnerable to herbivory (Bittick et al. 2010; Davis 2018). Although far less common, the two most frequently observed macroalgae species typically found with Turbinaria at the study site were a second fucoxid, Sargassum pacificum, and the red macroalga Amansia rhodantha. Surfaces of the bommies that were not otherwise occupied by living coral or macroalgae primarily were covered by closely cropped turf algae, sometimes along with crustose coralline algae (CCA), that can be colonized by coral or overgrown by macroalgae (Birrell et al. 2005; O’Brien and Scheibling 2018).

Multigenerational persistence of alternative states

We used both analysis of a 5-yr-long dataset and a field experiment to explore multigenerational persistence of alternative states. Temporal trajectories of macroalgal cover were based on 45 focal bommies at our site that we sampled for 5 yr (2015–2020). In 2015, all 45 bommies initially were dominated by Turbinaria and haphazardly assigned to one of two disturbance treatments (Fig. S1b): undisturbed (N = 15) where the replicate bommies were left undisturbed, and disturbed (N = 30) where all macroalgae were removed by divers in July 2015 to simulate a strong cyclone that scours macroalgae from reef surfaces (Schmitt et al. 2019). The surfaces of all disturbed bommies were rapidly colonized by a thin layer of turf algae. Each year during the Austral winter, the same observer quantified on each of the 45 bommies the cover and number of adult Turbinaria as well as the identity and cover of other macroalgae. The initial results revealed that the large disturbance we imposed in 2015 flipped the Turbinaria-dominated community to one where the bommie surface was covered almost entirely by cropped turf algae, and that these alternative benthic states persisted for 3 yr (Schmitt et al. 2019). In July 2018, the 30 replicate bommies in the disturbed treatment were cleared of any small amounts of macroalgae that had recolonized on some of the replicates since the clearing in 2015. We continued to follow these bommies for two additional years (until 2020).

We also conducted a field experiment to explore whether the observed multigenerational persistence of the two states was due to either (1) the year of the disturbance or (2) the particular set of bommies that were disturbed. To test this, in July 2018, 16 new Turbinaria-covered bommies that had not been used previously were selected haphazardly from within the study area (Fig. S1b) and cleared (once) of all macroalgae by the same divers using the same clearing technique as in 2015. The 15 undisturbed bommies selected in 2015 and sampled annually served as the unmanipulated control. Sampling of these 31 bommies ended in August 2020; the 25-month time span was sufficient for multiple (>4) complete turnovers of Turbinaria plants. For this experiment, the densities of Turbinaria were calculated by first estimating the surface area of each bommie, assuming a hemispherical shape with unequal length, width, and height, which enabled us to express Turbinaria as a density (number m$^{-2}$ of surface area).

We tested whether the 16 bommies cleared in July 2018 returned to their original macroalgal state using the analytical framework used by Schmitt et al. (2019). Briefly, for Turbinaria on the 15 undisturbed bommies (i.e., the unmanipulated controls), we estimated the relationship between initial and subsequent densities (number adult plants m$^{-2}$) at two time points: after 1 yr (in July 2019), and again after 2 yr (in August 2020). These relationships for the undisturbed bommies, estimated using a linear model on log transformed data, were then used to predict the expected density of Turbinaria for the 16 disturbed bommies 12 months (July 2019) and 25 months (August 2020) after macroalgae were cleared. The expectation was that a disturbed bommie that had returned to its original Turbinaria state would fall within the 95% prediction intervals of the estimated relationship (derived from the undisturbed bommies); the density of Turbinaria on a disturbed bommie that fell below the lower 95% prediction interval is evidence that the bommie had not returned to the Turbinaria state. We tested whether the number of disturbed bommies that fell below the 95% prediction interval after 25 months differed statistically between the disturbed and undisturbed treatments using a Chi-square contingency test.

Precariousness of the coral-invasible state

We conducted a 2-yr precariousness experiment to estimate how much herbivory had to be reduced before control of macroalgae was lost. To do this, we imposed a graded series of reductions in herbivory on bommies (all initially dominated by Turbinaria) after all macroalgae were removed by divers. The basic design was to create a stepped series of reduced herbivory levels below ambient by using semipermeable exclusion cages that had one of three different hole sizes to alter fishing intensities on the abundance of herbivorous fishes. Bottomless cages were constructed from plastic-coated 2.5 cm wire mesh that enclosed a natural, 625 cm$^2$ area of the cleared bommie surface (cage dimensions: 25 cm $\times$ 25 cm $\times$ 18 cm tall). We created 4 herbivory treatments by cutting progressively larger holes (apertures) in the mesh for 3 treatments (aperture hole sizes: 2.5 $\times$ 2.5 cm; 5 $\times$ 5 cm; 7.5 $\times$ 7.5 cm) and by creating an (uncaged) ambient herbivory treatment by demarking the corners of a 25 cm $\times$ 25 cm square (Fig. S2a). There were 10 replicates of each of the 4 herbivory treatments. We also established a cage control treatment (N = 5) consisting of two sides and a half top constructed with 2.5 cm mesh (Fig. S2b); cage artifacts were not detected when the accumulated biomass in the cage control and unmanipulated treatments were compared after 2 yr (Student’s t-test assuming unequal variances; t = 0.83, p = 0.45). A single cage was bolted to each of the focal bommies immediately after their
surfaces were cleared of macroalgae in July 2018. The four herbi-
vory treatments were intermingled across the study site; one rep-
licate of each herbivory treatment was assigned hapha-
ardly to a cluster of four neighboring bommies. Periodic inspec-
tion revealed that herbivory kept the cages relatively
unfouled, typically promoting the growth of a thin layer of
CCA on the mesh (Fig. S2b). Only macroalgae that had
attached to the bommie surface within the 625 cm$^2$ area
enclosed by a cage were included in analyses.

Previous tests of the effectiveness of these semipermeable
cages (Holbrook et al. 2016) using data from underwater video
showed that they created a graded series of herbivorous fish
visitation rates (number h$^{-1}$) and bite rates (number h$^{-1}$) by
the five most common herbivores at our study site (Table S1),
which comprised > 95% of total herbivore abundance. As a
consequence, there was a monotonic decline in the biomass
weighted herbivory index (gm fish min h$^{-1}$) (Holbrook
et al. 2016). Here, we conducted herbivory assays soon after
cages were installed to quantify ambient levels of grazing of
turf algae and browsing of macroalgae at the study site, as well
as the degree to which each cage treatment reduced these two
components of herbivory. Grazing assays used 7.5 × 7.5 cm
pieces of reef substrate covered by highly palatable species of
turf algae (e.g., Polysiphonia spp.), cut from gardens cultivated
by Dusky Farmerfish (Stegastes nigricans). One such piece was
affixed flat on the bottom within all 40 caged and uncaged
replicates. The percent of turf that was consumed on each
deployed piece was estimated after 48 h by the same observer;
two trials of the grazing assay were done several days apart
at the end of July 2018, with the two estimates averaged for a
given replicate. Separate browsing assays, also done twice sev-
eral days after in late July 2018, were done by affixing a
10 cm long × 2 cm wide piece of the palatable brown
macroalga, S. pacificum, within each of the 40 caged and
uncaged replicates. The length of the Sargassum piece was
measured after 48 h and used to estimate the percent con-
sumed (see Davis 2018), again with the two estimates averaged
for each replicate. Two-way permutational ANOVA, done
using the R package lmPerm (Wheeler and Torchiano 2016),
tested for differences among cage treatments and algae type
(turf vs. Sargassum), as well as an interaction between the two
factors, on the consumption rate of algae.

The precariousness experiment was terminated after
25 months (August 2020) at which time all macroalgae were
scraped and bagged by divers from the 625 cm$^2$ area within
each cage, cage control, and uncaged replicate. In the lab, the
macroalgae from each replicate were sorted by species and
damp weighed. At the same time in August 2020, macroalgae
in a 625 cm$^2$ area within a natural, undisturbed patch domi-
nated by Turbinaria were collected by divers from 12 hapha-
ardly chosen, previously unused bommies that were
interspersed among the bommies in the precariousness exper-
iment. These samples also were sorted by species and damp
weighed in the lab to provide the baseline for evaluation of
how each herbivory treatment altered the biomass of natural
patches of macroalgae that developed on macroalgae-free sur-
faces after 25 months. The comparison of interest is whether at
the end of the experiment (August 2020), a particular herbivory
experiment resulted in a biomass of macroalgae that was statisti-
cally different from that in undisturbed, natural patches of mac-
roalgae. Thus, the biomass density of macroalgae (g 625 cm$^{-2}$)
after 25 months in each of the four herbivory treatments was
compared separately to the biomass density (g 625 cm$^{-2}$) in the
naturally occurring patches of macroalgae using a t-test with a
Holm–Bonferroni correction for multiple comparisons.

To assess precariousness of the coral-invisible turf state, we
scaled the mean proportion of turf algae consumed in the
grazing assay for each treatment against the proportion con-
sumed at ambient herbivory. Our assays revealed that con-
sumption of macroalgae by browsing fishes was essentially
reduced to zero in all herbivory treatments below ambient, so
our index of herbivory was based only on the degree to which
the caged treatments reduced consumption of turf algae by
grazing herbivores (relative to the mean of the uncaged treat-
ment). Two nonlinear models (negative exponential, hyper-
bolic) and a linear model were fit to the data using the nls
function in R 4.0.2 (R Core Team 2020), and Akaike informa-
tion criterion (AIC) scores were then used to compare the
model fits against each other and a null intercept-only model.
The assemblage of herbivorous fishes was characterized by
visual counts by divers. Surveys conducted by the Moorea
Coral Reef Long-Term Ecological Research (MCR LTER) site
provided information on the species composition, body sizes
and abundances of roving herbivores at the study site over the
5 yr (Brooks and Moorea Coral Reef LTER 2021). Briefly,
annual surveys of all mobile taxa of fishes observed are
recorded by divers on four replicate 5 × 50 m permanent tran-
sects that extend from the surface of the reef to the surface of
the water column during the Austral winter at 18 different
sites on the island. The total length (TL) of each fish observed
is estimated to the nearest 0.5 cm. TLs are converted to fork
lengths (FLs) when necessary using the formula FL = aTL + b
where a and b represent published species-specific scaling
parameters. Fish biomass (g) then is calculated using the for-

mula w = aFL$^b$, where FL is the fish FL in cm and a and
b represent published species-specific scaling parameters (Brooks et al. 2019). Additional details concerning sampling
protocols can be viewed at: http://mcr.lternet.edu/data. Here,
we report time series data from two lagoon locations (LTER
1 and LTER 2) that bracket the study site and are
situated ~ 0.75 km to the east and ~ 2 km to the west, respec-
tively, of the study site.

Pattern of coral replenishment to disturbed and
undisturbed bommies

At each sampling date, the same diver quantified the coral
colonies on the 45 bommies followed since 2015 (disturbed:
N = 30; undisturbed: N = 15). All living colonies were
counted, identified to genus, sized (diameter), and classified as to whether they were within a macroalgae patch or not during each annual survey. No coral was observed in the midst of or under the canopy of macroalgae on these 45 bommies over the 5 yr. Because colonies could not be marked and followed individually, we considered an observed living coral to be a new recruit in a survey if it was small (≤ 4 cm diameter) and/or could not be accounted for in the survey of that bommie in the previous year. In the initial survey, live branching coral was rare (mean: 0.36 colonies m$^{-2}$), especially colonies ≤ 4 cm (mean 0.23 colonies m$^{-2}$), so the vast majority of corals observed between 2015 and 2020 recruited over that 5-yr period. To account for the fact that bommies differed in surface area, we analyzed the density of coral recruits (number m$^{-2}$). We tested whether cumulative coral recruitment differed among the two disturbance treatments with an ANOVA using log-transformed (log(x + 1)) data to improve distributional properties. To test whether the total density of living recruits at the end of the experiment differed between the two treatments, we used a generalized linear model (GLM) with a Tweedie distribution, a flexible distribution capable of fitting zero-inflated data (see Stears et al. 2020) using the “tweedie” package in R (Dunn 2017). Prior to analysis, we used maximum likelihood to estimate the variance power function for the distribution.

In addition to testing for differences in recruitment of coral among treatments, we were also interested in whether differences in coral recruitment could be explained by space preemption alone, or whether Turbinaria suppressed recruitment beyond what would be expected if space preemption was the sole mechanism (i.e., a neighborhood effect). Thus, we also tested whether coral recruitment per available substrate differed among the two disturbance treatments. To express coral recruitment as a function of suitable settlement space on a bommie, we estimated the surface area that was not covered by macroalgae or other unsuitable microhabitat (e.g., live scleractinian or fire coral). Differences among treatments were evaluated with ANOVA or a GLM as described in the previous paragraph.

Finally, we tested whether there was an association between the time-averaged cover of Turbinaria on a bommie and coral recruitment. Because coral recruitment was highly variable when cover of Turbinaria was low, we used quantile regression on the median and 75th quantile to test for relationships (1) between Turbinaria cover and cumulative coral recruitment and (2) between Turbinaria cover and the density of living recruits at the end of the experiment. Quantile regression was conducted using the quantreg package in R (Koenker 2020).

**Results**

Multigenerational persistence of alternative states

Data from the 45 focal bommies revealed that both a macroalgae state and a disturbance-induced turf algae state persisted over the 5 yr (Fig. 1; Fig. S3), a period that represents ≥ 10 complete turnovers of Turbinaria plants. Prior to manipulation, bommies in the undisturbed and disturbed treatments had similar cover of Turbinaria (means: 44.7% and 43.3%, respectively). Following the initial Turbinaria removal in 2015, macroalgae on the disturbed bommies remained at very low levels (≤ 2%) for the next 3 yr (Fig. 1; Fig. S4). Following the second disturbance to the same 30 bommies in July 2018, macroalgae again generally failed to recolonize, with the cover remaining reduced by > 95% compared to the macroalgae cover in the undisturbed treatment in 2020 (Fig. 1; Fig. S4).

In contrast with the disturbed treatment, macroalgae remained a major space holder on undisturbed bommies throughout the 5-yr period (Fig. 1; Fig. S4), although there was a decline in their cover during that time. By 2020, focal bommies in the undisturbed (macroalgae) state were characterized by an average Turbinaria cover of 30%, while the disturbed bommies had a mean cover of ~ 1%. Averaged over the 5-yr period, 95% of the surface of bommies in the non-macroalgae state (disturbed treatment) and 60% in the macroalgae state (undisturbed treatment) were covered by closely cropped turf algae with or without CCA (Fig. S5).

Disturbance to the previously unmanipulated set of 16 Turbinaria-dominated bommies in 2018 (Fig. S1) resulted in a transition to the closely cropped turf state that persisted until the experiment ended in 2020, a period sufficient for ≥ 4 complete turnovers of Turbinaria plants. None of these 16 disturbed
replicates returned to the original *Turbinaria* state by 2020 (Fig. 2). By contrast, 14 of the 15 bommies in the undisturbed treatment remained dominated by *Turbinaria* (Fig. 2). Thus, the disturbed bommies were significantly less likely to be dominated by *Turbinaria* after 2 yr compared to the undisturbed bommies (Chi-square = 23.6, *p* < 0.0001).

### Precariousness of the coral-invasible state

Under ambient conditions at the lagoon study site, herbivorous fishes that graze turf algae removed on average > 90% (median: 95%) of unprotected turf algae during 48-h assays (Fig. 3). By contrast, species of fish that browse on macroalgae consumed an average of 23% (median: 13%) of a similar, unprotected amount of the palatable brown alga *S. pacifica* in 48-h assays on the same bommies (Fig. 3). This disparity between ambient grazing and browsing rates (*p* < 0.001; Table S2) mirrors the great and temporally consistent differences in abundance and biomass between these two functional groups of herbivores around our study location (Fig. 4; Table 1; Table S1). Throughout the study, the group of herbivores that can suppress the establishment of macroalgae (i.e., “grazers” defined broadly to also include scrapers and excavators) was far more speciose and constituted the vast majority of herbivore abundance and biomass relative to the group of browsers that consume mature macroalgae (Fig. 4; Table 1; Table S1).

The three cage treatments of the precariousness experiment created a graded series of reduced grazing on surfaces of bommies that had been cleared of macroalgae (Fig. 3). The 48-h in situ herbivory assays revealed that the treatments sequentially stepped down the grazing rate to 56% (7.5 cm cage aperture, 9% (5 cm), and 1% (2.5 cm) of ambient. By contrast, there was very little consumption of *Sargassum* in any cage treatment (Fig. 3), which resulted in a significant interaction between algae type and cage treatment (PERMANOVA: *p* < 0.001; Table S2).

After 2 yr, virtually no macroalgae were present in the open control (ambient herbivory) treatment of the precariousness experiment (Fig. 5; Fig. S2). AIC scores of models fit to the data provided strong support that the relationship between biomass of macroalgae and grazing intensity was nonlinear; the two nonlinear models, the hyperbolic and negative exponential functions, both strongly outperformed a linear model (Fig. S6, Table S3). The biomass (mean ± SE: 276 ± 50 g 625 cm$^{-2}$) of macroalgae that accumulated in the lowest herbivory treatment was statistically indistinguishable from the macroalgae biomass (235 ± 20 g 625 cm$^{-2}$) on nearby, undisturbed bommies that were naturally dominated by *Turbinaria* (t-test: *t* = 0.77; *p* = 0.46). By contrast, the biomass of macroalgae that accumulated at all higher levels of grazing was significantly less than on undisturbed *Turbinaria* bommies (*p* < 0.01 after Holm–Bonferroni correction for multiple comparisons). The cage treatment that reduced grazing to 56% of ambient resulted in a standing biomass of macroalgae that was just 7% of that in natural patches of macroalgae (Fig. 5). Similarly, the biomass of macroalgae in the cage treatment that reduced grazing to 9% of ambient was < 40% of that in natural patches (Fig. 5).

### Pattern of coral replenishment to disturbed and undisturbed bommies

Overall, the rate of recruitment of branching corals (pocilloporids, acroporids) was low over the 5 yr following the experimentally imposed disturbance to macroalgae in 2015.
For the 30 focal bommies in the 2015-initiated disturbed (nonmacroalgal) treatment, the mean cumulative density of known branching coral recruits was 3.4 per m² of bommie surface. While low, this density of coral recruits to disturbed bommies was ~ 2.5 times greater than that in the undisturbed (macroalgae-dominated) treatment (mean: 1.35 per m²) (ANOVA on log transformed data: \(F_{1,43} = 13.9; p < 0.001\)). In addition, the percent of branching coral recruits that were still alive in 2020 was ~ 50% greater on the disturbed, non-macroalgae bommies compared to those where Turbinaria remained a major space holder. In the disturbed treatment, an average of 66% of observed coral recruits were alive in 2020 compared with just 45% on undisturbed bommies. As a result, the density of branching coral recruits that were alive in 2020 was ~ 3.5 times greater on the bommies in the original disturbed treatment (mean: 2.2 per m²) relative to those in the undisturbed treatment (0.6 per m²) (GLM: \(p < 0.0001\)).

Both the cumulative density of branching coral recruits and the density still alive in 2020 were inversely related to the time-averaged cover of Turbinaria plants on a bommie (Fig. 6). Specifically, the median density of cumulative coral recruits and the median density still alive at the end of the experiment were strongly negatively correlated with the cover of Turbinaria (quantile regression: \(p < 0.05\) for both comparisons).
addition, recruit densities greater than 3 per m$^2$ were only observed on bommies with very little or no *Turbinaria* (Fig. 6). Thus, the upper 75$^{th}$ quantiles of coral recruit density and living recruits also were strongly negatively correlated with the cover of *Turbinaria* (quantile regression: $p < 0.05$ for both comparisons). The relationships indicate that cover of *Turbinaria* as low as 10% is associated with suppression of coral recruitment as well as an increase in subsequent mortality of branching corals.

Our findings indicate that at least two mechanisms underlie the much faster colonization rate of branching corals to disturbed relative to undisturbed bommies. The first is pre-emption of space by macroalgae; no coral recruit was found within a patch of macroalgae over the 5 yr on any of the

---

**Table 1.** Time-averaged absolute and relative abundance and biomass of herbivorous fishes in two functional groups: Grazers that suppress the establishment of macroalgae, and browsers that consume mature macroalgae. Data are from annual estimates made between 2015 and 2019 from permanent transects at two locations that bracketed the experimental site; the cumulative number of species observed in each functional group is in parentheses. Table S1 gives the time-averaged abundance and biomass for each observed species, as well as their foraging mode.

| Herbivore functional group | Mean abundance | Mean biomass |
|----------------------------|----------------|-------------|
|                            | No. 100 m$^2$  | Percent total | g 100 m$^2$ | Percent total |
| Grazers (20 species)       | 97.7           | 99.8        | 4759.5      | 99.6          |
| Browsers (2 species)       | 0.2            | 0.2         | 16.8        | 0.4           |
| Total herbivores           | 97.9           | 100.0       | 4776.3      | 100.0         |

---

**Fig. 5.** Results of the precariousness experiment showing the biomass (mean $\pm$ SE) of macroalgae that accumulated on a bommie 2 yr after the disturbance plotted against relative grazing intensity (estimated from turf algae assays) from the caging experiment (closed circles, $N = 10$ per level of grazing intensity). The open circle is the biomass (mean $\pm$ SE) of macroalgae from natural *Turbinaria*-dominated bommies ($N = 12$). Biomass is expressed as damp weight (g 625 cm$^2$). Some error bars are hidden within a symbol.

**Fig. 6.** Patterns of coral replenishment to the 45 focal bommies sampled annually between 2015 and 2020 as a function of disturbance treatment. Data are (a) cumulative recruitment of branching corals (no. m$^{-2}$) and (b) branching corals alive in 2020 (no. m$^{-2}$) plotted against the time-averaged percent cover of *Turbinaria* between July 2015 and August 2020. White filled circles are the experimentally disturbed bommies ($N = 30$) and closed circles are the undisturbed bommies ($N = 15$).
45 bommies in the undisturbed or the disturbed treatments. Hence a much higher percent of the surface of a bommie was suitable for coral recruitment in the disturbed treatment (~95% suitable) compared to the undisturbed treatment (~60% suitable). Adjusting coral recruitment as a function of suitable settlement space on a bommie revealed that the cumulative recruitment of branching coral was still 1.5 times greater in the disturbed treatment (mean ± SE: 3.5 ± 0.8 per m² of suitable settlement area) than in the undisturbed treatment (2.2 ± 0.6 per m² of suitable area), a difference that was statistically significant ($F_{1,43} = 4.0, p = 0.05$). This is evidence of a second mechanism, a neighborhood effect of macroalgae that depresses early recruitment of branching corals on nearby surfaces covered by closely cropped turf algae. Furthermore, since all observed branching corals only recruited to bommie surfaces covered by turf algae (Figs. S2 and S5), the significant difference between the disturbed and undisturbed treatments in the recruits still alive in 2020 (GLM with a Tweedie distribution: $p < 0.01$) indicates that macroalgae also have an adverse neighborhood effect on longer-term survival of young branching coral. In 2020, only 34% of known recruits had died on disturbed bommies compared to 55% on undisturbed bommies.

**Discussion**

Our findings add to the mounting experimental evidence that on coral reefs, benthic communities dominated by self-sustaining populations of either macroalgae or coral are possible under the same set of environmental conditions. They also strongly support the theoretical prediction that when multiple attractors exist in an environment, a sufficiently large disturbance alone can flip a system between alternative stable states (Scheffer et al. 2001; Beisner et al. 2003). Of course, when multiple attractors exist on a coral reef, disturbance-induced mortality of coral or macroalgae does not result in an immediate switch to the alternative basin; rather disturbed reef surfaces first enter a transitional phase (thin epilithic turf algae) to which coral can invade, provided herbivores suppress macroalgae and keep the turf algae cropped (Kuffner et al. 2006; Bonaldo and Bellwood 2011; Goatley and Bellwood 2013; Wakwella et al. 2020). Here, we demonstrate that in our system, highly disturbed patch reefs previously dominated by macroalgae were not easily repopulated by macroalgae even when ambient herbivory was reduced by well more than half. The low precariousness of the invisible turf algae state is critically important because it allows sufficient time for coral colonization under levels of herbivory that might vary temporally, especially when the replenishment of coral is slow. The replenishment rate of coral to our experimentally disturbed patch reefs was ~3.5 times greater than to undisturbed reefs where macroalgae were a major space holder. The long-term persistence of the coral-invisible state on bommies likely reflected the great abundance of grazing herbivores that can prevent the establishment of macroalgae, while the long-term stability of the macroalgae state reflected the rarity of browsing herbivores that feed on mature macroalgae. By revealing processes that can foster bistability of coral and macroalgae-dominated states, our experiments and time series data help explain the rich dynamical behavior exhibited by coral reef benthic communities in Moorea and elsewhere.

Hysteresis in driver–response relationships creates the potential for bistability of alternative community states (Petraitis 2013), which has been demonstrated for the herbivory–macroalgae relationship at our study site (Schmitt et al. 2019). Our results here support the idea that macroalgae and coral may commonly be alternative attractors whenever there is a great disparity in the abundance of two general functional groups of herbivores: those that consume turf algae (grazers broadly defined) and those that consume mature macroalgae (browsers) (Han et al. 2016; Burkepile et al. 2020). While grazers can impede the establishment of macroalgae by consuming their early life stages, only browsers can reverse that shift by consuming mature plants (Bellwood et al. 2006; Burkepile and Hay 2010; Burkepile et al. 2020). A large number of species graze, scrape, or excavate epilithic and endolithic algae (Han et al. 2016) and thus can keep disturbed reef surfaces suitable for coral recolonization. Turf-consuming herbivores were by far the more specifico and numerically abundant functional group on lagoon reefs of Moorea. By contrast, only two, locally uncommon species of browsing herbivores were observed over the 5 yr of the current study (Table 1). Low species richness of browsing fishes, relative to those that consume turf algae, is a common pattern on coral reefs worldwide (Cheal et al. 2010). In addition, browser biomass appears to be particularly susceptible to fishing on many coral reefs globally (Edwards et al. 2014), a pattern that could be exacerbated in Moorea and elsewhere where local small-scale fisheries disproportionately target species of browsers (Rassweiler et al. 2020). Furthermore, movement patterns of fishers can further weaken resilience of the coral state after a large-scale coral mortality event if fishers avoid macroalgae-dominated areas and focus their fishing effort for herbivores on reefs that support the greatest remaining cover of coral (Rassweiler et al. In press).

In addition to attributes of the herbivore assemblage and dynamic feedbacks on patterns of fishing, certain traits found in some macroalgae likely promote hysteresis in an herbivory–macroalgae relationship. These traits are exemplified by *T. ornata*, the dominant macroalga in our system that is widely distributed throughout the Indo-Pacific (Stewart 2008). It becomes morphologically and chemically defended as it matures, becoming less palatable to herbivores (Stewart 2008; Davis 2018). Models have shown that this common biological feature, stage-structured vulnerability to consumption, promotes alternative stable states in general (Scheffer et al. 2001) and for *Turbinaria*—coral states in particular (Briggs...
et al. 2018). In addition, the dispersal distance of *Turbinaria* germlings typically is very short (<0.2 m), and young recruits gain an associational defense against herbivores when they recruit under the canopy of older, heavily defended plants (Davis 2018). This creates a positive feedback that reinforces a self-sustaining *Turbinaria* population once mature plants have become established (Davis 2018). These feedbacks, coupled with low levels of browsing, imply that *Turbinaria*-dominated patch reefs will tend to remain locked in that state until there is a sufficiently large disturbance that resets the system to the transitional turf algae state, or there is a sufficiently great increase in browsing pressure that is needed to extirpate macroalgae (i.e., the reverse tipping point is crossed).

While herbivory can enhance resilience of corals by maintaining disturbed reef surfaces in a condition suitable for coral recolonization (Burkepile and Hay 2010), the rate of return to a coral state (engineering resilience) depends on the input rate of coral propagules (Leichter et al. 2013; Holbrook et al. 2018; Cowles et al. 2021) and their subsequent growth and mortality rates (Connell et al. 1997; Lenihan et al. 2011; Kopecky et al. 2021). For example, when severe disturbances between 2007 and 2010 killed almost all coral on the fore reef surrounding Moorea, herbivory generally kept macroalgae under control (Adam et al. 2011; Holbrook et al. 2016). The return time for the coral to reach the predisturbance cover on the fore reef varied spatially around the island, mirroring spatial heterogeneity in recruitment of sexually produced colonists (Holbrook et al. 2018; Kayal et al. 2018). While the median time for coral cover to reach pre-disturbance levels was 8 yr, it ranged from <5 yr up to an estimated ~30 yr (Holbrook et al. 2018). This wide variation is similar to coral recovery times following mass mortality events observed elsewhere in the Indo-Pacific (Connell et al. 1997), which also ranged from <5 yr (Tomascik et al. 1996; Diaz-Pulido et al. 2009) to well over a decade (Halford et al. 2004; Van Woesik et al. 2011). Compared to macroalgae, however, coral populations typically have much slower dynamics that reflect characteristic differences in the dynamical properties of these taxa. As a consequence, resilience of a coral state will often hinge on the ability of herbivores to control macroalgae for a comparatively long time after a disturbance. Thus, management actions that focus on reducing the precariousness of the coral-invasive, transitional state are likely to be of universal importance.

While we have a growing understanding of the processes and mechanisms that maintain macroalgae and coral states, in general we have less knowledge of the mechanisms that induce a regime shift to the macroalgal state following a disturbance. Establishing such a trigger is challenging, in part because distinguishing transient dynamics from a persistent shift generally requires a long period of time, and as a consequence, most analyses of triggers of a state shift are retrospective explorations that often can be less definitive (Rassweiler et al. 2010). Herbivore dilution is a possible trigger for proliferation of macroalgae following widespread death of coral (Mumby et al. 2007; Baskett et al. 2014). However, relatively rapid increases in the biomass of key herbivorous fishes that kept macroalgae suppressed have been observed after large disturbances to several coral reef systems (Gilmour et al. 2013; Russ et al. 2021), including Moorea (Adam et al. 2011; Holbrook et al. 2016). One mechanism that could promote escape from herbivore control is a flush of nutrients, which has been observed after a massive disturbance to coral reefs (Delesalle et al. 1993). Similarly, a recent analysis of spatially explicit time series data revealed that shifts from coral to *Turbinaria* on lagoon reefs of Moorea were associated with regions of chronic nutrient enrichment, despite similar increases in the biomass of herbivorous fishes to lagoon regions of lower enrichment that did not undergo a shift to macroalgae (Adam et al. 2020). This suggests that excess nutrients can increase the precariousness of nonmacroalgae states, possibly by fueling a growth rate of macroalgae that can outstrip the capacity of grazing herbivores to respond. In Moorea, nutrient enrichment and fishing pressure on herbivores are inversely correlated in the cross-shore direction, but positively related in the along-shore direction (Holbrook et al. In press); this results in a predictable spatial pattern in the relative vulnerability of the coral state from human alteration of bottom-up and top-down forcing, and provides information valuable to spatially tailor management actions.

A major attribute that influenced the recolonization rate of coral on bommies in our study was the cover of macroalgae, primarily *Turbinaria*. Experimental bommies that remained almost entirely free of macroalgae had much faster coral colonization rates compared to undisturbed bommies with patches of macroalgae. This is consistent with other studies that found the recruitment of coral in Moorea (Mumby et al. 2016; Bulleri et al. 2018) and elsewhere (Johns et al. 2018; Evensen et al. 2019) was sensitive to the presence of macroalgae. Our data support two mechanisms by which macroalgae inhibited the replenishment of coral. The first is preemption of space by macroalgae (Nugues and Szmań 2006). In no case did we observe a new coral recruit within a patch of macroalgae on any bommie, an observation consistent with previous studies that have found macroalgae hinder the ability of coral larvae to reach primary surfaces (Birrell et al. 2008). The second mechanism was a negative neighborhood effect of macroalgae on the replenishment rate of coral (Bulleri et al. 2018; Johns et al. 2018; Evensen et al. 2019). When space already occupied was taken into account, the cumulative density of coral recruits was still much greater on bommies in the disturbed than undisturbed treatments, which indicates that macroalgae reduced successful early recruitment of coral to turf covered surfaces. Our data also suggest that macroalgae reduced longer-term survival of young coral in the neighborhood. In a similar set of in situ manipulations of *Turbinaria* in Moorea, Bulleri et al. (2018) found that *Turbinaria* greatly reduced successful settlement of coral larvae to nearby, macroalgae-free
substrate, and that this neighborhood inhibition was related to how the macroalgae altered the microbial assemblage of the reef surface. Such neighborhood effects are another mechanism that promotes hysteresis in driver–response relationships and strengthens the resilience of an alternative state (Briggs et al. 2018).

Finally, our findings shed light on an issue raised by Hughes et al. (2010) and others regarding how much macroalgae is too much before resilience of a coral state is impaired. Bruno et al. (2009) used the criterion of 50% or greater cover for a benthic assemblage to be considered dominated by macroalgae, which led to the conclusion that state shifts to macroalgae were infrequent on coral reefs throughout their global distribution. However, as pointed out by Hughes et al. (2010), the 50% threshold is exceptionally high relative to historical trends in abundance of either macroalgae or coral, and there is mounting evidence that abundances of macroalgae below this threshold can adversely impact coral dynamics and ecosystem processes. In our Moorea lagoon system, multiple field experiments have now shown that bommies where Turbinaria is a major space holder can represent an alternative basin of attraction. The overall mean cover of Turbinaria on unmanipulated bommies in our study (38%) was roughly the value for degraded reefs in the Caribbean (40%) reported in Hughes et al. (2010). However, there was considerable variation in the cover of Turbinaria (10–60%) among the 15 replicates of our undisturbed control treatment. While our data reveal that recruitment of branching coral generally declined with increasing macroalgae, a cover of Turbinaria as low as 10% still reduced the replenishment rate of coral by almost half (Fig. 6). Such a marked effect of such a relatively low cover of Turbinaria on the engineering resilience of coral is a mechanism that further reinforces macroalgae as an alternative basin of attraction. This emphasizes the urgent need to better identify tipping points to alternative states, assess the precariousness of the system to undesired shifts, and implement management actions that move the system away from regions of state space where bistability may be possible.

References
Adam, T. C., R. J. Schmitt, S. J. Holbrook, A. J. Brooks, P. J. Edmunds, R. C. Carpenter, and G. Bernardi. 2011. Herbivory, connectivity and ecosystem resilience: Response of a coral reef to a large-scale perturbation. PLoS One 6: e23717.
Adam, T. C., and others. 2020. Landscape-scale patterns of nutrient enrichment in a coral reef ecosystem: Implications for coral to algae phase shifts. Ecol. Appl. 31: e02227.
Baskett, M. L., N. S. Fabina, and K. Gross. 2014. Response diversity can increase ecological resilience to disturbance in coral reefs. Am. Nat. 184: E16–E31.
Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Front. Ecol. Environ. 1: 376–382.
Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. Nature 429: 827–833.
Bellwood, D. R., T. P. Hughes, and A. S. Hoey. 2006. Sleeping functional group drives coral-reef recovery. Curr. Biol. 16: 2434–2439.
Bestelmeyer, B. T., and others. 2011. Analysis of abrupt transitions in ecological systems. Ecosphere 2: 129. doi:10.1890/ES11-00216.1
Birrell, C. L., L. J. McCook, and B. L. Willis. 2005. Effects of algal turfs and sediment on coral settlement. Mar. Pollut. Bull. 51: 408–414.
Birrell, C. L., L. J. McCook, B. L. Willis, and G. A. Díaz-Pulido. 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Oceanogr. Mar. Biol. Ann. Rev. 46: 25–63.
Bittick, S. J., N. D. Bilotti, H. A. Peterson, and H. L. Stewart. 2010. Turbinaria ornata as an herbivory refuge for associate algae. Mar. Biol. 157: 317–323.
Bonaldo, R. M., and D. R. Bellwood. 2011. Spatial variation in the effects of grazing on epilithic algal turfs on the Great Barrier Reef, Australia. Coral Reefs 30: 381–390.
Briggs, C. J., T. C. Adam, S. J. Holbrook, and R. J. Schmitt. 2018. Macroalgae size refuge from herbivory promotes alternative stable states on coral reefs. PLoS One 13: e0202273.
Brooks, A., T. Adam, and Moorea Coral Reef LTER. 2019. MCR LTER: Reference: Fish taxonomy, trophic groups and morphometry. knb-lter-mcr.6001.6 doi:10.6073/pasta/f6feebdb7e4f3865ce4cd233a744b83
Brooks, A., and Moorea Coral Reef LTER. 2021. MCR LTER: Coral reef: Long-term population and community dynamics: Fishes, ongoing since 2005. knb-lter-mcr.6.58 doi:10.6073/pasta/a667eed481d9743e69c4209f6479ac4
Bruno, J. F., H. Sweatman, W. F. Precht, E. R. Selig, and V. G. W. Schütte. 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90: 1478–1484.
Bulleri, F., L. Thiault, S. C. Mills, M. M. Nugues, E. M. Eckert, G. Corno, and J. Claudet. 2018. Erect macroalgae influence epilithic bacterial assemblages and reduce coral recruitment. Mar. Ecol. Prog. Ser. 597: 65–77.
Burkepile, D. E., and M. E. Hay. 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. PLoS One 5: e8963.
Burkepile, D. E., M. H. Schmitt, K. Stears, M. K. Donovan, and D. I. Thompson. 2020. Shared insights across the ecology of coral reefs and African savannas: Are parrotfish wet wildebeest? Bioscience 70: 647–658.
Ceccarelli, D. M., R. D. Evans, M. Logan, P. Mantel, M. Puotinen, C. Petus, G. R. Russ, and D. H. Williamson. 2020. Long-term dynamics and drivers of coral and macroalgal cover on inshore reefs of the Great Barrier Reef Marine Park. Ecol. Appl. 30: e02008.
Cheat, A. J., M. A. MacNeil, E. Cripps, M. J. Emslie, M. Jonker, B. Schaffelke, and H. Sweatman. 2010. Coral–macroalgal phase shifts or reef resilience: Links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. Coral Reefs 29: 1005–1015.

Collins, S. L., J. B. Nippert, J. M. Blair, J. M. Briggs, P. Blackmore, and Z. Ratajczak. 2021. Fire frequency, state change and hysteresis in tallgrass prairie. Ecol. Lett. 24: 636–647. doi:10.1111/ele.13676

Connell, J. H., T. P. Hughes, and C. C. Wallace. 1997. A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol. Monogr. 67: 461–488.

Cowles, J., and others. 2021. Resilience: Insights from the U.S. Long Term Ecological Research Network. Ecosphere 12: e03434. doi:10.1002/ecs2.3434

Davis, S. L. 2018. Associational refuge facilitates phase shifts to macroalgae in a coral reef ecosystem. Ecosphere 9: e02272. doi:10.1002/ecs2.2272

Delesalle, B., M. Pichon, M. Frankignoulle, and J.-P. Gattuso. 1993. Effects of a cyclone on coral reef phytoplankton biomass, primary production and composition (Moorea Island, French Polynesia). J. Plankton Res. 15: 1413–1423.

Diaz-Pulido, G., and others. 2009. Doom and boom on a resilient reef: Climate change, algal overgrowth and coral recovery. PLoS One 4: e5239.

Dudgeon, S. R., R. B. Aronson, J. F. Bruno, and W. F. Precht. 2010. Phase shifts and stable states on coral reefs. Mar. Ecol. Prog. Ser. 413: 201–216.

Dunn, P. K. 2017. Tweedie: Evaluation of Tweedie exponential family models. R package version 2.3.

Edwards, C. B., and others. 2014. Global assessment of the status of coral reef herbivorous fishes: Evidence for fishing effects. Proc. R. Soc. B 281: 20131835.

Evensen, N. R., C. Doropoulos, K. M. Morrow, C. A. Motti, and P. J. Mumby. 2019. Inhibition of coral settlement at multiple spatial scales by a pervasive algal competitor. Mar. Ecol. Progr. Ser. 612: 29–42.

Gilmour, J. P., L. D. Smith, A. J. Heyward, A. H. Baird, and M. S. Pratchett. 2013. Recovery of an isolated coral reef system following severe disturbance. Science 340: 69–71.

Goatley, C. H. R., and D. R. Bellwood. 2013. Ecological consequences of sediment on high-energy coral reefs. PLoS One 8: e77737.

Graham, N. A. J., K. L. Nash, and J. T. Kool. 2011. Coral reef recovery dynamics in a changing world. Coral Reefs 30: 283–294.

Halford, A., A. J. Cheal, D. Ryan, and D. M. B. Williams. 2004. Resilience to large-scale disturbance to coral and fish assemblages on the Great Barrier Reef. Ecology 85: 1892–1905.

Han, X., T. C. Adam, R. J. Schmitt, A. J. Brooks, and S. J. Holbrook. 2016. Response of herbivore functional groups to sequential perturbations in Moorea, French Polynesia. Coral Reefs 35: 999–1009.

Holbrook, S. J., T. C. Adam, P. J. Edmunds, R. J. Schmitt, R. C. Carpenter, A. J. Brooks, H. S. Lenihan, and C. J. Briggs. 2018. Recruitment drives spatial variation in recovery rates of resilient coral reefs. Sci. Rep. 8: 7338.

Holbrook, S. J., R. J. Schmitt, T. C. Adam, and A. J. Brooks. 2016. Coral reef resilience, tipping points and the strength of herbivory. Sci. Rep. 6: 35817.

Holbrook, S. J., R. J. Schmitt, and A. J. Brooks. 2008. Resistance and resilience of a coral reef fish community to changes in coral abundance. Mar. Ecol. Prog. Ser. 371: 263–271.

Holbrook, S. J., R. J. Schmitt, V. Messmer, A. J. Brooks, M. Srinivasan, P. L. Munday, and G. P. Jones. 2015. Reef fishes in biodiversity hotspots are at greatest risk from loss of coral species. PLoS One 10: e0124054.

Holbrook, S. J., and others. In press. Spatial co-variation in nutrient enrichment and fishing of herbivores in an oceanic coral reef ecosystem. Ecol. Appl.

Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. Trends Ecol. Evol. 25: 633–642.

Hughes, T. P., and others. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr. Biol. 17: 360–365.

Hughes, T. P., and others. 2017. Coral reefs in the Anthropocene. Nature 546: 82–90.

Johns, K. A., M. J. Emslie, A. S. Hoey, K. Osborne, M. J. Jonker, and A. J. Cheal. 2018. Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. Ecosphere 9: e02349.

Kayal, M., H. S. Lenihan, A. J. Brooks, S. J. Holbrook, R. J. Schmitt, and B. E. Kendall. 2018. Predicting coral community recovery using multi-species population dynamics models. Ecol. Lett. 21: 1790–1799.

Koenker, R. 2020. quantreg: Quantile regression. R package version 5.67. Available from https://CRAN.R-project.org/package=quantreg

Kopecky, K. L., D. T. Cook, R. J. Schmitt, and A. C. Stier. 2021. Effects of corallivory and coral colony density on coral growth and survival. Coral Reefs 40: 283–288.

Kuffner, I. B., L. J. Walters, M. A. Becerro, V. J. Paul, R. Ritson-Williams, and K. S. Beach. 2006. Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar. Ecol. Prog. Ser. 323: 107–117.

Leichter, J. J., and others. 2013. Biological and physical interactions on a tropical island coral reef: Transport and retention processes on Moorea, French Polynesia. Oceanography 26: 52–63.

Lenihan, H. S., S. J. Holbrook, R. J. Schmitt, and A. J. Brooks. 2011. Influence of corallivory, competition, and habitat structure on coral community shifts. Ecology 92: 1959–1971.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450: 98–101.
Mumby, P. J., R. S. Steneck, M. Adjeroud, and S. N. Arnold. 2016. High resilience masks underlying sensitivity to algal phase shifts of Pacific coral reefs. Oikos 125: 644–655.

Mumby, P. J., R. S. Steneck, and A. Hastings. 2013. Evidence for and against the existence of alternate attractors on coral reefs. Oikos 122: 481–491.

Muthukrishnan, R., J. O. Lloyd-Smith, and P. Fong. 2016. Mechanisms of resilience: Empirically quantified positive feedbacks produce alternative stable state dynamics in a model of a tropical reef. J. Ecol. 104: 1662–1672.

Northrop, A. C., V. Avalone, A. M. Ellison, B. A. Ballif, and N. J. Gotelli. 2021. Clockwise and counterclockwise hysteresis characterize state changes in the same aquatic ecosystem. Ecol. Lett. 24: 94–101.

Nugues, M. M., and A. M. Szmant. 2006. Coral settlement onto Halimeda opuntia: A fatal attraction to an ephemeral substrate? Coral Reefs 25: 585–591.

O’Brien, J. M., and R. E. Scheibling. 2018. Turf wars: Competition between foundation and turf-forming species on temperate and tropical reefs and its role in regime shifts. Mar. Ecol. Prog. Ser. 590: 1–17.

Petraitis, P. 2013. Multiple stable states in natural ecosystems. Oxford Univ. Press, p. 202.

Petraitis, P. S., and S. R. Dudgeon. 2004. Detection of alternative stable states in marine communities. J. Exp. Mar. Biol. Ecol. 300: 343–371.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/

Rassweiler, A., R. J. Schmitt, and S. J. Holbrook. 2010. Triggers and maintenance of multiple shifts in the state of a natural community. Oecologia 164: 489–498.

Rassweiler, A., and others. 2020. Perceptions and responses of Pacific Island Fishers to changing coral reefs. Ambio 49: 130–143.

Rassweiler, A., and others. In press. How do fisher responses to macroalgal overgrowth influence the resilience of coral reefs? Limnol. Oceanogr. 67: S365–S377. doi:10.1002/lo.11921

Russ, G. R., J. R. Rizzari, R. A. Abesamis, and A. C. Alcala. 2021. Coral cover a stronger driver of reef fish trophic biomass than fishing. Ecol. Appl. 31: e02224.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413: 591–596.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. Trends Ecol. Evol. 18: 648–656.

Schmitt et al. Precariousness of coral recovery

Stears, K., M. H. Schmitt, C. C. Wilmers, and A. M. Shrader. 2020. Mixed-species herding levels the landscape of fear. Proc. R. Soc. B 287: 20192555.

Steneck, R. S., S. N. Arnold, and P. J. Mumby. 2014. Experiment mimics fishing on parrotfish: Insights on coral reef recovery and alternative attractors. Mar. Ecol. Prog. Ser. 506: 115–127.

Stewart, H. L. 2008. The role of spatial and ontogenetic morphological variation in the expansion of the geographic range of the tropical brown alga, Turbinaria ornata. Integr. Comp. Biol. 48: 713–719.

Suding, K. N., and R. J. Hobbs. 2009. Threshold models in restoration and conservation: A developing framework. Trends Ecol. Evol. 24: 271–279.

Tomascik, T., R. van Woesik, and A. J. Mah. 1996. Rapid coral colonization of a recent lava flow following a volcanic eruption, Banda Islands, Indonesia. Coral Reefs 15: 169–175.

Van Woesik, R., K. Sakai, A. Ganase, and Y. Loya. 2011. Revisiting the winners and the losers a decade after coral bleaching. Mar. Ecol. Prog. Ser. 434: 67–76.

Wakwella, A., P. J. Mumby, and G. Roff. 2020. Sedimentation and overfishing drive changes in early succession and coral recruitment. Proc. R. Soc. B 287: 20202575.

Wheeler, R., and M. Torchiano. 2016. lmPerm: Permutation tests for linear models. R package version 2.1.0. Available from https://CRAN.R-project.org/package=lmPerm

Acknowledgments

We thank K. Seydel, G. Bernardi, D. Cook, R. Honeycutt, K. Kopecky, J. Gallagher, K. Heimlich, S. Miller, M. Schmitt, and K. Stears for assistance in the field and lab, K. Kopecky and D. Burkepile for comments on the manuscript, and N. Davies, V. Brotherson, T. You Sing, and J. You Sing for logistical support at the University of California Berkeley Gump Research Station. The work was supported by the US National Science Foundation (OCE 1637396, BCS 1714704). This is a contribution of the Moorea Coral Reef (MCR) LTER Site. The study was approved by the University of California Santa Barbara Institutional Animal Care and Use Committee (IACUC, Protocol 918), and all experiments and other methods were performed in accordance with relevant guidelines and regulations. Research was completed under permits issued by the Government of French Polynesia (Délegation à la Recherche) and the Haut-commissariat de la République en Polynésie Française (DTRT) (Protocole d’Accueil for 2015–2020), whom we thank for their continued support.

Conflict of Interest

None declared.

Submitted 12 February 2021
Revised 27 May 2021
Accepted 10 August 2021
Associate editor: David Baker