



Experimental support for alternative attractors on coral reefs

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Edited by James A. Estes, University of California, Santa Cruz, CA, and approved December 21, 2018 (received for review July 18, 2018)

Ecological theory predicts that ecosystems with multiple basins of attraction can get locked in an undesired state, which has profound ecological and management implications. Despite their significance, alternative attractors have proven to be challenging to detect and characterize in natural communities. On coral reefs, it has been hypothesized that persistent coral-to-macroalgae “phase shifts” that can result from overfishing of herbivores and/or nutrient enrichment may reflect a regime shift to an alternate attractor, but, to date, the evidence has been equivocal. Our field experiments in Moorea, French Polynesia, revealed the following: (i) hysteresis existed in the herbivory–macroalgae relationship, creating the potential for coral–macroalgae bistability at some levels of herbivory, and (ii) macroalgae were an alternative attractor under prevailing conditions in the lagoon but not on the fore reef, where ambient herbivory fell outside the experimentally delineated region of hysteresis. These findings help explain the different community responses to disturbances between lagoon and fore reef habitats of Moorea over the past several decades and reinforce the idea that reversing an undesired shift on coral reefs can be difficult. Our experimental framework represents a powerful diagnostic tool to probe for multiple attractors in ecological systems and, as such, can inform management strategies needed to maintain critical ecosystem functions in the face of escalating stresses.

bistability | hysteresis | resilience | coral–algae phase shift | alternative stable states

Ecosystem dynamics can be highly nonlinear due to threshold rather than linear responses to incremental change in environmental drivers (1, 2). Abrupt transitions between ecosystem states have been documented in a number of terrestrial (e.g., grassland to shrubland), aquatic (oligotrophic to eutrophic lakes), and marine (coral to macroalgae) ecosystems. They typically have profound societal consequences, are challenging to forecast, and can be extraordinarily difficult to reverse (1–7). The two qualitatively different ways by which a newly formed alternative community can be maintained have very different implications for reversibility of the transition (5, 8). The less remarkable case is where the new state is maintained solely by a persistent change in the value of the underlying driver. In this situation, the system will return to its original state with small relaxation of the parameter across the threshold (i.e., the nonlinear relationship between state variables and environmental drivers remains unchanged). Of more interest, and concern from a management perspective, is the phenomenon of hysteresis, where, as before, a small change in a parameter produces a sudden shift in state, but a larger reverse change in that same parameter is required to restore the system to its original state (i.e., the relationship between state variables and environmental drivers is not the same before and after the shift). Systems with hysteresis can have multiple basins of attraction because more than one nontransient community state can exist for a given set of parameters. Thus, an alternative community that arises in a system with multiple attractors may not be easily reversed as reinforcing feedbacks can maintain the new regime even under

environmental conditions that existed before the transition (2, 6, 8–10). Furthermore, it is possible for a sufficiently large disturbance to flip a system with hysteresis to an alternative basin of attraction without any change in an underlying driver (2, 8, 9). As a consequence, alternative attractors make conservation and restoration particularly challenging (3–6, 11, 12).

Persistent community transitions in a number of terrestrial and aquatic ecosystems are believed to represent regime shifts between alternative basins of attraction (2, 6, 9, 12–16), although the evidence is equivocal in some cases (9, 11, 15, 17). Coral reefs, which are one of the most biodiverse and productive of all ecosystems, are among those where the evidence for alternative attractors continues to be the subject of debate (2, 5, 11, 13, 16–26). Over the past several decades, many coral reef ecosystems have transitioned, sometimes abruptly, from their historical coral state to another persistent assemblage dominated by noncoral organisms (12, 16, 26, 27), very often macroalgae (22, 28, 29). Coral-to-macroalgae “phase shifts” can alter biotic interactions, disrupt trophic structure, lower biodiversity, and change fisheries production of the reef (30–34). The societal and management implications are substantial if diverse and productive coral reefs become trapped in a less desirable state that is difficult or impractical to reverse (11, 12, 22, 35). Among the reasons why definitive evidence regarding multiple attractors on coral reefs has remained elusive is the scarcity of appropriate experimental

Significance

Ecological theory predicts that under the same environmental conditions, an ecosystem could have more than one community state that is maintained by reinforcing feedbacks. If so, a sufficiently large disturbance can flip the system to a less desired community that is difficult to reverse. Here, we demonstrate that a coral reef can become trapped in a seaweed-dominated state in the same conditions under which corals thrive. The implications are profound, particularly in light of the increasing occurrence of shifts to seaweed on coral reefs worldwide. Our results indicate that anticipatory management strategies that lessen the chance of a switch to seaweeds will be more effective than those aimed at restoring the coral community after a shift.

Author contributions: R.J.S., S.J.H., S.L.D., A.J.B., and T.C.A. designed research; R.J.S., S.J.H., S.L.D., A.J.B., and T.C.A. performed research; T.C.A. analyzed data; and R.J.S., S.J.H., and T.C.A. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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Data deposition: The data reported in this paper have been deposited in the Long Term Ecological Research Network database (<https://doi.org/10.6073/pasta/d9ec6d51af-b375e748298e72268198db>), <https://doi.org/10.6073/pasta/263faa48b520b7b2c964f158-c184ef96>, and <https://doi.org/10.6073/pasta/9041bae6c2a2c2c61eb2d48684f7ac1e>.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1812412116/-DCSupplemental.

Published online February 11, 2019.

explorations, including those that test across a wide range of parameter space of the underlying driver (11).

Field experiments can provide robust tests of alternative attractors in natural systems (8, 9, 15, 36, 37). At least two complementary approaches can be used (9). One is to seek experimental evidence of hysteresis in a driver–response relationship by quantifying whether the response of a system to an imposed gradient in an underlying driver depends on the initial community state (9, 15). If alternative attractors exist in a system, they likely will be restricted to a subset of parameter space (38). Thus, this type of press manipulation can delineate the region of potential bistability should hysteresis exist (9) and reveal where tipping points lie in parameter space relative to ambient conditions (39–42). Experimental manipulations to identify tipping points are uncommon (9) and have often involved highly simplified communities (40, 41, 43; cf. refs. 39, 42). In addition, experimental studies have rarely addressed the reversibility of state shifts by explicitly testing for hysteresis, that is, whether the relationship between state variables and environmental drivers changes from before to after an abrupt state shift (39–42; cf. ref. 43).

A second, more common manipulation to explore for alternative attractors is to test for recovery (resilience) following a disturbance (1, 9, 15, 44). This type of experiment involves the application of a pulse perturbation to a state variable to assess the local stability of the existing community. If alternative attractors exist under ambient conditions, the system theoretically should respond differently to a small-intensity versus large-intensity disturbance. If the predisturbed system was initially above the unstable equilibrium of the hysteresis, the community should tend to return to its predisturbance state after a small perturbation, but it could flip to a new dynamic regime (an alternative basin of attraction) following a disturbance sufficiently large to push the system below the unstable equilibrium (9, 15, 36, 37, 45). While this approach can provide robust support for multiple attractors, it can only test whether they exist under ambient environmental conditions (9).

With respect to coral reefs, the benthic community that develops immediately after a disturbance kills coral typically is composed of a thin layer of turf algae. This is a transient state that is highly invasible by young coral (46–48). However, the initial postdisturbance turf algae state can instead transition to macroalgae if herbivores fail to keep them under control (5, 29, 49, 50), a state that is highly resistant to colonization by coral (48, 51, 52). A key issue is whether, for a given level of herbivory, a self-replicating macroalgae state as well as a turf state invasible by coral can both persist.

We applied a framework that encompassed both types of field experiments described above to probe for multiple attractors in two different coral reef habitats of Moorea, French Polynesia: the fore reef (outer slope) and the back reef of the lagoon (*SI Appendix, Fig. S1*). In Moorea, community responses to coral-killing disturbances have differed substantially between these two habitats. Although macroalgae occur at low densities on the fore reef (39, 53, 54), over the past four decades, this outer slope habitat consistently has returned to high coral cover following multiple large disturbances without macroalgae becoming a dominant space holder (54–57). The largest and most recent of these perturbations occurred in 2007–2010, which drove the initially high cover of coral to near zero on the fore reef (Fig. 1A). Despite this massive mortality (58), the coral community recovered rapidly (Fig. 1A) (54–57), with spatial variation in return rate driven primarily by recruitment of coral (57, 59). These time series data reveal the extraordinary resilience of the coral community on the fore reef and suggest that only one basin of attraction (the coral state) exists under current conditions on this outer slope habitat. By contrast, disturbed patch reefs in the lagoons show divergent community responses, even between

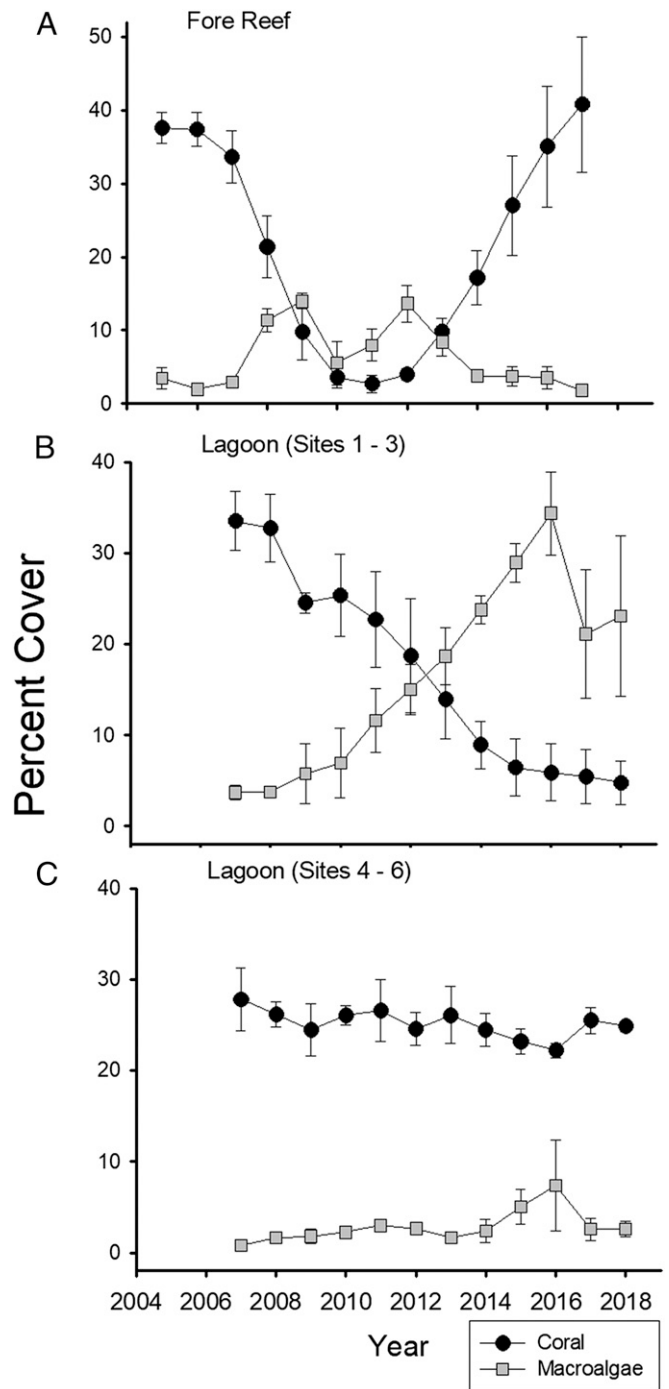


Fig. 1. Temporal trends in the cover of coral (black circles) and macroalgae (gray squares) on the fore reef (A) and lagoon patch reefs (B and C) of Moorea. Data are mean \pm 1 SE. All fore reef sites ($n = 6$) showed similar dynamic patterns through time, whereas lagoon reefs showed two distinct patterns: one where the coral declined and macroalgae increased (B, $n = 3$) and another where coral remained relatively high and constant and macroalgae remained relatively low (C, $n = 3$).

adjacent patch reefs in the same locality at times. Disturbed lagoon reefs can either return to the coral state or transition to a distinctly different, persistent assemblage characterized by low cover of coral and dense stands of macroalgae (Fig. 1B and C), primarily the brown macroalga *Turbinaria ornata* (53, 60–62). This suggests a potential for macroalgae to be an alternative

attractor to the coral state under prevailing conditions in the lagoons of Moorea.

To probe whether the macroalgae state might be an alternative basin of attraction in either the lagoon or fore reef habitat, we first used a hysteresis test that subjected two different initial community states to the same experimental gradient in herbivory that broadly mimicked the effects of variation in fishing intensity (39, 63). Herbivorous fishes are the principal agents that control macroalgae on the reefs of Moorea (50, 54, 61) and most coral reefs elsewhere (26, 27, 29, 49, 64). Based on results of our probe for hysteresis, we then used a resilience approach for lagoon patch reefs that initially were dominated by *Turbinaria* to explore local stability properties of the macroalgae state. We mimicked storms of different strengths to evaluate whether the responses of macroalgae revealed hysteretic dynamics, specifically testing whether the probability that a patch reef returned to its pre-disturbed level of *Turbinaria* was related to the intensity of the disturbance. If the *Turbinaria*-dominated state was maintained by a localized, chronic change in a driver (e.g., herbivory), then disturbed reefs should all have the same tendency to return to high abundance of macroalgae independent of disturbance treatment. By contrast, if the system was above an unstable equilibrium due to hysteresis in the herbivory–macroalgae relationship, reefs subjected to a less intense disturbance should tend to return to dominance by macroalgae, whereas those subjected to high disturbance should have a much greater probability of switching to a persistent macroalgae-free state.

Results

Test for Hysteresis. The hysteresis experiments, which subjected two different initial community states to the same experimental gradient in herbivory (from none to ambient), provided statistical support for the presence of hysteresis in the herbivory–macroalgae relationship for both the fore reef and lagoon sites (Fig. 2 and *SI Appendix*, Fig. S2 and Table S1). In both habitats, the relationship between the herbivory treatment and the biomass of macroalgae present at the end of the experiment depended on whether the initial community state was *Turbinaria* or cropped turf algae (initial state \times herbivory interaction; fore reef: $P = 0.008$, lagoon: $P = 0.016$; *SI Appendix*, Table S1; both interactions were due to divergence among treatments). In both cases, less herbivory was needed to keep macroalgae suppressed than to eradicate plants (thalli) already established.

The fore reef and lagoon differed with respect to how close the two systems were to the region of potential bistability created by the hysteresis. On the fore reef, the bistability region was far below ambient herbivory, apparent only in the second lowest herbivory treatment (Fig. 2A and *SI Appendix*, Fig. S2A). Macroalgae were not able to persist above the lowest two levels of herbivory on the fore reef, regardless of the initial community state (Fig. 2A). By contrast, the prevailing level of herbivory at the lagoon site placed the system near the region of hysteresis (Fig. 2B). When turf was the initial assemblage in the lagoon, virtually no macroalgae were present above the second lowest level of herbivory. However, when *Turbinaria* was the initial state, herbivores were unable to completely eliminate macroalgae in any treatment, even at ambient herbivory. For example, when *Turbinaria* was the initial state, the median herbivory treatment resulted in a biomass of macroalgae that was 30% of the maximum attained in the complete absence of herbivory; macroalgal biomass was still 5–12% of this maximum under the two highest levels of herbivory (Fig. 2B).

Batch-marked cohorts of *Turbinaria* in experimental treatments revealed that the duration of the hysteresis experiments spanned multiple complete turnovers of *Turbinaria* individuals (fore reef: two or more turnovers, lagoon: five or more turnovers; *SI Appendix*, Fig. S3). Further, when *Turbinaria* was the initial state, the mean ($\pm 95\%$ confidence interval) number of

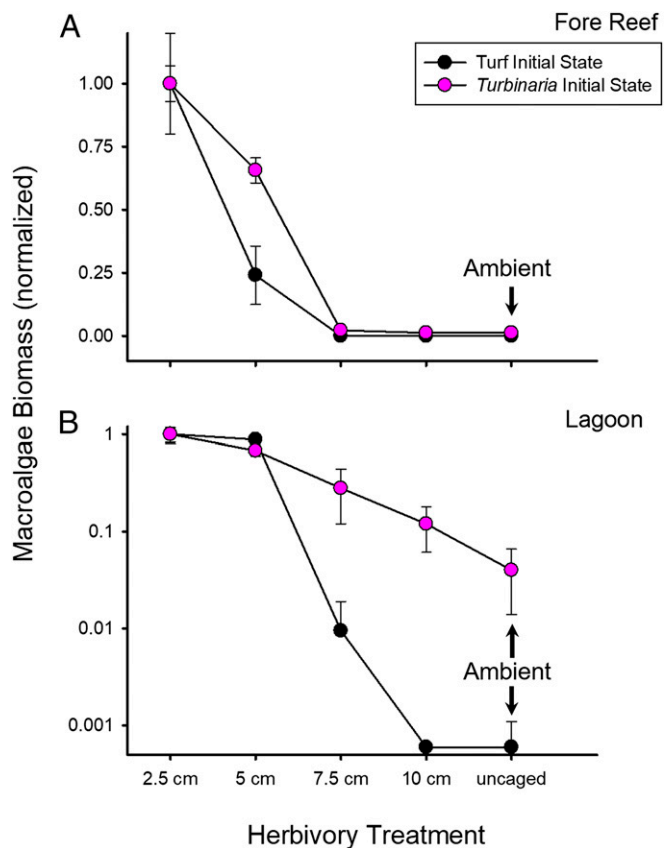


Fig. 2. Results of the hysteresis experiments showing the final biomass of macroalgae across a gradient of reduced herbivory as a function of initial community state (turf, black circles; *Turbinaria*, pink circles) for the fore reef (A) and the lagoon (B). For visualization purposes, data for each initial state were standardized by dividing each replicate by the mean of biomass in the 2.5-cm herbivory treatment (i.e., the highest mean) of that state; plotted are the standardized mean ± 1 SE (fore reef: $n = 5$ for the *Turbinaria* initial state treatment, $n = 10$ for the turf initial treatment; lagoon: $n = 5$ for the *Turbinaria* initial state treatment, $n = 3$ for the turf initial treatment). Plots of nonnormalized data are given in *SI Appendix*, Fig. S2.

adult plants increased by 78.8% (± 46.3) in the lowest two herbivory treatments from the beginning to the end of the experiment. Together, these results indicate that the *Turbinaria* state was self-replenishing in the low herbivory treatments where it was able to persist and that the persistence of macroalgae did not represent a transient state.

Resilience Test. Results of the hysteresis experiments suggest that under ambient conditions, the *Turbinaria* state might be an alternative basin of attraction on lagoon patch reefs but not on the fore reef. This motivated a pulse manipulation of whole patch reefs in the lagoon as a direct test, which revealed compelling evidence for alternate basins of attraction. *Turbinaria*-dominated patch reefs were highly resilient to a moderate disturbance (simulated disturbance from a large wave event that removes buoyant adult plants; *SI Appendix*, Fig. S4) but not to a severe disturbance (simulated cyclonic storm that removes both adult and nonbuoyant juvenile stages). Patch reefs (bommies) in the no disturbance treatment remained dominated by *Turbinaria* throughout the 26-mo course of the experiment (Figs. 3 and 4A), a period when there were at least five complete turnovers of individuals. For bommies subjected to a moderate disturbance event, adult *Turbinaria* returned to dominance on 88% (13 of 15) of the replicates by the end of the experiment (Figs. 3 and 4B),

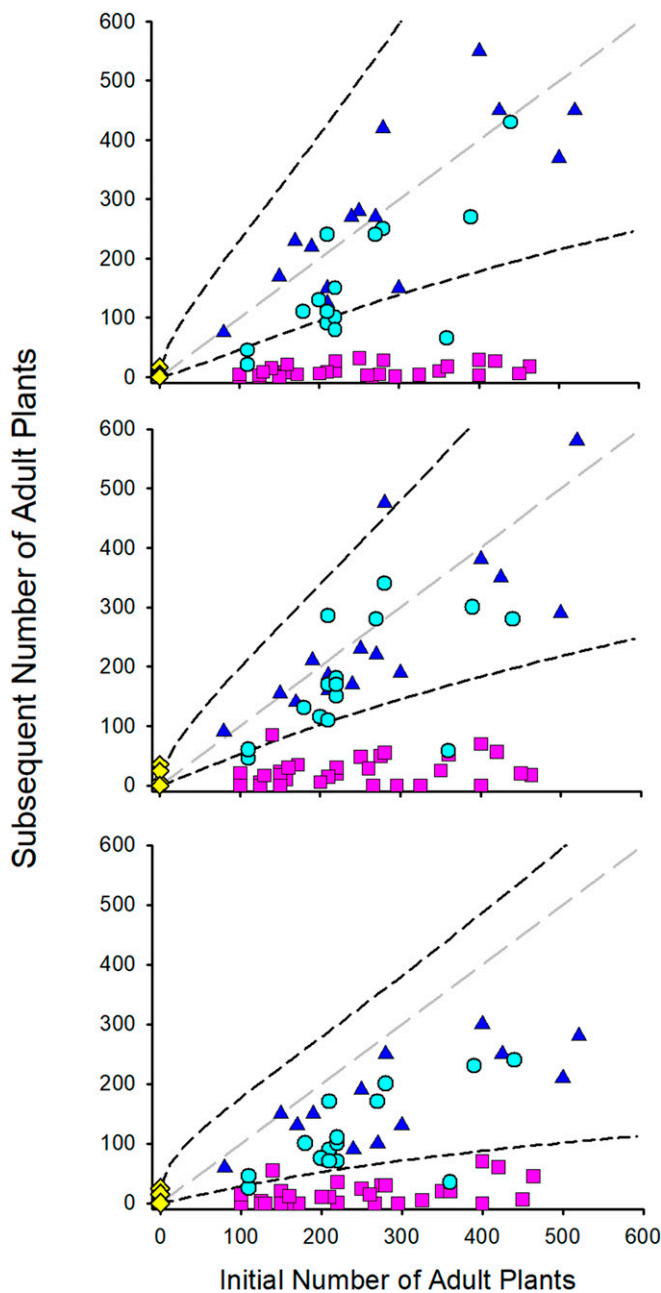


Fig. 3. Results of the lagoon resilience experiment that tested the local stability of natural patches of the brown alga *T. ornata* to three levels of a simulated pulsed disturbance, at three time periods. Each point represents an individual patch reef (bommie), the 45° line (light dashed line) represents the no change reference line, and the heavier dashed lines demarcate the 95% prediction interval based on the no disturbance treatment for a given time period. Treatments included the following: no disturbance (dark-blue triangles, $n = 15$); moderate disturbance (light-blue circles, $n = 15$), which mimicked a single episode of large waves that would remove only buoyant adult plants; and high disturbance (pink squares, $n = 30$), which simulated a large cyclonic storm that would remove both adults and juveniles (with half having a small herbivore exclusion cage; data are for the unprotected bommie surface). Also presented are data for nonexperimental bommies selected at the study site because they naturally lacked *Turbinaria* at the start of the experiment (yellow diamonds, $n = 15$).

which was not significantly different from the no disturbance treatment (Fisher's exact $P = 0.96$ after Holm correction); the majority (60%) of moderate disturbance reefs returned to the

macroalgae state within a year (Fig. 3). Unlike the moderate disturbance treatment, only one of the 30 replicates (3%) subjected to high disturbance returned to the original *Turbinaria* state within 26 mo (Figs. 3 and 4C). The remaining 29 bommies in the high disturbance treatments remained dominated by closely cropped turf algae (Fig. 4C and *SI Appendix*, Fig. S5). In marked contrast to the no disturbance controls, which remained dominated by *Turbinaria* throughout the experiment, *Turbinaria* that managed to colonize these 29 bommies remained in very low abundance throughout the experiment (Fisher's exact $P < 0.0001$ after Holm correction).

Temporal data from repeated sampling (Fig. 3) over the 2-y-long experiment did not provide evidence that any of the 29 bommies in the high disturbance treatment were transitioning back to *Turbinaria* dominance. The time series did provide evidence of a general, ~34% site-wide decline in *Turbinaria* abundance at the experimental site during the last 6 mo of the trial (Fig. 3). Finally, bommies selected because they initially lacked *Turbinaria* (and hence were not randomly assigned to a disturbance treatment) remained free from macroalgae for the duration of the experiment (Fig. 3). Based on our estimates of *Turbinaria* turnover rates, at the beginning the experiment, we set an elapsed time of 2 y as the end point of the experiment (i.e., five or more population turnovers), at which time we collected some specimens of macroalgae. However, we resampled all experimental bommies after 3 y to determine whether the global decline in abundance of adult *Turbinaria* observed in the last 6 mo of the experiment had continued. Data collected 37 mo after the pulse disturbance manipulations (*SI Appendix*, Fig. S6) revealed two important points: (i) There was no further site-wide change in the abundance of adult *Turbinaria*, and (ii) experimental bommies continued to persist in their respective states for a third year (*SI Appendix*, Figs. S6 and S7), providing further evidence that the "*Turbinaria*-free" condition was not a transient state.

Failure of severely disturbed bommies to return to their original state was not a result of our manipulation altering the reefs in a manner that inhibited colonization of macroalgae, and it was not due to lack of input of *Turbinaria* propagules. A subset of 15 (of 30) bommies in the high disturbance treatment had a small exclusion cage to prevent herbivore access to a small patch (0.06 m² in area) of the experimentally denuded surface. Within 12 mo, *Turbinaria* and other macroalgae had successfully colonized and matured on those bommies, but almost exclusively where the reef surface was protected from herbivorous fishes (*SI Appendix*, Fig. S5A). At the end of the experiment (26 mo postmanipulation), the biomass density of macroalgae in these cages (mean \pm SE: 21.5 g of damp weight 100 cm⁻²) was an order of magnitude greater than on adjacent, unprotected surfaces of these bommies (1.0 ± 0.2 g 100 cm⁻²; Student's t test with unequal variance: $t = 8.64$, $df = 32$, $P < 0.001$). Analysis of in situ video recordings made 15 mo after the manipulation points to grazing by herbivorous fishes as the mechanism preventing the widespread return of *Turbinaria*; the overall feeding rate (bites time⁻¹ area⁻¹) by herbivorous fishes on the surface of a patch reef was about fivefold greater on high disturbance bommies compared with the no disturbance treatment (Student's t test: $t = 4.49$, $df = 6$, $P < 0.005$; *SI Appendix*, Fig. S8). Many species of herbivorous fishes occurred at this location (*SI Appendix*, Table S2), and their feeding activity, particularly by species of parrotfishes, kept turf algae well cropped over most of the surface of bommies in the high disturbance treatment throughout the duration of the experiment (*SI Appendix*, Fig. S5B).

Discussion

The general issue of multiple basins of attraction has received considerable theoretical and empirical attention, yet it is not especially well resolved for natural ecosystems because of

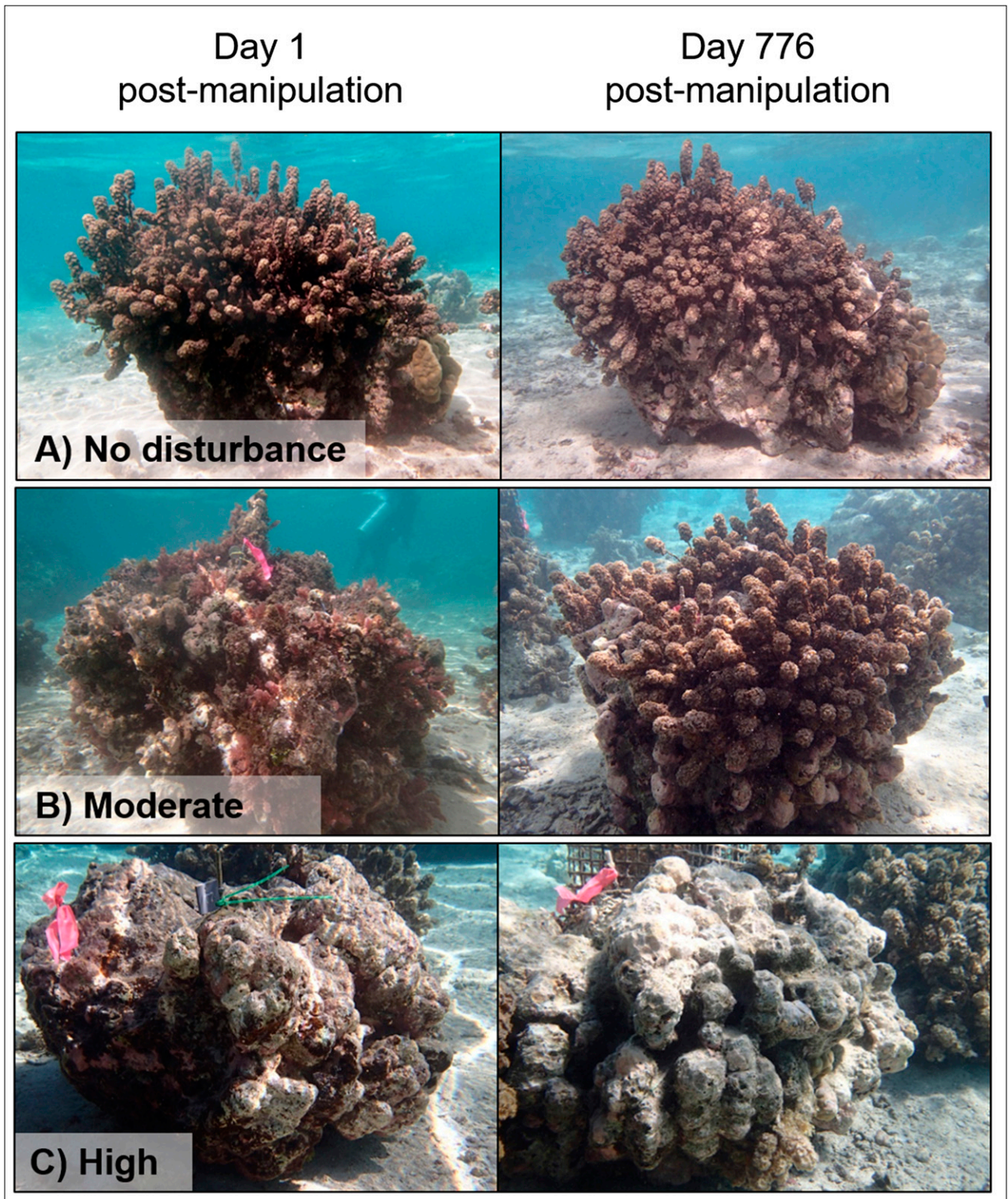


Fig. 4. In situ photographs of a representative bommie in each of the three major disturbance treatments of the resilience experiment just after the pulse disturbance treatments and at the end of the experiment 26 mo later. All 60 experimental bommies initially had high cover of *T. ornata* similar in density to that in the no disturbance treatment (A, Left). (A–C, Left) Images (day 1 postmanipulation) were taken the day after the simulated pulse disturbance was completed. (A–C, Right) Images (day 776 postmanipulation) show the same bommies near the end of the 26-mo experiment. Rows are representative bommies in each disturbance treatment: no disturbance (A), moderate disturbance (B; large swell event, only adult *Turbinaria* removed), and high disturbance (C; cyclonic storm, adult and juvenile *Turbinaria* removed). Images of these same bommies 37 mo after initiation of the experiment are shown in *SI Appendix*, Fig. S7.

inherent challenges in demonstrating their existence and characterizing their nature (2, 9, 11, 15). This is particularly the case for coral reefs (11, 16, 17, 22, 24), where an important but unresolved issue is whether coral and macroalgae can be multiple attractors under the same environmental conditions or whether a persistent phase shift to macroalgae simply reflects a long-term change in the value of an underlying driver (e.g., chronically reduced herbivory and/or increased nutrient flux). Using complementary experimental approaches, we showed that a state transition to macroalgae can represent a switch to an alternative basin of attraction. In addition, our manipulations revealed that macroalgae-dominated reefs in the lagoons of Moorea currently exist in an environment that has more than a single basin of attraction. Under the same conditions, lagoon reefs could persist for years in either a macroalgae-dominated or macroalgae-free state, depending on initial conditions. In contrast, herbivory on the fore reef of Moorea was sufficiently high to exclude macroalgae irrespective of initial conditions. These results help explain why reefs on the fore reef of Moorea have consistently recovered to a coral-dominated state following disturbances, while reefs within the lagoons have sometimes shifted to a persistent macroalgae-dominated state.

While our experiments demonstrate that coral reefs can persist in alternate states under the same set of environmental conditions, multiple lines of other evidence suggest that macroalgae could be an alternate basin of attraction in other coral reef systems. For example, by fitting time series data to mechanistic models with and without alternate attractors, Mumby et al. (5, 11) have shown that some Caribbean reefs may exhibit bistability between macroalgae-dominated and coral-dominated states. Similarly, spatial patterns of coral cover on reefs in the Tropical Eastern Pacific were consistent with a model that included feedbacks resulting in alternate states but inconsistent with models lacking these feedbacks (65). The existence of alternate states on coral reefs has vast implications for the understanding and management of these diverse ecosystems. In particular, our results suggest that proactive management strategies that lessen the chance of a switch to macroalgae will be more effective than those aimed at restoring the coral community after a shift (also ref. 5).

Our resilience experiment that tested the stability of the macroalgae state on lagoon reefs provided robust evidence for bistability. Nonetheless, direct tests of the stability of a community state can provide evidence of alternative attractors only for ambient conditions. The region of potential bistability created by hysteresis in a system, should it exist, almost certainly will be restricted in parameter space (38) such that the bifurcation point may often lie below the ambient conditions of a given environment (39). Thus, the lack of support for alternative attractors from a resilience test is not evidence that they are absent under all conditions (11). Further, it frequently is not sufficient to just know whether or not alternative attractors exist in a system. Management goals are better served by also knowing whether a tipping point is being approached and whether the system would become trapped in an alternative state. Although the issue of early warning has received considerable attention (6, 40, 41, 66), experimental tests to identify and characterize hysteresis across a wide range of parameter space remain scarce (9, 15).

There is a small but growing number of studies where a relevant driver was varied experimentally to explore aspects of abrupt state transitions, very commonly focused on a single species in simplified systems in laboratory settings (40, 41, 43; cf. refs. 39, 42). However, for almost all such manipulations to date, only one initial state was subjected to the imposed variation in the driver (cf. ref. 43). For example, Sirota et al. (42) varied the amount of prey (organic matter) that entered the aquatic

microecosystem that forms in the leaves of a carnivorous pitcher plant, and found that a modest enrichment of food induced a sudden transition of the pool from the initial aerobic state to an anaerobic state. Although subsequent modeling suggests the presence of hysteresis in this system (67), there was not an empirical test for discontinuity in the driver–response relationship by also evaluating whether the threshold for the pool to switch back to the aerobic state occurred at the same or lower level of enrichment as the switch to the anaerobic condition. Here, we tested explicitly for such initial state dependence of the driver–response relationship.

Our hysteresis experiments that tested for discontinuity in the herbivory–macroalgae relationship revealed evidence of hysteresis on both fore reef and lagoon habitats of Moorea. In both environments, a greater level of herbivory was needed to remove mature macroalgae than to prevent them from becoming established. Importantly, the prevailing level of herbivory on the fore reef was far above the experimentally delineated tipping point to macroalgae, whereas it fell on the cusp of the bistability region in the lagoon. This is a concrete demonstration of the major strengths of the approach. It not only distinguishes hysteresis from simple nonlinear tracking of a driver but can indicate how close the current environment is to a tipping point and provide insight into how much relaxation in the driver is likely to be needed for a switch back to the original state. Such information is critical for forecasting ecosystem responses to changing environmental drivers and can be especially useful for guiding ecosystem-based management and setting targets (68). For example, our work implies that under current levels of herbivory, macroalgae-free reefs within the lagoons of Moorea are at risk for transitioning to a persistent macroalgae-dominated state rather than to a coral state, and that once flipped, a disproportionately large (and impractical) increase in herbivory would be needed to restore lagoon reefs to a nonmacroalgae state. On the fore reef, by contrast, the bifurcation point currently is far below ambient herbivory. Hence, sensible management might be to initiate proactive means to increase levels of herbivory within the lagoon but merely to monitor herbivory on the fore reef unless it begins to decline.

Results of our resilience experiment were consistent with the hypothesis from the hysteresis experiment that the prevailing level of herbivory on lagoon reefs was within a region of bistability. On lagoon reefs, the macroalga *T. ornata* behaved dynamically as a basin of attraction under the same environmental conditions where coral-dominated and cropped turf communities also co-occurred. The alternative community to macroalgae when our resilience experiment was terminated consisted of closely cropped turf algae and some crustose coralline algae (CCA) that developed rapidly after *Turbinaria* was completely removed (Fig. 4C and *SI Appendix*, Fig. S5). This benthic state is regarded as transitional to a coral-dominated community because, unlike macroalgae, it is suitable for colonization and subsequent survival of coral, which easily can overgrow cropped turf algae and CCA (46–48, 51, 52, 69). While we did not assess how disturbance treatments may have influenced settlement patterns of coral larvae, a shorter term study by Bulleri et al. (70) did so for similar patch reefs in the lagoons of Moorea using almost the same manipulations of *Turbinaria* as in our resilience experiment. While overall settlement rates of coral were low in their study, *Turbinaria* greatly suppressed colonization by coral larvae, which was approximately fivefold greater where the macroalga was completely removed compared with even the presence of just its juvenile stages. The reduction in settlement likely was mediated by *Turbinaria* enhancing the abundance of epilithic microbes that can harm juvenile and adult corals and inhibit the settlement of coral larvae (70).

While several mechanisms are known by which *T. ornata* can inhibit the return of coral, at least one stabilizing feedback has

been identified that could account for the ability of local populations of this alga to self-replenish under moderate levels of herbivory. *Turbinaria* plants have both structural and chemical defenses against herbivory that develop ontogenetically and become most effective in mature thalli (53, 71). As a result, palatability to fish herbivores declines sharply once an individual grows out of the highly vulnerable early recruit stage (62). Germlings of *T. ornata* settle very close to the parent thalli, with the bulk dispersing <0.2 m from the parent (72). Once a patch of mature *Turbinaria* forms, the early palatable life stages that settle under the canopy of much less palatable adults gain an associational defense against herbivores that greatly enhances their probability of surviving to maturity (62).

A model based on the Moorea system (73) revealed that stage structure in the vulnerability of macroalgae to herbivores (i.e., palatable as juveniles but not as adults) similar to that of *Turbinaria* (62) can result in bistability of coral and algae states across a wide range of herbivory. Indeed, this mechanism appears to create a much broader region of bistability compared with other mechanisms that have been modeled for coral reefs to date (73). It is common for organisms to grow out of high-risk life stages, and this type of stage structure generally has been shown to promote bistability (74). This size-related vulnerability mechanism differs from others that have been explored for coral reefs. A common mechanism that also has empirical support, especially from Caribbean reefs, involves the dilution of herbivory as corals die and provide surfaces on which rapidly growing algae can colonize (5). These surfaces can transition to macroalgae if herbivores are incapable of responding fast enough to keep the expanded surface area sufficiently grazed (5, 11). This result is not universal, however, as several studies have found rapid increases in herbivore biomass following a sudden mass mortality of coral that facilitated the return to a coral state (39, 54, 61, 75). Parameterized models that capture the particular mechanism(s) underlying bistability in a system can be especially useful for management as they reveal the most important parameters that drive system dynamics (11, 73). For example, such models can guide development of strategies to strengthen resilience of a desired state before a switch to an alternative basin, and also identify the feedbacks that must be broken to restore the system if it does become locked in a less desired state (73).

While our findings warrant further exploration of underlying mechanisms, we gained considerable insight into the qualitatively different community dynamics that lagoon and fore reef habitats of Moorea have displayed over the past four decades. In particular, the high resilience of coral on the fore reef is facilitated by levels of herbivory that are well above a potential bifurcation point delineated by our hysteresis experiment; as a result, grazing intensity was sufficient to keep the substrate suitable for coral settlement following a massive disturbance (49, 54, 59, 61, 64). Our experiments also help explain the divergent dynamics of the benthic community on lagoon patch reefs (60, 76, 77), specifically why some lagoon reefs return to a coral state (albeit slowly at times), whereas other reefs nearby can transition to a persistent, self-replicating community dominated by macroalgae (Fig. 1). Our experiments revealed that bistability of macroalgae and coral is a possible outcome at the level of herbivory that prevailed in the lagoon. Thus, the experimental framework we used is a potentially powerful tool to probe for multiple attractors in complex natural systems and, as such, can provide valuable insight to guide management and conservation in the face of mounting local and global stresses.

Methods

Study Site and Permitting. Moorea (17.54°S, 149.83°W) is in the central South Pacific 20 km west of Tahiti in the Society Island archipelago of French Polynesia. The triangular volcanic high island has an ~50-km perimeter and an offshore barrier reef that encloses a shallow lagoon. In the past decade,

Moorea experienced an outbreak of coral-eating crown-of-thorns seastars that reduced the cover of live coral from ~40% to <5% on the fore reef, with corals in the lagoon experiencing less loss (Fig. 1) (54, 58, 78). The large amount of suitable reef substrate that became available immediately following the loss of coral from the fore reef afforded ample opportunity for macroalgae to become established. However, herbivorous fishes have kept cover of macroalgae low on the fore reef, and coral cover has since returned to its high, predisturbance levels at many locations around the island (39, 54, 57). By contrast, disturbed patch reefs in the lagoon have either transitioned to high cover of macroalgae (largely *T. ornata*) or remained dominated by turf algae and/or live coral (Fig. 1). *T. ornata* is a brown alga (class Pheophyceae, order Fucales) whose adult stage is morphologically and chemically defended (53, 71), and which produces germlings throughout the year (72, 79). Germlings typically disperse short distances (<0.2 m from parental thallus), although longer distance dispersal occurs when buoyant thalli are detached from the substrate and transported by water flow (53, 72, 79).

Time series patterns for corals and macroalgae (Fig. 1) are from data collected by the Moorea Coral Reef Long Term Ecological Research project, which has censused the coral reef communities annually around Moorea since 2005. Diver surveys and photoquadrats provide estimates of percent cover of major benthic substrate categories (e.g., coral, macroalgae, turf/CCA, sand), with most benthic taxa (including corals) resolved to species or genus level. Details concerning sampling protocols and the data can be viewed at mcr.lternet.edu/data. Data are reported here for lagoon reefs (80) and for the fore reef (81).

The study was approved by the University of California, Santa Barbara Institutional Animal Care and Use Committee (Protocols 639 and 918), and all experiments and other methods were performed in accordance with relevant guidelines and regulations. Permits for field work were issued by the Haut-Commissariat de la République en Polynésie Française (Protocole d'Accueil 2010–2011, 2011–2012, 2012–2013, 2013–2014, 2014–15, 2015–16, and 2016–17 to R.J.S. and S.J.H.).

Test for Hysteresis. The same hysteresis experiment was conducted at a paired fore reef site and back reef site on the north shore of the island (*SI Appendix, Fig. S1*). Both sites had very low cover of macroalgae (<5%) throughout the duration of the experiments. The basic design principle was to create a series of herbivory levels by using semipermeable exclusion cages that had one of several different hole sizes to allow herbivorous fishes of certain body sizes to gain entrance. This broadly mimics the effects of different levels of fishing intensity on the abundance and body sizes of herbivorous fishes (39, 63). Preliminary tests of cage designs (different dimensions, with natural or terra cotta substrates) revealed that periodic very strong hydrodynamic forces on the fore reef dictated we use a box design bolted to the bottom, with a relatively small footprint (0.14 m²) that encased a standard substrate [unglazed terra cotta tiles mounted rough (bottom) side up]. This and similar designs previously have been used successfully in Moorea (39, 63). We used the same cage design in the lagoon as on the fore reef to enable comparison. Cages were constructed from plastic-coated wire mesh, and each measured 37 × 37 × 22 cm, except for cages on the fore reef, where turf was the initial state, which had a height of 12 cm to further reduce drag and minimize the potential for the cages to become dislodged during large swell events. We created five herbivory treatments by cutting progressively larger holes in the mesh for five treatments (hole sizes: 2.5 × 2.5 cm, 5 × 5 cm, 7.5 × 7.5 cm, and 10 × 10 cm) and by eliminating the mesh from the entire upper portion of the cage to create an ambient herbivory treatment. A cage control (full sides, no top) was included for the turf initial state treatment to test whether alterations in abiotic conditions from the cage structure influenced the development of algae communities. No cage artifacts were detected (cage control vs. uncaged treatment; Student's *t* test assuming unequal variances: *t* = 1.63, *P* = 0.13). Previous tests of the effectiveness of this set of cage designs showed it created a graded series of herbivore visitation rates, bite rates, and biomass-weighted herbivory index (grams of fish per min·h⁻¹) (39). For the current experiments, each replicate had four unglazed terra cotta tiles that had been seasoned in the ocean for 3 mo but brushed clean just before use. After deployment, the mesh of cages was kept free of fouling organisms by periodic *in situ* cleaning by divers using scrub brushes and by replacing cages annually.

The experiment consisted of two initial community states: a cropped layer of turf algae (on all four tiles in a cage) or *T. ornata* plants (on two of the four tiles, with cropped turf on the remaining two tiles). For the *Turbinaria* treatments, a small piece of natural substrate on which several plants were attached was carefully chiseled from the reef, returned submerged in seawater to the laboratory, and glued underwater to a designated tile using a nontoxic underwater epoxy (Z-Spar A-788 Splash Zone Epoxy). The biomass

of adult *Turbinaria* we affixed to each tile was based on the average we estimated for lagoon patch reefs that were heavily dominated by the macroalgae (mean \pm 1 SE: 370 ± 30 g of damp mass 0.1 m^{-2} ; visualization of this density is shown in Fig. 4A). Replicates were interspersed along the 12-m isobath across an $\sim 225\text{-m}$ stretch of coastline on the fore reef and at a depth of ~ 2 m within an $\sim 3,600\text{-m}^2$ area within the lagoon (SI Appendix, Fig. S1). Due to logistical constraints, replication was uneven among treatments (fore reef: $n = 5$ replicates of *Turbinaria* treatment, $n = 10$ replicates for the turf treatment; lagoon: $n = 5$ replicates for the *Turbinaria* treatment, $n = 3$ replicates for the turf treatment). The turf initial state treatments were terminated when the biomass of macroalgae in the lowest herbivory treatment reached the starting biomass in the *Turbinaria* initial state treatment (i.e., the average biomass on *Turbinaria*-dominated lagoon reefs), which occurred after 24 mo in the lagoon and after 36 mo on the fore reef. *Turbinaria* initial state treatments were terminated after 24 mo in the lagoon and 12 mo on the fore reef. Cohorts of *Turbinaria* were batch-marked by loosely ringing individuals with small (10-cm-long) colored cable ties around the base of the stipe (the lower thallus portion that lacks branchlets) at different sampling times and counting individuals in each uniquely marked cohort at each successive sampling date. This revealed that the experiment spanned multiple complete turnovers of *Turbinaria* individuals, at least two full replacements for the fore reef experiment and five for the lagoon experiment (SI Appendix, Fig. S3). Cages were treated as replicates in all analyses.

The appropriate time scale of this and the resilience experiments described below is a critical consideration because of the time frames needed to assess the stability of a state (9, 15, 82). The accepted convention is that a state can be concluded as stable when it exhibits self-replenishment for at least one complete turnover of individuals (9, 82). In our case, the longevity of the individual *Turbinaria*, the dominant space-holding macroalgae on patch reefs in Moorea (60, 62, 70), is short (< 1 y; SI Appendix, Fig. S3), which is not unlike most macroalgae in coral reef ecosystems (83). Our field manipulations all ran for multiple complete turnovers of *Turbinaria*, which satisfies this essential requirement.

The biomass of macroalgae that grew on the tiles was quantified when treatments were terminated. Cages were transported to the laboratory in seawater, where each tile was gently rinsed to remove loose sediments. All macroalgae present were then carefully removed by hand, identified, and weighed damp. Subsamples of each algal species were weighed damp and dried in a drying oven until they reached a constant weight so that we could obtain relationships between damp mass and dry mass. For graphical purposes, we use standardized macroalgal biomass estimates to compare between the initial community states. We calculated these separately for the two initial community states by dividing each replicate of each treatment by the mean biomass of the lowest herbivory treatment for that state. To determine if there was statistical evidence for hysteresis, we tested whether the relationship between herbivory and macroalgal biomass at the end of the experiment was dependent on the initial community state. Specifically, we used a permutational ANOVA to ask whether there was an initial community treatment effect; a herbivory treatment effect; and, most importantly, an interaction between the two treatments. Data were log-transformed before analysis using the following transformation:

$$Y = \log(x + d) - c,$$

where d is a decimal constant determined by the lowest nonzero value in the dataset and c is the antilog of that constant. An advantage of transformation is that it preserves the relative order-of-magnitude differences in the data and results in values of zero when the original data are zeros (84). The permutational ANOVA was implemented in R using the `lmp` package (85). P values were calculated using unique sums of squares with 10^7 iterations. Strong evidence for hysteresis would include both a significant interaction between the herbivory and initial state treatments and evidence that the interaction was due to divergence among the initial state treatments at intermediate levels of herbivory. To explicitly test this hypothesis, we visually assessed where the two initial state treatments appeared to diverge (Fig. 2 and SI Appendix, Fig. S2) and then ran separate permutational ANOVAs on these treatments. These analyses provided statistical support of divergence among treatments on both the fore reef and lagoon (SI Appendix, Table S1).

Resilience Test. We conducted a pulse manipulation at a back reef (lagoon) site on the north shore of Moorea to test the resilience of the *Turbinaria*-dominated state (SI Appendix, Fig. S1). Based on the results of the hysteresis experiments, we hypothesized that bommies on the back reef could potentially exist in either the turf state or *Turbinaria* state under ambient

conditions. On the back reef, we tested the resilience of the *Turbinaria* state by simulating two pulse disturbances of different magnitudes on individual coral bommies. The experiment was conducted at a single back reef site, where many similar sized ($\sim 1\text{--}4 \text{ m}^2$), semiisolated (nearest neighbor $\sim 0.5\text{--}5 \text{ m}$) coral bommies were interspersed (SI Appendix, Fig. S1). Coral cover at the site was low, and many bommies harbored abundant macroalgae (primarily *T. ornata*). Others were free of macroalgae and covered primarily with closely cropped filamentous turf algae. If the *Turbinaria*- and turf-dominated states represent alternate attractors, we then predicted that the *Turbinaria* state would be resilient to a moderate disturbance but that a larger disturbance could result in a persistent switch to the turf state.

To test whether the *Turbinaria* state was resilient to disturbance, we subjected bommies dominated by *Turbinaria* to three levels of disturbance. For the high disturbance treatment, we simulated a cyclonic storm event, which can scour all macroalgae from the surface of bommies (86), by removing all *Turbinaria* individuals from a patch reef (i.e., bommie). Divers did this by hand (adults and large juveniles) and using small knives to remove smaller recruits and any remaining pieces of holdfast. For the moderate disturbance treatment, we mimicked a more moderate swell event, which, due to ontogenetic changes in *Turbinaria* morphology, results in the tall, buoyant adult thalli being detached from the substrate and swept away, but which leaves short, juvenile *Turbinaria* unaffected (53). Thus, for the moderate level of disturbance, we removed all large *Turbinaria* but left individuals < 3 cm intact (SI Appendix, Fig. S4). In addition to the two manipulated treatments, we tracked the fates of two different types of no disturbance control reefs (those that initially had *Turbinaria* and those that were *Turbinaria*-free). Finally, to ensure that our pulse manipulations did not alter the suitability of coral bommies for *Turbinaria*, we placed a small ($25 \times 25 \times 18$ cm) herbivore exclusion cage over a portion (SI Appendix, Fig. S5A) of the cleared surface on 15 of the 30 bommies in the high disturbance treatment. Our expectation was that *Turbinaria* and other macroalgae should readily recruit to the cages following the manipulation. Unlike the hysteresis experiment, the mesh of cages in the resilience experiment was not kept cleaned because the goal was to simply allow macroalgae to colonize an area protected from herbivory. Replicates ($n = 15$ of each treatment) were assigned randomly while making sure to intersperse all treatments throughout the study site. The experiment was run for 26 mo, with reefs sampled at three time points (12 mo, 18 mo, and 26 mo). After the experiment was terminated, all reefs were resampled a year later (37 mo after the pulse manipulation) to assess whether macroalgae were declining site-wide at the study location.

At each sampling point, we estimated the relationship between the abundance of *Turbinaria* at the onset of the experiment and its current abundance on the unmanipulated controls using a linear model on log-transformed data. There was a strong positive relationship throughout the experiment ($P < 0.01$ and $r^2 > 0.5$ for all dates), indicating that for the unmanipulated bommies, the abundance of *Turbinaria* at the onset of the experiment predicted well its abundance at each of the sampling points. Thus, for each sampling period, we used this relationship to predict the abundance of *Turbinaria* on the manipulated reefs. The expectation was that manipulated reefs that had returned to the *Turbinaria* state would fall within the 95% prediction intervals of the relationship. In contrast, reefs with few *Turbinaria* would fall outside of this range, illustrating a failure to recover to the *Turbinaria* state following the pulse disturbance. We tested whether the number of bommies falling below the prediction interval differed among the treatments at the conclusion of the experiment using a χ^2 contingency test. Given that the overall test was significant, we performed post hoc tests using Fisher's exact test for all pairwise comparisons, followed by an adjustment for multiple comparisons using the "Holm" method (87).

To gain insight into the mechanisms potentially maintaining the alternate states, ~ 15 mo after the initiation of the experiment, we made video recordings of four bommies from the no disturbance treatments (each with a high density of *Turbinaria*) and four nearby bommies in the high disturbance treatment using underwater video cameras for ~ 1 h each. We scored videos for herbivory by counting bites by herbivorous fishes (primarily Acanthuridae and Scaridae) in a standardized 0.25-m^2 area on each bommie. We differentiated whether bites were taken from the primary surface of the bommie or on macroalgae, and used two sample t tests to test whether the total number of bites per hour by herbivorous fishes and the number of bites on the primary surface differed between the two treatments. Analyses were conducted using R 3.3.2 (88).

Data Availability. Data for this study (80, 81, 89) are available on the website of the Moorea Coral Reef Long Term Ecological Project (mcr.lternet.edu/data).

ACKNOWLEDGMENTS. We acknowledge technical assistance from Keith Seydel, Jessica Nielsen, Juliette Verstaen, Katrina Munsterman, and Melissa H. Schmitt; information management support from M. Gastil-Buhl; field and laboratory assistance of University of California, Santa Barbara interns: E. Barba, E. Dille, J. Mandoske, and B. Ulaski; and logistical help from the staff of the University of California, Berkeley Richard B. Gump South Pacific Research Station: N. Davies, H. Murphy-Teurumeariki, V. Brotherson, T. You Sing, J. You Sing, and I. You Sing. We thank the French Polynesian

Government (Délégation à la Recherche) and the Haut-Commissariat de la République en Polynésie Française (DTRT) for continued support. The work was supported by the US National Science Foundation (Grant OCE 16-37396 and earlier awards) and by a generous gift from the Gordon and Betty Moore Foundation. Research was completed under permits issued by the French Polynesian Government (Délégation à la Recherche) and DTRT (Protocole d'Accueil 2005–2017). This work is a contribution of the Moorea Coral Reef LTER Site.

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