

ARTICLE

Material legacies can degrade resilience: Structure-retaining disturbances promote regime shifts on coral reefs

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Abstract

Standing dead structures of habitat-forming organisms (e.g., dead trees, coral skeletons, oyster shells) killed by a disturbance are material legacies that can affect ecosystem recovery processes. Many ecosystems are subject to different types of disturbance that either remove biogenic structures or leave them intact. Here we used a mathematical model to quantify how the resilience of coral reef ecosystems may be differentially affected following structure-removing and structure-retaining disturbance events, focusing in particular on the potential for regime shifts from coral to macroalgae. We found that dead coral skeletons could substantially diminish coral resilience if they provided macroalgae refuge from herbivory, a key feedback associated with the recovery of coral populations. Our model shows that the material legacy of dead skeletons broadens the range of herbivore biomass over which coral and macroalgae states are bistable. Hence, material legacies can alter resilience by modifying the underlying relationship between a system driver (herbivory) and a state variable (coral cover).

KEY WORDS

alternative stable states, coral reefs, disturbance, hysteresis, macroalgae, material legacies, regime shifts, resilience

INTRODUCTION

Major disturbances, such as fire, drought, storms, and heat waves, can abruptly kill the structure-forming species that create the foundations of ecosystems. When the dead structures of these organisms are left behind, these material legacies can alter recolonization rates and interactions among species in the recovering system (Johnstone et al., 2016). For example, standing or fallen

dead trees can affect establishment success of new colonizing individuals in forests (Johnstone et al., 2016), shells of dead oysters can provide substrate for new settling larvae to facilitate recoveries on oyster reefs (Lenihan & Peterson, 1998), and skeletons of dead corals can either serve as settlement substrate or harbor macroalgae that compete with live corals for attachment space on coral reefs (Vieira, 2020). Because material legacies can have powerful effects on ecological processes, they have the potential to

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also alter how ecosystems resist and recover from disturbance—that is, ecosystem resilience. For example, if dead structures occupy significant amounts of habitat space for extended durations, these legacies can prolong the time for new colonists to reseed a disturbed area and for that ecosystem to regain its predisturbance condition. Alternatively, if dead structures facilitate colonization by a functionally different guild of organisms, these structures may facilitate a regime shift in ecosystem state.

To better understand the role of material legacies, we can directly compare how disturbances that either remove or leave in place dead biogenic structures affect resilience. Some disturbances both kill structure-forming organisms and remove their biogenic structure, opening up unoccupied habitat spaces between surviving individuals (hereafter, structure-removing disturbances). Examples include intense fires, floods, storms (Fukami, 2015), deforestation, landslides, avalanches (Swanson et al., 2011), dredging, and ice scour (Lenihan & Peterson, 1998). By contrast, other disturbances kill structure-forming organisms but leave their structures intact, resulting in patchworks of live and dead organisms or dense stands of dead individuals that can restrict the amount of unoccupied space for new colonists and surviving individuals (hereafter, structure-retaining disturbances). Examples include drought, disease, predator or pest outbreaks (Johnstone et al., 2016), thermal stress (e.g., heat waves; Folke et al., 2004), and hypoxic events (Lenihan & Peterson, 1998). In this study, we use a model to quantify how the resilience of coral reef ecosystems may be differentially affected following structure-removing and structure-retaining disturbance events.

Coral reefs serve as a timely model system to explore the effects of material legacies on resilience. Disturbance regimes are changing such that acute events that either remove or retain structure are increasing in frequency, severity, or both (Oliver et al., 2018; Uthicke et al., 2015; Wehner et al., 2018). For example, structure-removing events (e.g., tropical storms) appear to be increasing in intensity (Vecchi et al., 2021), while structure-retaining events (e.g., marine heat waves that cause coral bleaching, predator/disease outbreaks) are becoming more widespread, frequent, and severe (Hughes et al., 2017; Lough et al., 2018; Pratchett et al., 2013). Storm disturbances can remove the entire coral colony, creating planar reef surfaces (Gardner et al., 2005), whereas structure-retaining disturbances kill the soft tissue of corals while leaving their skeletons intact (Baker et al., 2008; Pratchett et al., 2013). Coral taxa that are most sensitive to both disturbance types tend to have greater structural complexity (e.g., branching, corymbose, and tabular colony morphologies), but how their dead structures influence the recovery potential of reefs remains poorly understood. Some disturbances can

tip a coral reef ecosystem from a coral-dominated state to one where macroalgae or other benthic taxa are the more common space holder (Schmitt et al., 2022). There is mounting empirical and theoretical evidence supporting the idea that these can be alternative basins of attraction (alternative stable states in models) when hysteresis creates a region of bistability that includes the ambient environmental conditions (Briggs et al., 2018; Folke et al., 2004; McManus et al., 2019; Mumby, 2006; Mumby et al., 2013; Muthukrishnan et al., 2016; Schmitt et al., 2019; Schröder et al., 2005). Yet the resilience of coral to disturbance is tremendously variable across coral reef ecosystems, with rapid recovery in some reefs and continued coral decline or shifts to macroalgae in others (Baumann et al., 2022; Holbrook et al., 2018). The presence or type of material legacies has the potential to account for some of the observed variability in resilience of coral following a disturbance.

Competing hypotheses exist regarding the role of dead coral structures in fostering return of coral on disturbed tropical reefs. High structural complexity can promote faster or more successful recovery of corals if it provides habitat for coral-associated organisms that benefit coral growth and/or settlement substrate with refuge spaces for colonizing corals that would otherwise be consumed by predators (Graham et al., 2015). Alternatively, the retention of dead coral skeletons may diminish coral resilience if skeletons facilitate the establishment of macroalgae—major competitors of coral for attachment space on the reef—by, for example, creating physical refugia from herbivores for vulnerable, early-life-stage macroalgae (Bennett et al., 2010; Puk et al., 2020). Indeed, flat reef surfaces are readily grazed by herbivorous fish and sea urchins, preventing the establishment of macroalgae (Adam et al., 2011, 2015; Bellwood et al., 2006; Holbrook et al., 2016). This grazing helps maintain reef surfaces in a suitable condition for the settlement of new coral colonies and, thus, can be a crucial stabilizing feedback during periods of coral reef recovery (Adam et al., 2015; Holbrook et al., 2016; Schmitt et al., 2022). Following reductions in herbivory, some coral reefs have transitioned to a degraded ecosystem state in which macroalgae become the dominant space holder (Hughes, 1994; Mumby et al., 2013; Vieira, 2020). Once mature, macroalgae can become physically and/or chemically defended against herbivory (Davis, 2018) and compete directly with corals for reef space by overgrowing live colonies and preempting settlement space for coral larvae (McCook et al., 2001; Vieira, 2020). This suggests that macroalgae that are initially protected by dead coral structures could persist on the reef well after the dead structures have completely eroded away, potentially trapping the system in the alternative, macroalgae-dominated state.

Here we integrate herbivory and retention of biogenic structure using a conceptual framework derived from catastrophe theory (Jones, 1977; Loehle, 1989) to explore how material legacies could act to modify the coral reef resilience landscape (Figure 1). At low amounts of algal refugia, the coral-dominated state is resilient to disturbances that do not increase algal refugia (i.e., structure-removing disturbances). However, disturbances that substantially decrease coral abundance and simultaneously increase the level of algal refugia (i.e., structure-retaining disturbances) can move the system to a region of state space in which coral and macroalgae states become bistable, thereby triggering shifts from coral to macroalgae dominance (Figure 1, red line and bottom right). Material legacies of structure-retaining disturbances may act to modify the resilience landscape and change the underlying relationship between herbivores (a biological driver) and equilibrium coral abundance (a state variable) by increasing the degree of hysteresis

(Figure 1, blue dashed arrow). Importantly, the material legacy in this case causes an effective reduction in the capacity of herbivores to control macroalgae (i.e., the rate of herbivory) without actually changing the biomass of herbivores present in the system.

To investigate the effect of material legacies on coral reef resilience, we explored the consequences of structure-removing and structure-retaining disturbances using a model that simulated how the fraction of reef space occupied by key interacting benthic space holders (corals, macroalgae) changes following these two types of disturbance events. We address three main questions. First, how do the material legacies of structure-retaining disturbances affect the presence of alternate states? Second, what disturbance conditions (i.e., intensity and type) are required to trigger shifts between coral and macroalgae states? Finally, do structure-retaining disturbances speed or slow shifts to alternate states or recoveries to the predisturbance state?

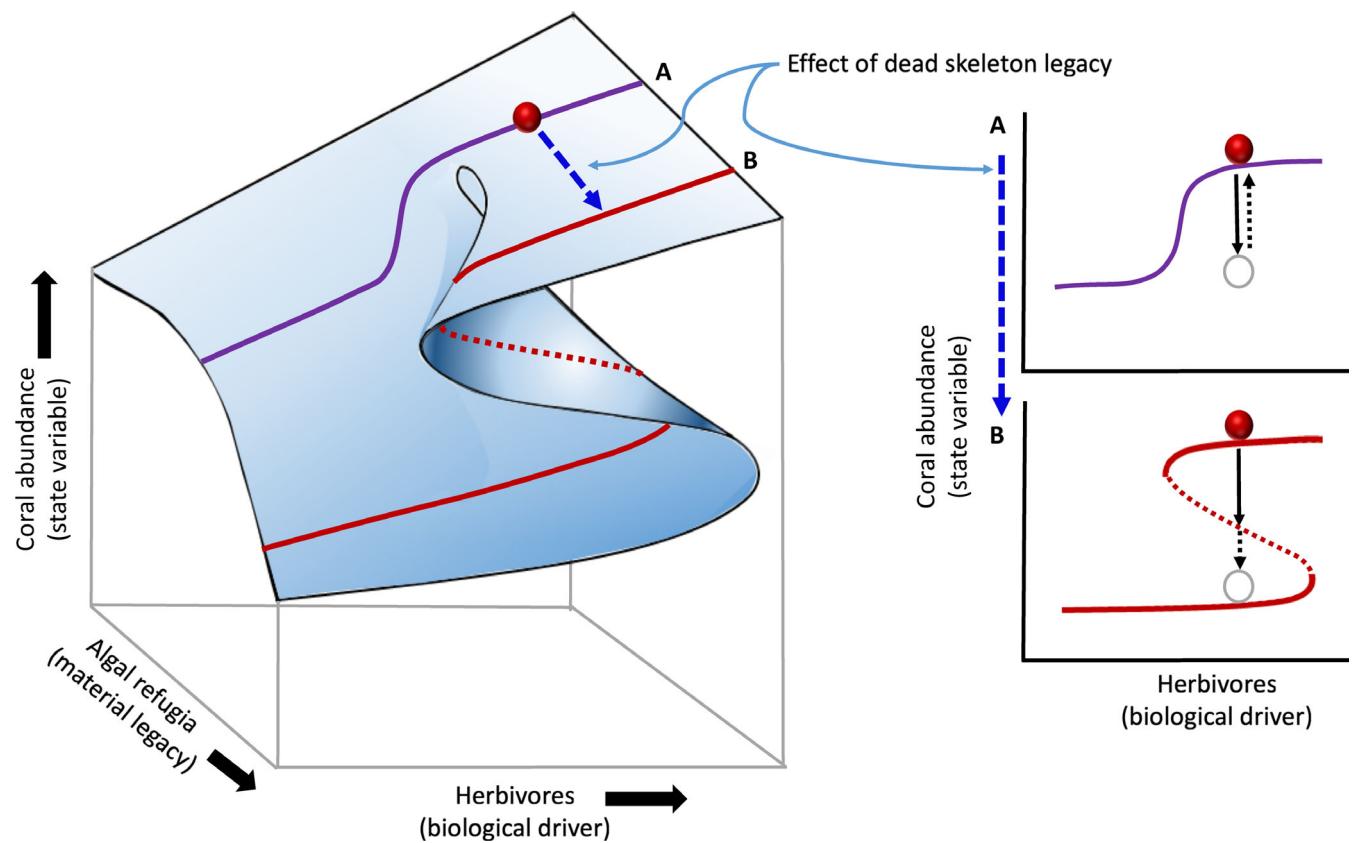


FIGURE 1 (Left) A hypothetical response surface showing how the equilibrium abundance of coral might vary as a function of herbivory and the amount of physical refugia in the environment that facilitate the proliferation of macroalgae; for heuristic purposes, we assume the response surface for macroalgae is the inverse of that shown for coral. The material legacies of structure-retaining disturbances (dead coral skeletons) provide vulnerable stages of macroalgae with refuge space from herbivores, potentially moving the system into a region of state space where hysteresis exists in the relationship with herbivory (blue dashed arrows). Such hysteresis promotes the bistability of coral and macroalgae for some range of herbivory. (Top right) In regions of state space without hysteresis, coral would return to its predisturbance state (upward dotted black arrow) after a high-intensity disturbance (downward solid black arrow). (Bottom right) By contrast, for regions of state space with hysteresis, the same intensity of disturbance could flip the system to a macroalgae stable state without any change in herbivory.

METHODS

Model description

To quantify the effects of disturbance type on coral reef community structure, we developed a model that describes how benthic cover changes over time. Building on previous work (Briggs et al., 2018; Mumby, 2006), we divided benthic cover on hard substrate into a set of classes representing the fraction of reef space occupied by coral C, macroalgae M, and “empty” space S. In this model, empty reef space is functionally equivalent to hard substrates occupied by a thin layer of turf or crustose coralline algae, which can be colonized or overgrown by either coral or macroalgae (Birrell et al., 2005; O’Brien & Scheibling, 2018; Schmitt et al., 2022). To compare structure-removing and structure-retaining disturbances and model the effects of the dead skeleton legacy, we further subdivided the coral cover class into live colonies growing on primary reef substrate (C_L), live colonies growing on dead colonies (C_P), and standing dead skeletons (C_D). Similarly, because dead skeletons may influence herbivory rates on macroalgae (Bennett et al., 2010; Puk et al., 2020), we partitioned macroalgal cover into two classes that differ in the substrate they occupy: macroalgae that grow on open reef spaces and are

fully exposed to herbivory (M_E) and macroalgae that grow amid the branches of dead coral colonies and are protected to some degree from herbivory (M_P).

We described changes in the proportions of the biotic cover classes (corals and macroalgae) using a system of five differential equations that capture transitions between empty space, live and dead branching coral cover, and macroalgal cover on the reef (Figure 2). First, live coral (C_L) grows onto empty reef spaces at rate g_c . Our model also allows for open recruitment, with coral settlers arriving into empty space at rate γ_c . Live coral can die in two ways: It can experience natural mortality at a rate d_c , which causes transitions from live to dead coral, or it can be overgrown by either exposed or protected macroalgae at rate g_{mc} , which causes transitions directly from live coral to protected macroalgae. The balance of these gain and loss processes produces the change in proportional live coral on the reef over time:

$$\frac{dC_L}{dt} = g_c C_L S + \gamma_c S - g_{mc} C_L (M_E + M_P) - d_c C_L. \quad (1)$$

When corals die naturally, their skeletal structures remain on the reef and continue to occupy benthic space as they gradually erode over several years (Adam et al., 2014).

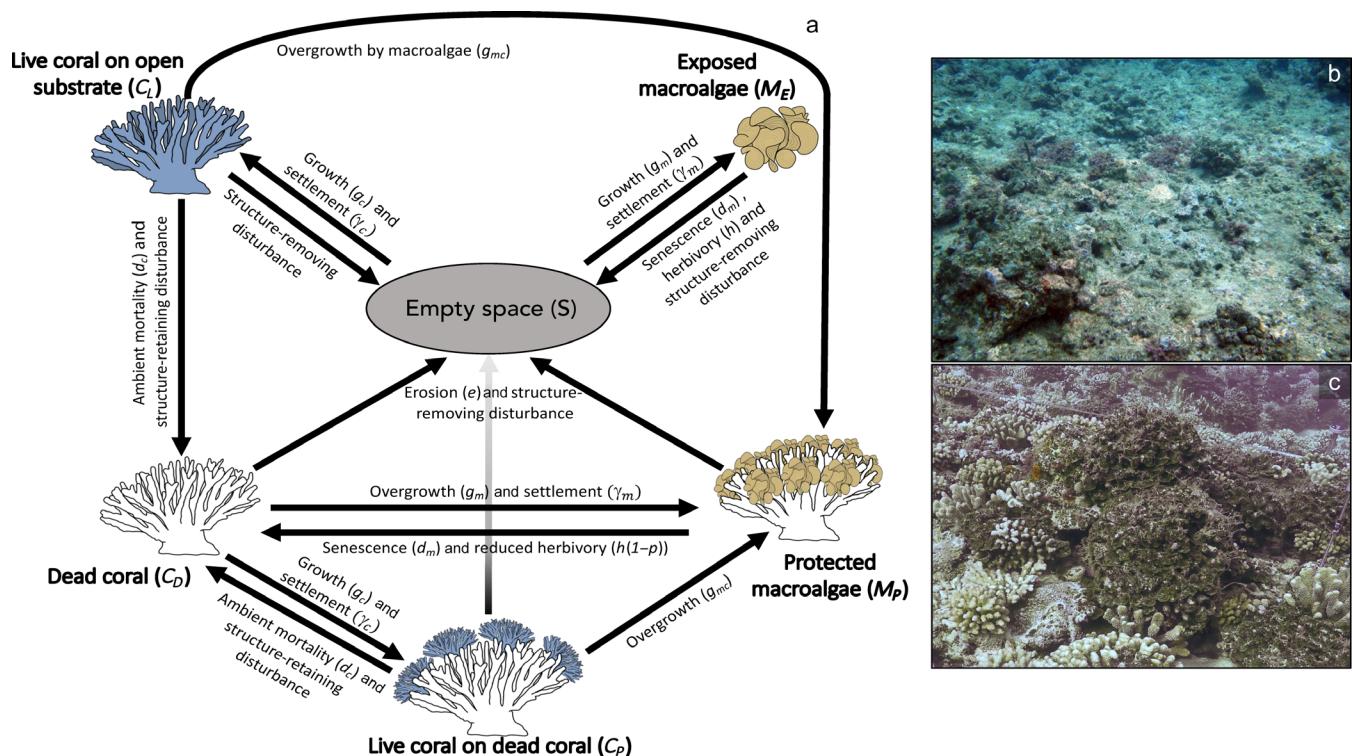


FIGURE 2 (a) Graphical depiction of interactions among state variables via model parameters (shown in parentheses). Arrows indicate the transfer of spatial occupation from one state variable to another by the associated process (e.g., dead coral transitions to open space via erosion). (b) Photograph of a coral reef following a structure-removing disturbance event (cyclone) that created bare, unoccupied reef space (photo credit: Russell Schmitt). (c) Photograph of a coral reef following a structure-retaining disturbance event (coral bleaching) that left in place dead coral skeletons (a material legacy) that are being overgrown by macroalgae (photo credit: Kai Kopecky).

We represented this as C_D , or the fraction of reef space occupied by standing dead coral skeleton. Transitions from live coral to dead coral result from the natural mortality of live coral ($d_c C_L$). Further, herbivores can remove macroalgae from dead coral structure, but at a reduced rate $h(1-p)$ compared to herbivory on exposed macroalgae, representing the product of the ambient rate of herbivory h scaled by the degree of protection afforded by a dead coral skeleton (p), resulting in a transition from *protected macroalgae* to dead coral. Dead coral is lost in three ways: It is removed via erosion at a fixed rate, e ; it can be settled and grown on by live coral at rates γ_c and g_c , respectively; and it can be settled onto or overgrown by macroalgae at rates γ_m and g_m , respectively. We thus describe the change in proportional cover of standing dead coral over time as

$$\frac{dC_D}{dt} = d_c(C_L + C_P) + M_P(h(1-p) + d_m) - g_c C_P C_D - s\gamma_c C_D - g_m C_D(M_E + M_P) - \gamma_m C_D - eC_D. \quad (2)$$

Standing dead coral provides a secondary substrate on which corals can settle and grow, and we represented this in our model as C_P or live coral that grows specifically on dead coral structure. Corals of this class arise only as a result of settlement (γ_c) and subsequent growth (g_c); lateral overgrowth by mature colonies does not tend to occur in structure-forming coral species, so we did not include this process in our model. We included a multiplier, s , for the rate of settlement of live coral onto dead coral relative to open substrate, where values less than one correspond to reduced settlement, and values greater than one correspond to increased settlement relative to that on open substrate. As a default, we set the settlement rate on dead coral equal to that on open substrate (i.e., $s=1$). Similar to live coral that grows on primary reef substrate, live coral that grows on dead coral can be lost via ambient mortality, at rate d_c , as well as overgrowth by macroalgae, at rate g_{mc} . This class of coral can also be lost via erosion, at rate e , to capture the transient nature of standing dead coral as a substrate. We thus describe the change in proportional cover of live coral growing on dead coral over time as

$$\frac{dC_P}{dt} = g_c C_P C_D + s\gamma_c C_D - g_{mc} C_P(M_E + M_P) - d_c C_P - eC_P. \quad (3)$$

We tested the sensitivity of our model's predictions to coral settlement on a dead structure by varying the parameter s .

Macroalgae growing within or beneath complex structures—such as the skeletons of dead corals—tend to have reduced rates of herbivory relative to more planar,

exposed reef surfaces (Bennett et al., 2010). To capture this, we subjected the exposed and protected macroalgae classes to different levels of herbivory. Exposed macroalgae (M_E) are removed at the ambient rate of herbivory, h . Protected macroalgae (M_P), by contrast, experience reduced herbivory pressure, $h(1-p)$, where p is a value between 0 and 1 that decreases the ambient level of herbivory by a designated amount (hereafter, referred to as *algal protection*). Both exposed and protected macroalgae can grow (at rate g_m) and settle (at rate γ_m) into empty space (S), which increases exposed macroalgae (M_E), and onto dead coral, which increases protected macroalgae (M_P). Both classes of macroalgae can overgrow either class of live coral, but at a slower rate, g_{mc} , resulting in a transition from live coral to protected macroalgae. Finally, both classes of macroalgae are lost via senescence (i.e., natural mortality) at a fixed rate, d_m . The rates of change in proportional cover for these two classes of macroalgae are given by the following equations:

$$\frac{dM_E}{dt} = g_m M_E S + g_m M_P S + \gamma_m S - M_E(h + d_m), \quad (4)$$

$$\begin{aligned} \frac{dM_P}{dt} = & g_m M_P C_D + g_m M_E C_D + g_{mc} C_L (M_E + M_P) \\ & + g_{mc} C_P (M_E + M_P) + \gamma_m C_D \\ & - M_P(h(1-p) + d_m + e). \end{aligned} \quad (5)$$

Finally, because our state variables represent the fraction of space occupied by any given class, we note that the fraction of empty space can be described as

$$S = 1 - C_L - C_D - C_P - M_E - M_P. \quad (6)$$

Disturbance

To model an acute disturbance, such as a storm event (structure-removing disturbance) or bleaching episode (structure-retaining disturbance), we used a kick-flow approach in which the “flow” of the system described by Equations (1) to (6) is paused, the system is instantaneously perturbed by a “kick” (e.g., an acute mortality event), and then the simulation is resumed. During these perturbations, the fraction of reef occupied by each space holder is reduced, increased, or unchanged to simulate pulse disturbance events of each type. Specifically, structure-removing disturbances reduce all space holders to a designated percentage of their predisturbance levels (increasing empty space), where the percentage represents the intensity of the disturbance. Structure-retaining disturbances affect only the three coral classes (i.e., live coral on open substrate or on dead coral, and standing dead coral).

In these instances, both classes of live coral are reduced by a fixed proportion (again, representative of disturbance intensity), and dead coral increases by the amount that live coral is reduced.

Model parameterization and analysis

We parameterized the model following ranges of parameters published by Fung et al. (2011) for reef systems not subjected to anthropogenic stressors (e.g., overfishing and sedimentation) and default values used by Briggs et al. (2018) (Table 1). We modified some of the parameters and added additional ones to account for the addition of the new state variable representing dead coral skeletons. In particular, we reduced the coral mortality rate (production of dead skeletons) and estimated a new parameter, the erosion rate of dead coral skeletons, as 10 times greater than the

TABLE 1 Variable and parameter symbols, descriptions, and default values.

Symbol	Description	Default value (range)
Variable		
C_L	Live coral on open substrate	
C_D	Dead coral	
C_P	Live coral on dead coral	
M_E	Exposed macroalgae	
M_P	Protected macroalgae	
S	Empty space; colonizable by coral or macroalgae	
Parameter		
g_c	Growth rate of coral	0.1 year ⁻¹
g_m	Growth rate of macroalgae	0.6 year ⁻¹
g_{mc}	Overgrowth rate of macroalgae onto live coral	0.06 year ⁻¹
d_c	Death rate of coral	0.001 year ⁻¹
d_m	Senescence rate of macroalgae	0.05 year ⁻¹
e	Erosion rate of dead coral	0.01 year ⁻¹
γ_c	Open settlement rate of coral	0.001 year ⁻¹
s	Multiplier for rate of coral settlement onto dead coral	1 (0–2)
γ_m	Open settlement rate of macroalgae	0.001 year ⁻¹
h	Ambient herbivory rate	0.3 (0–0.4) year ⁻¹
p	Algal protection; degree to which ambient herbivory is reduced for protected macroalgae	0.5 (0–1)

Note: Units for all parameters are change in proportional cover per year. Values in parentheses indicate the ranges used for sensitivity analyses.

mortality rate of live corals to ensure that the abundance of dead skeletons remained within a range typically observed in nature (Appendix S1). Our estimated erosion rate of 1% per year falls within published estimates of bioerosion of calcium carbonate structures on reefs of 0% to 5% per year (Silbiger et al., 2014). Importantly, these published rates estimate annual volumetric loss, not two-dimensional surface loss, as modeled here. Nonetheless, a volumetric loss of this magnitude translates to a comparable loss of two-dimensional area (Appendix S1). Because this lower coral mortality rate resulted in a reduced rate of production of empty space, we increased macroalgal growth and settlement rates to allow macroalgae to colonize this reduced open space efficiently.

We first explored the sensitivity of equilibrium conditions to variation in key parameters without disturbance using bifurcation diagrams. For this analysis, we solved for the equilibria of our model equations numerically (using MATLAB version R2016a, MathWorks, Natick, MA, USA) and assessed the equilibrium cover of each class of space holder across selected ranges in key parameters. This analysis focused on how variation in algal protection from herbivory (p) affected equilibrium values of live coral and total macroalgae ($M_E + M_P$) cover. Independent simulations were run for values of algal protection ranging between 0 and 1 (i.e., from no protection to complete protection for M_P). Further, we analyzed the model's sensitivity to variation in algal protection for starting conditions that reflect either a coral-dominated or macroalgae-dominated equilibrium to test for bistability between these two ecosystem states (i.e., hysteresis). We then explored equilibrium conditions of coral cover as a response surface determined by the degree of algal protection, p , and the ambient level of herbivory, h . For this analysis, we constrained the maximum level of herbivory to 0.4 to represent a realistic range in this parameter (Mumby et al., 2007). Lastly, we conducted a sensitivity analysis in similar fashion to explore equilibrium conditions of coral and macroalgae cover as a function of the erosion rate of dead coral (e) and coral mortality rate (d_c) (Appendix S1).

Over the range in algal protection that produced alternative stable states, we used numerical simulations (in R version 4.0.0) to explore how the model responded to structure-removing and structure-retaining disturbances of various intensities (fractional mortality of the affected space holders). Beginning with a coral-dominated state, we simulated the fraction of space occupied through time by each space holder following single disturbances that ranged in intensity from no mortality to complete mortality of the affected space holders (i.e., 0 to 1). We evaluated the equilibrium cover of each class of space holder via simulation by determining proportional cover after disturbance once the rates of change all reached zero. We then

designated the state of the system as either a coral or macroalgae equilibrium based on which organisms were the predominant space holders (a low equilibrium cover of coral always corresponded to a high equilibrium cover of macroalgae). We identified the intensity of each disturbance type that was required to trigger a shift from a coral to macroalgal state for each value of algal protection. This analysis was repeated for an ecosystem state that initially was dominated by macroalgae such that the initial cover of each space holder reflected that of a macroalgae equilibrium. Finally, we quantified the time taken to reach equilibrium for each combination of algal protection and disturbance intensity. All analyses and figures were produced using R version 4.0.0 (R Core Team, 2020), RStudio version 1.2.5042 (RStudio Team, 2020), the fields package (Nychka et al., 2015), and MATLAB version R2016a. All model code is permanently archived on Zenodo (Kopecky, 2023): <https://doi.org/10.5281/zenodo.7556007>.

RESULTS

Algal protection creates alternative stable states

As is common among models of benthic cover on coral reefs (Briggs et al., 2018; Fung et al., 2011; McManus

et al., 2019; Mumby, 2006; Muthukrishnan et al., 2016; Sandin & McNamara, 2012), our model predicted the existence of alternative stable states dominated by either coral or macroalgae (Figure 3). The magnitude of hysteresis between these states depended both on the amount of herbivory and the strength of algal protection (Figure 3c). A sensitivity analysis of equilibrium coral cover as a function of the erosion rate of dead coral (e) and coral mortality rate (d_c) revealed that bistability between the coral and macroalgae states exists when erosion occurs relatively slowly (i.e., the material legacy is more persistent), but only the coral state exists at higher rates of erosion when the material legacy becomes more ephemeral. Additionally, this analysis also showed that higher erosion rates allow the system to tolerate higher rates of coral mortality without transitioning to dominance by macroalgae (Appendix S1).

Structure-retaining disturbances promote and maintain shifts from coral to macroalgal states

Overall, structure-retaining disturbances were more likely to drive transitions to and maintain the macroalgae-dominated state (Figures 4 and 5). For example, coral-dominated systems that were perturbed by a structure-removing

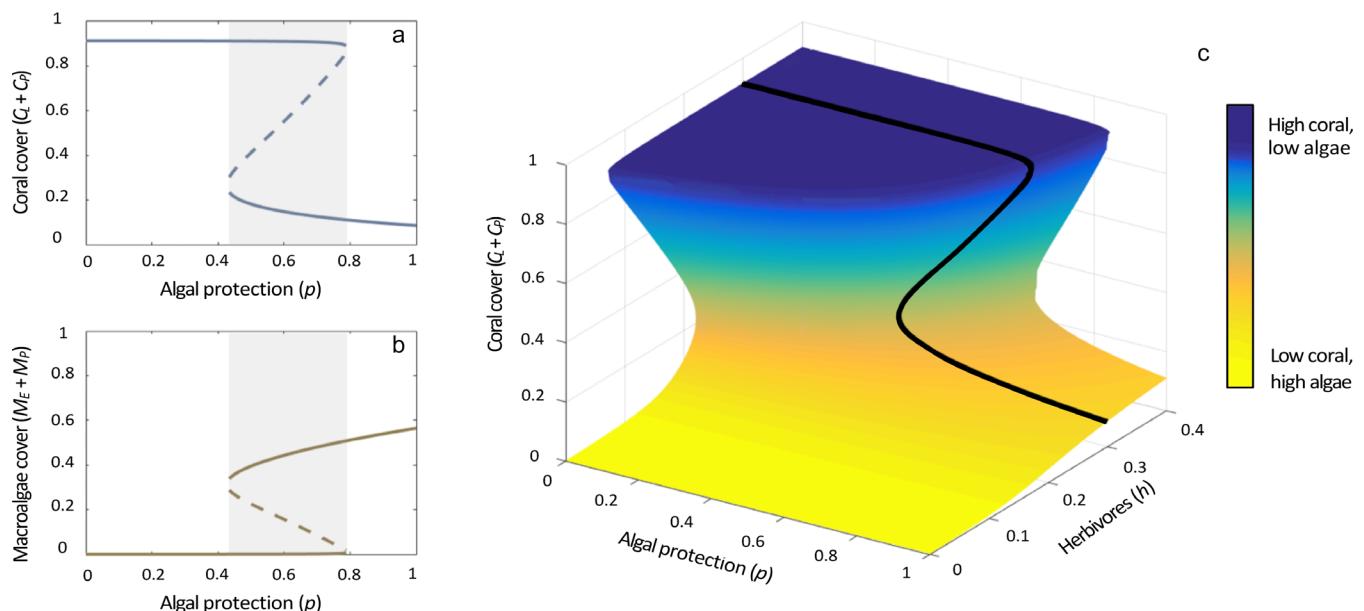


FIGURE 3 (a, b) Bifurcation diagrams showing (a) equilibrium cover of total live coral ($C_L + C_P$) and (b) total macroalgae ($M_E + M_P$) as a function of algal protection from herbivory, p . Solid lines indicate stable equilibria (i.e., values of the state variable to which the system will return after perturbations in either direction), and dotted lines indicate unstable equilibria (i.e., values of the state variable from which the system will diverge if perturbed). Equilibria were determined via numerical solving of our model equations. Shaded portions of each plot illustrate the regions of bistability (the range of algal protection over which coral and macroalgae are alternative stable states). (c) Response surface displaying the resultant equilibrium cover of coral at varying values of both algal protection, p , and herbivores, h . Blue shading represents high-coral equilibria, and yellow represents low-coral equilibria. The black line indicates equilibrium coral cover at the default value of herbivores but across the range of algal protection.

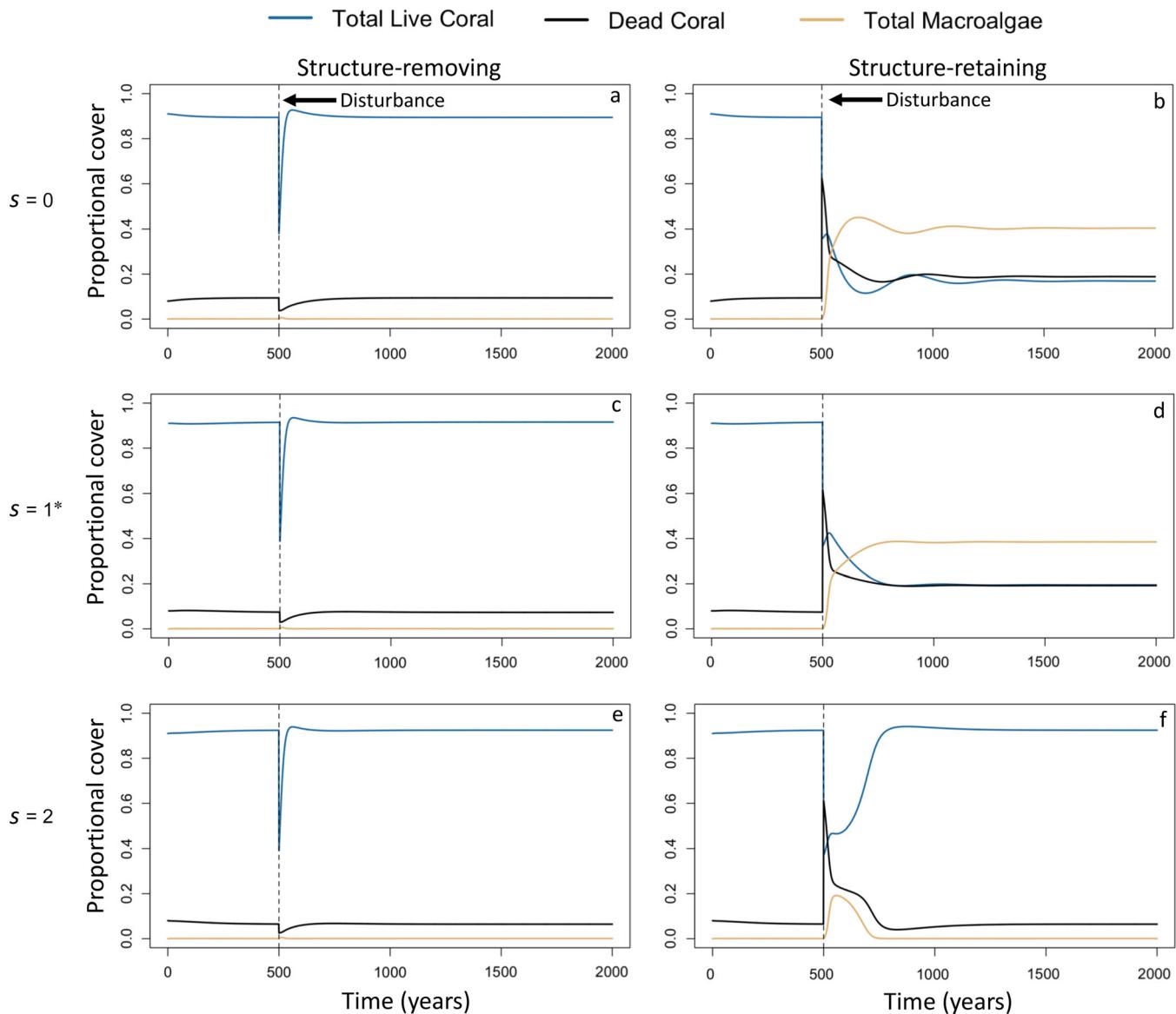


FIGURE 4 Time series of an initially coral-dominated community subjected to either a moderate structure-removing disturbance (a, c, e) or a moderate structure-retaining disturbance (b, d, f). Results are shown for settlement rates onto dead coral that were set to 0, 1, or 2 times the rate of settlement on open substrate (i.e., $s = 0, 1$, or 2 ; asterisk indicates default value). Blue lines (total live coral) show combined proportional cover of live coral that grows on open substrate and dead coral ($C_L + C_P$), while brown lines (total macroalgae) show combined proportional cover of macroalgae that grow on open substrate and dead coral ($M_E + M_P$). In both cases, the model system was subjected to a 60% intensity disturbance (indicated by dashed vertical black lines), where 60% of all space holders were removed in panels (a), (c), and (e), and 60% of each class of live coral cover was converted to dead coral in panels (b), (d), and (f) at the time of disturbance.

disturbance with an intensity of 0.6 (i.e., all space holders instantaneously reduced by 60%) rapidly regained pre-disturbance levels of live coral and macroalgal cover (Figure 4a,c,e). By contrast, a structure-retaining disturbance of the same intensity (i.e., where 60% of space occupied by live coral on open substrate and on dead coral was converted to standing dead coral) triggered persistent shifts to the macroalgal state (Figure 4b,d). In this case, live coral cover continued to drop after the disturbance and eventually stabilized far below its predisturbance equilibrium cover. Both exposed and protected macroalgae sharply

increased after the disturbance and achieved an equilibrium cover substantially higher than their predisturbance levels, surpassing coral as the dominant space holders on the reef (Figure 4b,d). When varying the rate of live coral settlement onto dead coral, we found that this outcome held when settlement onto dead coral was less than or equal to the rate of settlement on open substrate (i.e., when $s \leq 1$) (Figure 4a-d). However, when settlement on dead coral was doubled relative to open substrate, the system was able to recover from structure-retaining disturbance at this intensity, though at a slower rate than when the structure was removed (Figure 4f).

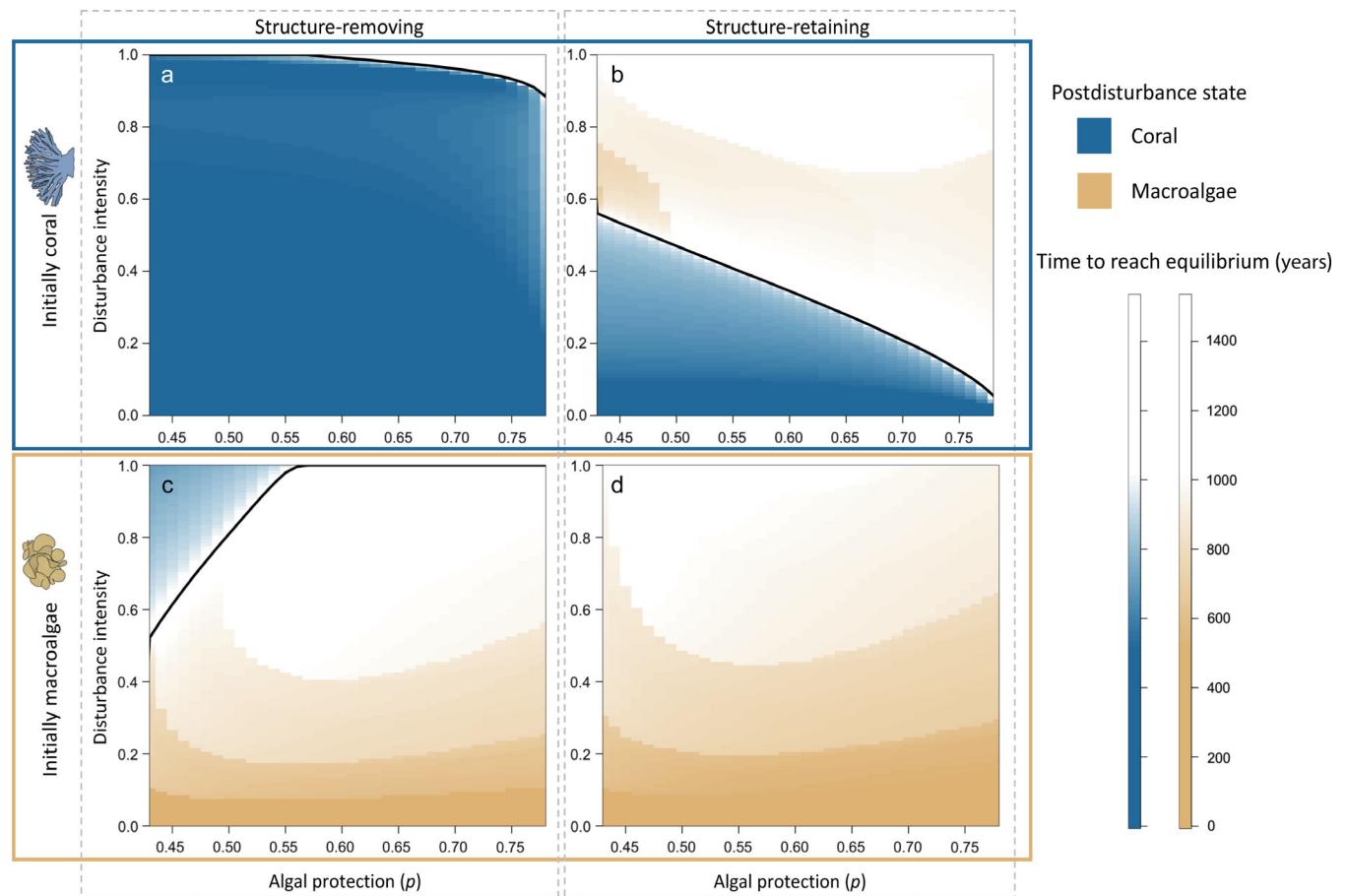


FIGURE 5 Equilibrium community states following structure-removing (a, c) and structure-retaining (b, d) disturbances plotted across a range of algal protection, p , and disturbance intensity. Model outputs for initial conditions that reflect a coral-dominated state are shown in panels (a) and (b), while panels (c) and (d) show outputs for an initially macroalgae-dominated state. Blue shading depicts a coral equilibrium after disturbance; brown depicts a macroalgae equilibrium. Black lines indicate the level of disturbance required to trigger a state shift at the corresponding level of algal protection (the tipping point). The saturation of each color represents the time taken for the system to reach equilibrium at a given value of algal protection and disturbance intensity. The range of macroalgal protection from herbivory shown is the region of bistability (the range in values over which alternative stable states exist, indicated by the shaded regions in Figure 3). Output is shown for all intensities of disturbance (i.e., from no disturbance to complete mortality).

Across the range of algal protection that created bistability, the thresholds for state shifts from coral- to macroalgae-dominated reefs were lower for structure-retaining disturbances relative to structure-removing disturbances. When the initial state was dominated by coral, the system returned to coral dominance following nearly all intensities of a structure-removing disturbance. However, when algal protection was sufficiently high, large structure-removing disturbances tipped the reef into macroalgal dominance (Figure 5a). By contrast, much lower intensities of structure-retaining disturbance were needed to tip the system from coral- to macroalgal-dominance, and the intensity required to do so was inversely related to the strength of algal protection offered by the dead skeletons (black line, Figure 5b). When the system was instead initially dominated by macroalgae (Figure 5, bottom row), only high-intensity structure-removing disturbances at low

levels of algal protection resulted in shifts to coral dominance (Figure 5c). The tipping point in disturbance intensity required to do so increased with increasing algal protection (Figure 5c, black line). Importantly, the macroalgal state was maintained following all intensities of structure-retaining disturbance and at all values of algal protection, revealing that shifts from the macroalgal to the coral state were not possible with disturbances that leave dead structure in place across this range of algal protection (Figure 5d).

Equilibration times varied with disturbance intensity and level of algal protection

Generally, rapid returns to a coral equilibrium occurred following most intensities of disturbance and at most

values of algal protection. However, some slower return times resulted from disturbances near the threshold value of disturbance intensity and at higher values of algal protection (Figures 5a,b). In these situations, macroalgae temporarily achieved a higher cover following the disturbance and, thus, delayed slightly the return to a coral equilibrium. By contrast, systems that shifted to the macroalgal state had longer equilibration times overall, the longest of which followed the most intense disturbances (Figure 5b). This reflects the time taken for macroalgae to take up the newly available substrate (i.e., dead skeletons). When shifts from macroalgae to coral took place, equilibration times were also generally longer for systems near the tipping point of disturbance intensity (Figure 5c). When the system returned to macroalgal dominance after disturbance, the time to reach equilibrium was generally longer following higher-intensity disturbances of both types (Figure 5d).

DISCUSSION

Material legacies shape the resilience landscape

Globally, ecosystems are increasingly crossing tipping points, in many cases to degraded states that offer diminished ecosystem services (Fagre et al., 2009; Millennium Ecosystem Assessment Program, 2005; Scheffer et al., 2001). Knowledge of the factors that either enhance resilience and foster recoveries or reduce resilience and promote shifts to alternate states is central to our ability to understand resilience now and forecast trajectories of community reassembly as disturbance regimes change in the future. Here, we showed that disturbances that leave dead skeletons (material legacies) can erode coral resilience, either prolonging the return to a coral-dominated state or causing a regime shift from a coral to a macroalgae community. Our findings suggest that better integration of material legacies into studies of resilience may offer key insight into when and where ecosystems that are dominated by structure-forming organisms will cross tipping points.

Disturbance-driven shifts between alternative ecosystem states (i.e., those that occur without changes to underlying drivers) have traditionally been thought to depend on whether the intensity of a disturbance is sufficient to push the system across the unstable equilibrium value of a state variable (Beisner et al., 2003; Fabina et al., 2015; Scheffer & Carpenter, 2003; Suding & Hobbs, 2009). Our findings add nuance to this, showing that even at the same intensity, different disturbance types can lead to divergent outcomes (i.e., recovery versus

regime shift) if there is differential production of a material legacy that modifies a stabilizing feedback. Our model exhibited high resilience to structure-removing disturbances, showing very low hysteresis (Figure 1, blue lines). Nonlinear systems with little (or no) hysteresis tend to be resilient to disturbance, and abrupt shifts between ecological states occur only if the threshold value of a system driver is crossed (Beisner et al., 2003; Suding & Hobbs, 2009). By contrast, our model suggests that coral-dominated reefs were resilient only to low intensities of structure-retaining disturbance, while moderate to intense disturbances caused shifts from coral to macroalgae because of the great increase in the amount of algal protection afforded by the dead skeletons. When bistability exists across a wide range of the driver in this fashion (Figure 1, red lines), an abrupt shift in ecosystem state is possible with a disturbance that displaces the system across a tipping point without any change to the underlying driver (e.g., herbivore biomass). Consistent with the dynamics we hypothesized in Figure 1, our results suggest that material legacies hold the capacity to shape the landscape of resilience in which a system operates by determining the magnitude of hysteresis between a system variable and its driver.

The importance of material legacies in preventing or driving regime shifts is likely to depend on the type of stabilizing feedback that promotes recovery in a given system. For our coral reef example, the material legacy (dead coral skeletons) acts to weaken a stabilizing feedback (the rate of herbivory), but the possibility also exists that a material legacy could instead strengthen a stabilizing feedback. For example, oyster reefs provide a soft sediment analog to coral reefs, as oysters are structure-forming organisms that are periodically killed by disturbances that either remove shell structures (e.g., dredging) or leave shell structures intact (e.g., hypoxic events). Disturbances that leave shells intact may in fact promote recoveries on oyster reefs, as oyster shells provide substrate for larvae to settle on and reduce impacts from seafloor sediments that can smother young oysters (Lenihan & Peterson, 1998). This contrasts with coral reefs where coral larvae that recruit to dead skeletons may be doomed to early death by erosion of their dead host structure (Swanson, 2016). In our model, high recruitment of coral onto dead structure could prevent tipping into the macroalgal state by pre-empting algal settlement (Figure 4f). However, it is important to note that in our model, this high recruitment does not come at a cost to coral settlement in empty space; in other words, dead coral does not act as an “ecological trap” for larvae (Battin, 2004). If a settlement tradeoff did exist, dead coral could act as a “sink” for larval propagules and erode coral persistence (Kopecky et al., 2021). In forests, the removal of tree roots during disturbance can increase the erosion of

topsoil and destabilize the forested ecosystem state. If tree roots are instead retained through a disturbance, topsoil will persist afterward and can increase the colonization success of new trees (Flores et al., 2020). However, there is evidence that standing or fallen dead trees could decrease resilience by negatively affecting the establishment of new individuals (Johnstone et al., 2016; Swanson et al., 2011). These examples illustrate the importance of considering context dependency in assessing how a material legacy may affect the stabilizing and destabilizing feedbacks that govern alternative states of an ecosystem.

The dead coral skeleton legacy decreases recovery potential on coral reefs

Building on previous models of alternative stable states in coral reefs (e.g., Briggs et al., 2018; Mumby, 2006), we explored the effects of disturbances that either remove or leave in place dead coral skeletons on resilience by incorporating three novel components: (1) the occupation of space by dead coral skeletons (i.e., a material legacy); (2) the (transient) substrate these dead structures provide for corals and macroalgae; and (3) the protection from herbivores that these dead coral structures provide for macroalgae. The dead skeleton legacy produced by structure-retaining disturbances effectively reduced the strength of herbivory and produced a relatively high degree of hysteresis in our coral-macroalgae system compared to a relatively low degree of hysteresis when this legacy was removed by disturbance. The retention of this structure created a higher incidence of coral-macroalgae shifts (lower chance of recovery) when the dead skeleton legacy was in place to inhibit herbivory. These results indicate that coral-dominated reefs are likely to be more resilient to disturbances that remove dead skeletons (e.g., storm-generated waves), while disturbances that leave dead skeletons intact (e.g., predator outbreaks or bleaching) greatly lower the threshold of disturbance intensity required to trigger a regime shift to macroalgae dominance. We note that our model does not account for dynamical responses by herbivores that could result from changes in the amount of complex reef structure that provides habitat. Indeed, the degree of habitat complexity has been found to positively affect abundances of reef fishes, including herbivores (Blackwood et al., 2011; Bozec et al., 2013; Holbrook et al., 2003); however, increases in herbivore abundance associated with higher habitat complexity may not directly translate to increased rates of herbivory if the habitat provides a high degree of protection for macroalgae. Nevertheless, future investigations into the role of the dead coral skeleton legacy on coral-algae dynamics could consider dynamical responses

by herbivores to the removal or retention of dead coral skeletons with varying degrees of algal protection.

Our results suggest that the degree of hysteresis in the relationship between coral cover (the state variable) and herbivory (a system driver) depends on the type of disturbance that occurs. More specifically, the amount of macroalgal refugia generated during a disturbance event (via coral skeletons that are left on the reef) determines the degree of bistability between coral-dominated and macroalgae-dominated reef states. In turn, the amount of spatial refugia generated depends on the intensity of the disturbance, while the strength of protection offered by the skeletons likely depends on the morphological traits of the affected coral species, such as the three-dimensional structural characteristics of the coral skeleton. The genera of coral that are most sensitive to bleaching mortality from marine heatwaves tend to be those with higher structural complexity (e.g., branching, corymbose, and tabular colony morphologies). These growth forms are also preferred by crown-of-thorns seastars (*Acanthaster planci*) (COTS), a coral predator that similarly leaves behind intact coral skeletons by removing coral tissue. Populations of this predator can exhibit “boom-and-bust” outbreaks that periodically cause widespread mortality of coral tissue over landscape scales (Pratchett et al., 2013, 2017).

The findings described here are likely most representative of reefs dominated by complex, branching coral morphologies. Reefs dominated by massive or mounding coral morphologies have skeletons that may not provide as much protection for algae. Massive and mounding corals tend to be less susceptible to disturbance in general (Zawada et al., 2019) and, therefore, were not the main focus of our model. Nonetheless, these reef types were captured in our sensitivity analysis of algal protection, p , when p was set to extremely low levels (Figure 3c). Further, we parameterized our model to the level of dead coral cover observed in natural systems (i.e., <10% for a coral-dominated reef state). Although our estimated rate falls within observed bioerosion rates (Silbiger et al., 2014), erosion of dead coral likely varies widely with flow rates, wave exposure, coral skeleton morphology/structural composition, and the presence of bioeroding organisms. Indeed, when erosive forces such as storms act to rapidly remove coral skeletons, reef recovery to coral-dominated states can be rapid (Holbrook et al., 2018). Additionally, we found that the rate at which coral skeletons are produced via mortality can be counteracted by the rate at which these skeletons are removed via erosion (i.e., higher erosion allows for higher coral mortality without a transition to macroalgal dominance; Appendix S1). This underscores the importance of considering how multiple processes could interact to modify the strength of the material legacy effect and, thereby, equilibrium conditions.

Theoretical work and empirical work support the notion that the skeletons of dead branching corals could facilitate the proliferation of macroalgae. Many primary producers (both terrestrial and marine) show stage-dependent vulnerability to herbivory, where early life stages are palatable to herbivores but become physically and/or chemically defended as they mature or increase in size (Barton & Korichev, 2010; Cronin & Hay, 1996; Davis, 2018). On coral reefs, this well-known life history trait of macroalgae has been proposed as a mechanism that contributes to shifts from coral to macroalgal states (e.g., Davis, 2018). Theory shows not only that stage-dependent vulnerability in macroalgae can produce alternative stable states between coral and macroalgae, but also that the rate of maturation from the vulnerable to invulnerable stage influences the magnitude of hysteresis between herbivory and coral cover (Briggs et al., 2018). Further, empirical studies have revealed that vulnerable (juvenile) macroalgae escape herbivory by receiving associational refuge from unpalatable adults (Davis, 2018) or reef structures that hinder herbivore access (Puk et al., 2020), both of which can lead to multigenerational persistence of stands of macroalgae (Schmitt et al., 2019, 2022). Thus, dead coral skeletons could provide a key spatial refuge for vulnerable life history stages of macroalgae and could be a critical element contributing to transitions to macroalgae-dominated reef states. This is highly problematic for conservation and restoration because reversing shifts when hysteresis exists requires either a large relaxation of the underlying driver or a subsequent large disturbance to reset the system (Beisner et al., 2003). Further, structure-retaining disturbances—particularly coral bleaching events—are increasing in prevalence and severity due to elevated sea temperatures associated with global climate change (Donovan et al., 2021; Hughes et al., 2018, 2019; Lough et al., 2018; Pratchett et al., 2017; Uthicke et al., 2015). This changing disturbance regime may lead to more reefs becoming trapped in the macroalgae state (Fabina et al., 2015), which has potentially far-reaching consequences for human populations who rely directly on coral reefs for a wide array of ecosystem services.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts to declare.

DATA AVAILABILITY STATEMENT

All model code (Kopecky, 2023) is publicly available in Zenodo at <https://doi.org/10.5281/zenodo.7556007>. Data sets utilized for this research are available from the Environmental Data Initiative (EDI) Data Portal as follows: time series for cover of hard corals at the NSF Moorea Coral Reef Long Term Ecological Research (MCR LTER) site (Edmunds, 2022; <https://doi.org/10.6073/pasta/913b1532594fcacf02de7671ed940b4c5>); time series for cover of benthic algae at the MCR LTER site (Carpenter, 2022; <https://doi.org/10.6073/pasta/69b6927cca72a5893573276c9b0dc2a0>); and cover of dead coral at the MCR LTER site (Adam et al., 2012; <https://doi.org/10.6073/pasta/23157cfedcc6522c999e593d83007c9>).

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SUPPORTING INFORMATION

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

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APPENDIX S1

Journal name: Ecology

Title: Material legacies can degrade resilience: Structure-retaining disturbances promote regime shifts on coral reefs

Authors: Kai L. Kopecky, Adrian C. Stier, Russell J. Schmitt, Sally J. Holbrook, and Holly V. Moeller

Field observations to corroborate model predictions and parameter values

Here, we show a time series of coral and macroalgae cover (Figure S1) from the Moorea Coral Reef Long Term Ecological Research site (<http://mcr.lternet.edu/>) for the fore reef on the northern shore of Moorea that shows divergent recovery patterns following a cyclone (in 2010), and more recently, a mass coral bleaching event (in 2019). Following the cyclone, we observed a marked recovery of coral in which pre-disturbance coral cover was regained 5 years after the disturbance, then far exceeded pre-disturbance levels in the following years before the bleaching event. A similar trajectory is shown by our theoretical time series plot for a reef subjected to a severe structure-removing disturbance (Figure 4a). By contrast, following the recent bleaching event, coral cover has continued to decline and macroalgae have shown a marked increase, primarily growing within dead coral structures. These patterns are consistent with our model's predictions for a reef subjected to a severe structure-retaining disturbance event (Figure 4b).

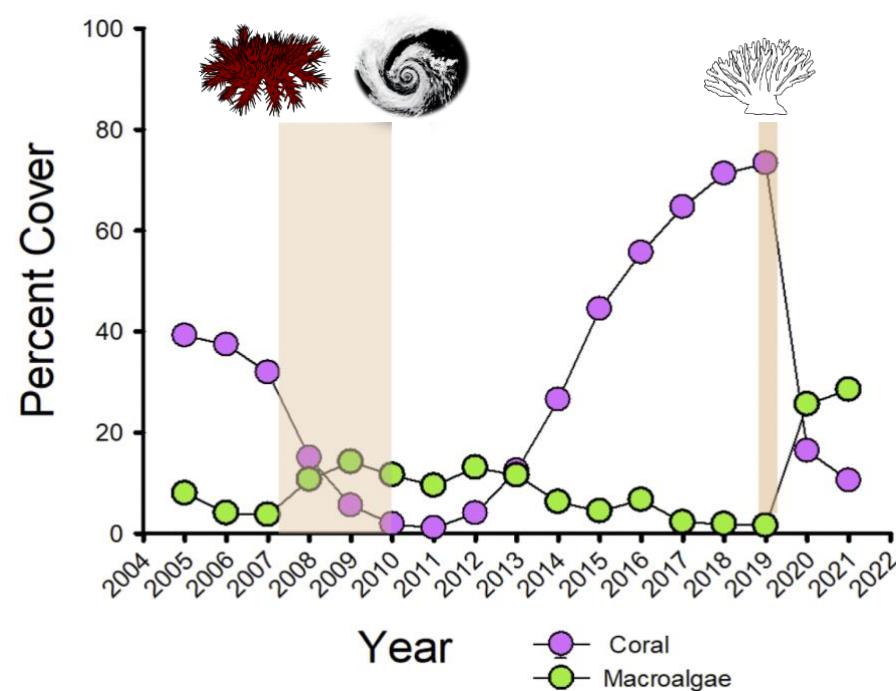


Figure S1. Time series of live coral cover (magenta dots) and macroalgae cover (green dots) following different disturbance types on the north shore fore reef of Moorea, French Polynesia. An outbreak of predatory Crown-of-Thorns Seastars occurred from 2007-2009, followed by a powerful cyclone that removed nearly all live and dead coral structure at these sites in 2010. In 2019, a marine heat wave triggered a coral bleaching event that resulted in significant coral mortality, leaving the dead skeletons intact.

Because previous models did not explicitly simulate cover of dead coral or integrate it as a separate substrate, we felt that the coral mortality rates used in these models were not appropriate for our model. We instead adjusted our rate for coral mortality to create a realistic amount of dead coral in our system (<10%), that is, the amount that would be present at 'equilibrium' or pre-disturbance. This value of dead coral cover is corroborated by field data from the Moorea Coral Reef Long Term Ecological Research project, which show the areal coverage of dead coral during four different years in the time series. In 2006 (the only year in the

4-year dataset before the outbreak of the Crown-of-Thorns Seastar), the island-wide mean percent cover of dead coral (i.e., across all 6 fore reef sites) was $7.1 \pm 3.1\%$ (mean \pm SD; Table S1; Adam *et al.* 2012). With the default value we chose for coral mortality, the percent cover of dead coral at equilibrium (in the coral-dominated state) in our model system is 7.6%, and thus closely aligns with these field observations.

Table S1. Mean cover (and standard deviation) of dead coral at 6 long term monitoring sites for the year 2006 (the only year with data on dead coral cover prior to the outbreak of predatory seastars and subsequent coral mortality).

site	year	mean_dead_coral	standard_deviation
LTER_1	2006	6.97	4.42
LTER_2	2006	8.67	7.67
LTER_3	2006	4.05	3.38
LTER_4	2006	9.09	13.82
LTER_5	2006	10.99	3.45
LTER_6	2006	2.84	4.23

Translating volumetric loss to areal loss for carbonate structures

Our estimated erosion rate of 1% per year falls within published estimates of bioerosion of calcium carbonate structures on reefs of 0 to 5% per year (Silbiger *et al.* 2014); however, these published rates estimate annual volumetric loss, not two-dimensional surface loss, as modeled here. We made a simple calculation (see 1-5 below) to compare how the reduction in volume of a hemisphere (a commonly used shape to estimate the volume of a coral colony; e.g., see Konh and Parry 2019, Shlesinger and van Woesik 2021) relates to a reduction in the area of a circle - the two-dimensional footprint of a hemisphere - using the change in radii from the hemisphere. We found that a 0-5% reduction in hemispheric volume translates roughly to a 0-3.3% reduction in the area of a circle with the same changes in radii:

- 1) Volume of a hemisphere: $100cm^3 = \frac{2\pi r^3}{3}$, radius = $3.63cm$
- 2) Initial, circular footprint of $100cm^3$ hemisphere: $\pi(3.63cm)^2 = 41.40cm^2$
- 3) Volume of hemisphere, reduced by 5%: $95cm^3 = \frac{2\pi r^3}{3}$, radius = $3.57cm$
- 4) Circular footprint of reduced, $95cm^3$ hemisphere: $\pi(3.57cm)^2 = 40.04cm^2$
- 5) % reduction of circular footprint: $\frac{Final - initial area}{initial area} = \frac{40.04cm^2 - 41.40cm^2}{41.40cm^2} = -0.033,$

$$-0.033 * 100 = 3.3\%$$

Thus, our estimate of a 1% annual loss in two-dimensional area of dead coral skeletons via erosion fits within the range of 0-5% found by Silbiger *et al.* (2014) for volumetric losses of carbonate structures.

Sensitivity analyses of other parameters – erosion rate and coral mortality

To understand how the erosion rate of dead corals interacts with the mortality rate of live corals to affect equilibrium conditions, we created response surfaces (Figure S2) to explore the sensitivity of equilibrium coral and macroalgae cover to variation in the erosion rate of dead coral (e) and coral mortality rate (d_c). For coral mortality, we explored a range from 0 to 0.02, the lowest value that has been used in previous models. Not unexpectedly, higher erosion rates allow the system to tolerate higher rates of coral mortality. Generally, high erosion rates tend to produce coral-dominated reefs. This is because only dead coral skeletons (populated by macroalgae or not) erode, and when they erode quickly enough, the effect of this material legacy (i.e., protecting macroalgae from herbivory) is not sufficiently strong to facilitate the proliferation of macroalgae. Specifically, higher rates of erosion reduce the abundance of protected macroalgae, thereby reducing the overgrowth of live coral by that macroalgae. Importantly, this response surface shows that our model still exhibits bi-stability between coral and algae at a coral mortality rate $> 10x$ our default rate (~ 0.015), or within an order of magnitude of the lowest rate used in previous models.

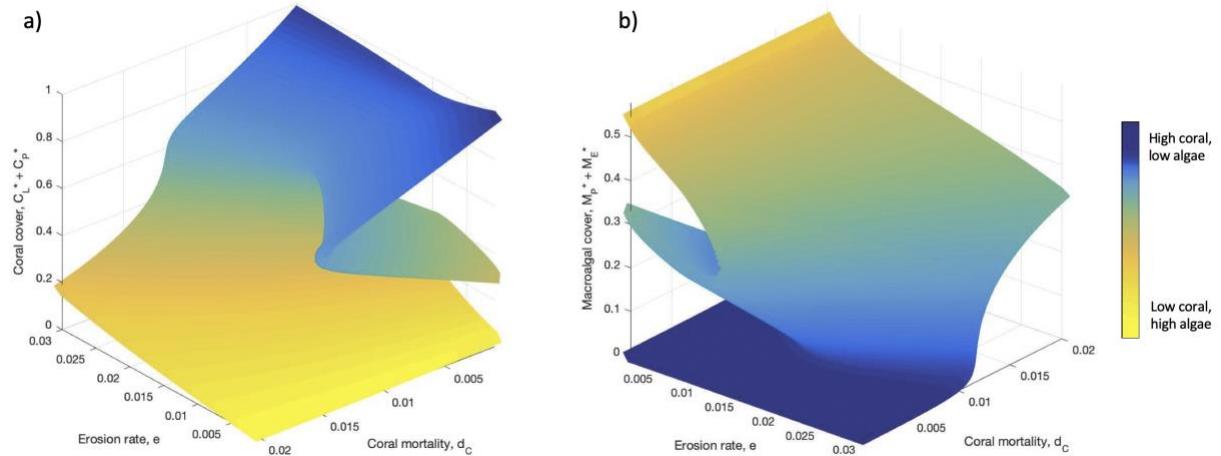


Figure S2. Response surface displaying the resultant equilibrium cover of a) live coral and b) macroalgae and at varying values of both the erosion rate of dead corals, e , and coral mortality, d_c . Blue shading represents high-coral, low-macroalgae equilibria, and yellow represents low-coral high, macroalgae equilibria.

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