



Research



Cite this article: Chakraborty S, Bejarano S, Kooi B, Merico A. 2026 Impacts of different recruitment density-dependences on post-disturbance coral reef recovery. *J. R. Soc. Interface* **23**: 20250281. <https://doi.org/10.1098/rsif.2025.0281>

Received: 2 April 2025

Accepted: 29 October 2025

Subject Category:

Life Sciences—Mathematics interface

Subject Areas:

biomathematics, ecosystem

Keywords:

coral–algae competition, recruitment density-dependence, alternative stable states, hysteresis, coral recovery, mathematical model

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Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.8283125>.

Impacts of different recruitment density-dependences on post-disturbance coral reef recovery

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Coral reefs, among the most productive and diverse ecosystems on our planet, are rapidly degrading and losing corals through a variety of disturbances. Post-disturbance reef recovery rates depend strongly on local community structure and recovery processes. Larval recruitment, a fundamental process regulating reef recovery, is closely related to adult coral cover (i.e. it is a density-dependent process). However, it remains unclear how the form of this density-dependence relationship influences post-disturbance trajectories of coral populations. Here, we use a coral–macroalgae competition model to examine how different functional forms of recruitment density-dependence (linear, convex and concave) affect coral recovery. Our results reveal that coral species characterized by a concave density dependence are more likely to recover following disturbances. By contrast, species with a convex density dependence can recover only when the disturbance is weak or when maximum local recruitment rates are high. We argue that a comprehensive understanding of coral recovery after disturbances requires detailed examination of recruitment processes, particularly their density dependence. Selecting corals expressing concave density dependences and high maximum recruitment rates could lead to more effective reef restoration practices because these corals are more likely to regain ecological dominance following a disturbance.

1. Introduction

Coral reefs are highly productive ecosystems. They play essential roles in marine biodiversity, create habitats for many marine species, provide important economic, social and aesthetic services, and contribute significantly to ocean health [1]. Most coral reefs are affected by various threats due to an array of physical and biological disturbances [2]. Historically, cyclones, diseases and predation by crown-of-thorns starfish have posed serious challenges to coral reefs [3–5]. In the last few decades, marine heatwaves have impacted coral reefs to a much larger spatial extent than any other stressor [6], causing severe coral bleaching events [7], which often resulted in mass coral mortality and shifts in species composition [8]. In March 2024, the National Oceanic and Atmospheric Administration (NOAA) and the International Coral Reef Initiative (ICRI)¹ announced that a new global mass bleaching event (the fourth since 1982) had severely affected reefs globally since the start of the austral summer in 2023. Various ecosystem pathways can emerge after such disturbances. Certain coral populations exhibit some resilience, defined as the ability to return to pre-disturbance ecological conditions, enabling them to recover from bleaching

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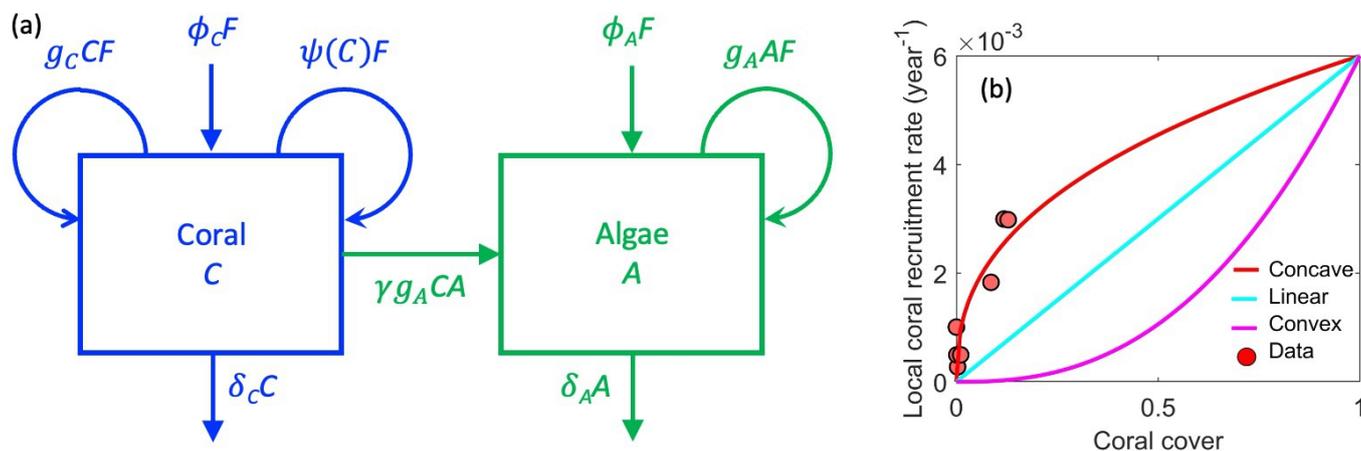


Figure 1. Schematic representation of the model considering coral and algal recruitment. (a) The rectangular boxes represent coral (C) and algal (A) cover. Model processes are represented by arrows; they include: external coral recruitment, $\phi_C F$, local coral recruitment, $\psi(C)F$, lateral coral growth, $g_C C F$, loss of coral cover, $\delta_C C$, external algal recruitment, $\phi_A F$, combination of algal local recruitment and lateral growth, $g_A A F$, loss of algal cover, $\delta_A A$, and coral overgrowth by algae, $\gamma g_A C A$. (b) The shape of the curve describes the relationship between coral cover and local coral recruitment rate (e.g. linear and concave or convex power-laws). The exact shape of the concave power-law was determined by calibration against field data (red circles) from Bramanti & Edmunds [9].

and mortality events [9,10]. However, most corals fail to regain their pre-disturbed ecological state [11], often leading to macroalgae [12] or turf algae [13] dominance. Understanding the underlying processes governing the recovery of coral populations is critically important to evaluate the resilience of reef ecosystems and to formulate effective conservation and management strategies [14].

The recovery of corals can be influenced by a variety of interacting physical and biological processes [14]. Among biological factors, coral recruitment (i.e. the addition of new individuals to populations) is considered one of the most important processes [15,16]. Adult corals produce propagules via both sexual and asexual reproductive modes. Through sexual reproduction, adult corals spawn gametes (eggs and sperm) that fertilise in the water and form larvae (spawners) or release fully developed larvae following internal fertilisation (brooders) [17,18]. Coral larvae remain in a planktonic stage for varying periods of time before settling on a hard surface [17]. The process of asexual reproduction produces free fragments or buds that break off from the parent colony. The successful settlement of propagules on suitable substrates initiates the recruitment process. Newly settled propagules encounter numerous survival challenges, including predation and algal overgrowth [18]. Only a small portion of propagules develop successfully into recruits, juveniles and ultimately adult corals, thus driving population recovery [15]. Therefore, effective recruitment is the result of the successful settlement of propagules and their subsequent post-settlement survival.

A coral recruit is defined as the first detectable individual in a population that appears between two surveys, and, consequently, the recruitment rate is the rate at which these individual coral larvae settle onto a unit area [15]. Naturally, we can expect to record a high number of recruited individuals if surveys are infrequent. Recruits are often defined as small settlers of at least 4 cm in diameter [19]. Environmental factors that affect the rate of recruitment include wave exposure, light, availability of suitable substrate and water quality [20,21]. Once settled, coral recruits are vulnerable to predation (e.g. by parrotfishes) and to overgrowth by fast-growing benthic organisms (e.g. algae) [22,23]. Although coral recruitment rates are negatively affected by conspecific interactions such as competition [24], they can be both positively [25–27] and negatively [9] correlated with adult coral cover. Coral cover is considered one of the best predictors of coral recruitment rate [26].

The shape of the density-dependence relationship between local recruitment rate and coral cover, hereafter the recruitment density-dependence, differs between coral species and is mainly determined by their reproductive strategy [9,25]. The dependence can be both positive and negative as population density increases [28]. A positive effect arises from the enhancement of population-level fecundity and recruitment by high densities of adults, whereas a negative effect arises from conspecific interactions such as competition. The functional form of the recruitment density-dependence can be positive linear [29], positive power-law [9], negative exponential and negative power-law [9]. Previous studies indicate that broadcast spawners often exhibit a power-law relationship [9], whereas brooders tend to follow a linear relationship [29]. Importantly, mathematical models aimed at understanding reef recovery trajectories and coral persistence have mainly assumed a positive linear density-dependent recruitment [30–32]. This oversimplifies and biases the trajectory of reef recovery because the shape of the recruitment density-dependence affects recruitment dynamics and thus influences the way coral populations respond to disturbances [9]. Some studies suggest that nonlinear recruitment rates facilitate coral recovery [9,33]. However, the specific mechanisms of how different functional forms of recruitment density-dependence regulate coral recovery following a disturbance remain unknown.

Here, we present a coral–macroalgae competition model that explicitly incorporates different forms of recruitment density-dependence. We consider three common density-dependence forms, which have a positive effect on coral survival: (i) linear, (ii) convex, and (iii) concave. The exact shape of the concave curve is determined using field data for *Acropora* spp. [9], and the other parameter values are taken from a combination of empirical studies and established coral reef modelling literature. We simulate coral recovery following a number of natural disturbances that result in drastic losses of coral cover, including cyclones, bleaching and intense grazing by crown-of-thorns starfish. We aim to (i) examine the effects of the form of recruitment density-dependence on the post-disturbance trajectory of reefs (§3.1), (ii) understand the underlying mechanisms of coral

Table 1. Model parameters with corresponding literature sources. Parameter values are obtained from a combination of empirical studies and established coral reef modelling literature. Note that, for the sake of generality and due to spatial independence, we considered normalized parameter values.

symbol	description	value	unit	source
ϕ_C	external coral recruitment rate	0.0005	year ⁻¹	[32]
ϕ_A	external algal recruitment rate	0.0001	year ⁻¹	[37]
r	maximum local coral recruitment rate	0.006	year ⁻¹	calibrated
α	exponent of local coral recruitment	0.4, 1, 2.5	—	[9]
g_C	lateral growth rate of corals	0.1	year ⁻¹	[32]
g_A	algal growth rate, combining lateral expansion and local recruitment	0.5	year ⁻¹	[37]
γ	growth of algae over corals	0.5	—	[37]
δ_C	rate of loss of coral cover	0.02	year ⁻¹	[32]
δ_A	rate of loss of algal cover	0.355	year ⁻¹	[32]

recovery following a disturbance for different types of recruitment density-dependence (§3.2), (iii) investigate the interactive effects of maximum local coral recruitment rate and coral mortality on coral recovery for different types of recruitment density-dependence (§3.3), and (iv) assess the interactive effects of continuously varying types of recruitment density-dependence together with coral mortality and maximum local coral recruitment rate on coral recovery (§3.4).

2. Methods

2.1. Model structure

To examine how different coral species recover following disturbances, we extend the coral–macroalgal model developed by Mumby *et al.* [34] by incorporating external recruitment from neighbouring sites and different functional forms of recruitment density-dependence, representing different coral species. The model is independent of any specific spatial location.

The model describes the temporal dynamics of the fractional areas occupied by corals (C) and by macroalgae (A) on a coral reef. A schematic representation of the processes and the interaction between these two components is provided in figure 1a. To concentrate on the recovery of a particular coral species, we assume that the coral reef is composed of a single population representing that species. While macroalgae are typically considered the primary competitors of corals [35], dense algal turfs are becoming more abundant and emerging as strong coral competitors [36]. Therefore, in our model, the term ‘algae’ represents primary competitors in general, which may include macroalgae, dense algal turfs or both. We refer to ‘remaining area’ as the free space (F). Free space corresponds to ‘bare’ substrate and includes recently freed space through coral or algal mortality as well as space occupied by sparse algal turfs that can be easily colonized by corals and algae. At any point in time, all space on the reef is occupied by one of these three entities, so that $C + A + F = 1$. The equations governing the temporal dynamics of corals and algae can be written as

$$\frac{dC}{dt} = \phi_C F + \psi(C)F + g_C CF - \gamma g_A CA - \delta_C C, \quad (2.1)$$

$$\frac{dA}{dt} = \phi_A F + g_A AF + \gamma g_A CA - \delta_A A. \quad (2.2)$$

Here, both coral and algae recruits originate either locally or from neighbouring reefs (external recruitment). External recruitment can only colonize free space at rates ϕ_C and ϕ_A for corals and algae, respectively. g_A is the rate at which free space is taken up by algae due to both local algal recruitment and lateral algal growth. Additionally, algae can overgrow corals, but the rate of algal growth over coral is usually slower than over free space. Hence, the algal growth rate over coral is γg_A with scaling factor $\gamma \leq 1$. Since we aim to investigate the effects of different functional forms of recruitment density-dependence on coral recovery, we separate local coral recruitment, $\psi(C)F$, from corals’ lateral growth, $g_C CF$, where $\psi(C)$ represents the functional form of recruitment density-dependence and g_C represents the lateral growth rate of corals. δ_C and δ_A are the rates of coral and algal cover loss, respectively, through natural mortality, which includes predation. An increase in loss rate is thus attributed to additional mortality from environmental stress.

2.2. Functional forms of recruitment density-dependence

In nature, the form of recruitment density-dependence varies among locations and coral species. In Moorea, French Polynesia (central South Pacific Ocean), for example, the recruitment density-dependence of *Pocillopora* spp. and *Acropora* spp. follow a power-law function [9]. By contrast, in the Great Barrier Reef, mean recruit density is linearly related to mean adult coral density [29]. Previous modelling studies considered a linear function between recruitment rate and coral cover [30–32].

In the present study, we consider a recruitment density-dependence of the following general form:

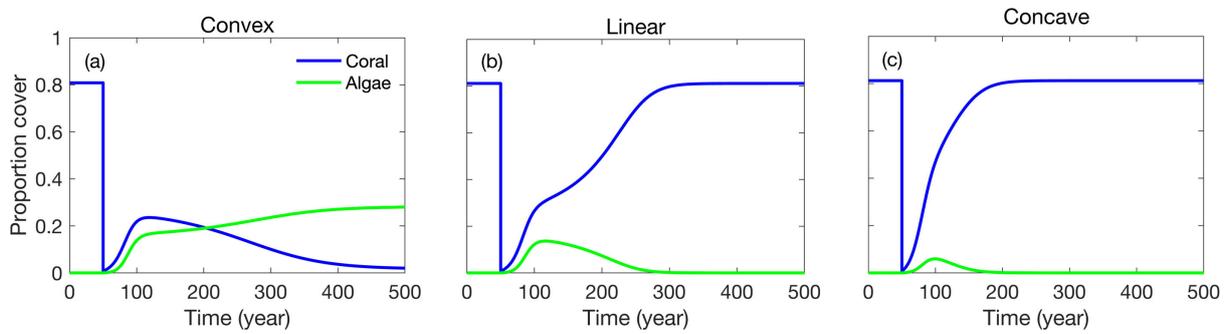


Figure 2. Post-disturbance long-term trajectories of coral and algal cover under different functional forms of recruitment density-dependence: (a) convex power-law, $\alpha = 2.5$, (b) linear, $\alpha = 1$, and (c) concave power-law, $\alpha = 0.4$. The disturbance consists of a sudden and drastic 99% decrease in coral cover at year 50, reflecting a mass bleaching event. Simulations are run for 500 years to allow for the system to reach a stable steady state. The other parameter values are listed in table 1.

$$\psi(C) = rC^\alpha, \quad (2.3)$$

where r is the maximum local coral recruitment rate and the parameter $\alpha > 0$ determines the shape of the recruitment curve (figure 1b). Our analyses focus on positive density-dependent recruitment forms. The implications of negative density-dependence are addressed in §4 based on the obtained results. Here, we examine the effects and mechanisms of coral recovery following a disturbance under three specific scenarios: (i) $0 < \alpha < 1$, i.e. $\psi(C)$ is a concave curve, (ii) $\alpha = 1$, i.e. $\psi(C)$ is a linear function, and (iii) $\alpha > 1$, i.e. $\psi(C)$ is a convex curve. For the case of the concave function, we calibrate the value of α using field data collected in Moorea by Bramanti & Edmunds [9]. The value of α for the convex form is chosen arbitrarily, satisfying $\alpha > 1$, due to the unavailability of data. All other parameter values are taken from the literature, encompassing multiple geographic regions and diverse coral species (table 1). To examine the robustness of model parameters, we performed an in-depth sensitivity analysis (electronic supplementary material, text 1 and figure S1).

2.3. Model simulations

We performed numerical simulations to examine how different forms of recruitment density-dependence affect coral survival and recovery after disturbances. The model was solved numerically using the MATLAB ‘ode45’ solver [38], except for the bifurcation diagrams, which were produced using the software package AUTO [39].

Given the uncertainties involved due to scant observations and lack of laboratory data, we examined the impact of different forms of recruitment density-dependence on coral recovery and analysed simulated time series for convex ($\alpha = 2.5$), linear ($\alpha = 1$) and concave ($\alpha = 0.4$) forms (figure 2). Although the model has multiple equilibria, only two were found to be stable: one dominated by corals (approx. 80%), with a minimal algal cover (approx. 0.03%), and another dominated by algae (approx. 30%), with a minimal coral cover (approx. 2%). We chose the coral-dominated stable equilibrium point as the starting point to represent a healthy reef prior to disturbance. At year 50, we introduced a disturbance reflecting a mass bleaching event by imposing a sudden and severe reduction (99%) in coral cover—comparable to losses observed following an unprecedented heatwave in 2014 at Kapou (Lisianski) in Papahānaumokuākea [40]. We then ran the time series for 500 years to ensure that a stable steady state was reached and to illustrate the long-term system dynamics. This allowed us to investigate how different functional forms of recruitment density-dependence influence the pathway to recovery and whether the system returns to coral dominance or shifts to algal dominance. Coral dominance was defined as the case in which the fractional coral cover exceeds the fractional algal cover.

To understand the mechanisms determining post-disturbance dominance under different density-dependence scenarios, we performed phase plane analyses showing the long-term behaviour of the system (figure 3). First, we examined the undisturbed system by inspecting (i) the trajectories of coral and algal cover and (ii) the equilibrium points reached for different combinations of initial coral and algal cover. We then plotted the trajectory of the coral-dominated stable equilibrium state after introducing the same type of disturbance used in figure 2 (a 99% reduction in coral cover); that is, the path followed by the system from post-disturbance states to new equilibrium points. The analyses were performed for different functional forms of recruitment density-dependence: (i) convex power-law, $\alpha = 2.5$, (ii) linear, $\alpha = 1$, and (iii) concave power-law, $\alpha = 0.4$. We also calculated the likelihood of coral recovery, defined as the fraction of the phase plane where long-term trajectories reach a coral-dominated state, by continuously varying the exponent of coral recruitment (α), which determines the type of recruitment density-dependence, within the range $0 < \alpha < 2.5$ (figure 4). Note that the shift from low to high values of α results in a progression from concave ($\alpha < 1$) to linear ($\alpha = 1$) and, ultimately, to convex forms ($\alpha > 1$).

To better understand the mechanisms underlying the observed variations in basins of attraction (figure 3), we analysed a one-parameter bifurcation diagram to visualize equilibrium points and their stability under a varying rate of coral loss (δ_c) (figure 5) and across three functional forms of recruitment density-dependence: convex power-law ($\alpha = 2.5$), linear ($\alpha = 1$) and concave power-law ($\alpha = 0.4$). A detailed description of the bifurcation analysis is provided in electronic supplementary material, text 2. In our model, loss of coral cover due to disturbance includes impacts from diseases, predation by crown-of-thorns starfish, and environmental events such as cyclones and marine heatwaves. We varied the loss rate between 0 and 0.1 year⁻¹, a range that is consistent with empirical estimates from long-term monitoring (0.005–0.035 year⁻¹ [41,42]) and short-term severe

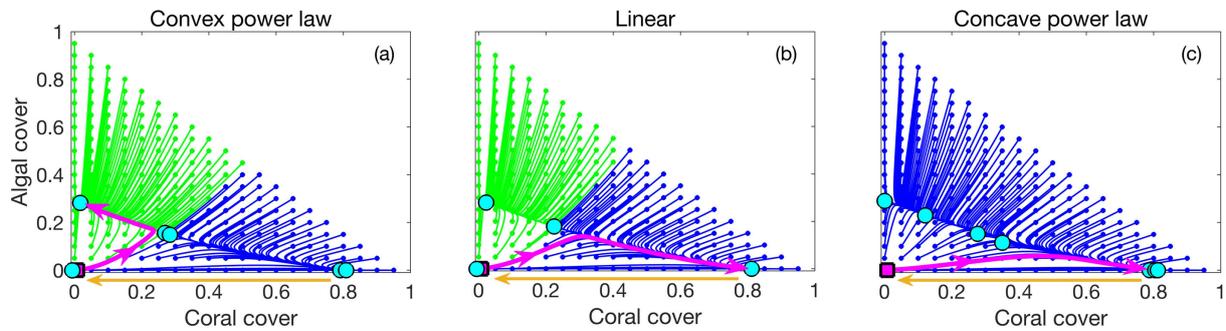


Figure 3. Phase plane analyses showing the fraction of coral and algal cover at equilibrium and long-term trajectories starting at different initial conditions for coral and algal cover. Phase plane analyses are performed for different functional forms of recruitment density-dependence: (a) convex power-law, $\alpha = 2.5$, (b) linear, $\alpha = 1$, and (c) concave power-law, $\alpha = 0.4$. Algal and coral covers at equilibrium are represented by cyan circles for the three different density-dependence forms. The basins of attraction are indicated by green lines for algal-dominated equilibrium and by blue lines for coral-dominated equilibrium. The magenta squares indicate coral cover after disturbance (figure 2), and the yellow arrows indicate the magnitude of the shifts from pre-disturbance coral cover. The magenta lines show the trajectories of the coral-dominated stable equilibrium state after introducing the same type of disturbance used in figure 2, which reflects a system characterized by either algal dominance (a) or coral dominance (b,c). The other parameter values are listed in table 1.

disturbance events (up to 0.2 year^{-1} [43]), thereby encompassing both mild chronic losses and acute bleaching-induced declines. Accordingly, we interpret increases in coral loss rates above 0.02 year^{-1} (2% cover per year) as reflecting additional mortality from external stressors—an issue of particular relevance in the current context of global warming [44].

To determine how the three alternative states (i.e. exclusive coral dominance, alternative stable states and exclusive algal dominance) vary with coral loss rates (δ_c) and maximum local coral recruitment rates (r) under different density-dependence scenarios, we analysed the stabilities of the equilibrium points (figure 6). In the context of global warming, r is another parameter of particular interest [28]. In this analysis, we varied these parameters within ranges obtained from modelling literature [32,37] and inspected the final state of the system.

By continuously varying the local recruitment exponent α (which determines the shape of the recruitment density-dependence) as a function of coral loss rate (δ_c) and maximum local coral recruitment rate (r) independently, we further investigated how different density-dependence forms affect the three alternative states (figure 7).

3. Results

3.1. Effects of recruitment density-dependence forms on coral recovery following disturbance

From the time series, we find that both coral and algae start increasing just after the disturbance, irrespective of the shape of density-dependence (figure 2). However, when the recruitment density-dependence follows the convex function ($\alpha = 2.5$), benthic cover ultimately shifts from a coral-dominated to an algal-dominated state (figure 2a). In the other two cases, corals recover to pre-disturbance levels, the stable equilibrium point corresponding to coral dominance (figure 2b,c).

3.2. Mechanisms of coral recovery

Due to the nonlinear nature of the system, varying initial combinations of algal and coral cover reach distinct equilibrium states (figure 3). Although many equilibrium points exist, only two of them are stable under both convex and linear recruitment forms; one is characterized by coral dominance and the other is characterized by algal dominance (figure 3a). Distinct basins of attraction are observed for both states. This means that the final state of the system depends on the initial coral and algal cover. When the recruitment density-dependence follows the convex function ($\alpha = 2.5$), a disturbance involving a 99% reduction in coral cover forces the system to change its basin of attraction from coral to algal dominance (figure 3a). By contrast, in the linear case ($\alpha = 1$), a disturbance does not change the basin of attraction and the system returns to a steady state characterized by coral dominance (figure 3b). Note that the trajectory following a disturbance largely depends on the strength of the disturbance. Interestingly, when the recruitment density-dependence follows a concave form ($\alpha = 0.4$), multiple equilibrium points exist, but only one of the coral-dominated states is stable (figure 3c). As a result, the system returns to a coral-dominated state, regardless of the initial coral cover, indicating a robust tendency for recovery.

A continuous variation of the exponent of coral recruitment (α), which determines the type of recruitment density-dependence, shows that low values of α ($\alpha < 0.45$; strong concavity) ensure a high recovery likelihood of corals (figure 4). However, with an increase in α , the recovery likelihood decreases and remains low for high values of α .

Our bifurcation analysis shows that regardless of the shape of recruitment density-dependence, very low coral loss rates (δ_c lower than approx. 0.01 year^{-1}) lead to coral dominance, whereas high coral loss rates (δ_c higher than approx. 0.043 year^{-1}) result in low coral cover and, consequently, in algal-dominated states (figure 5). Interestingly, with intermediate coral loss rates, we find alternative stable states with the initial condition of coral cover determining the trajectory towards coral or algal dominance. The change in dominance following a disturbance is possible only when the system is in alternative stable states.

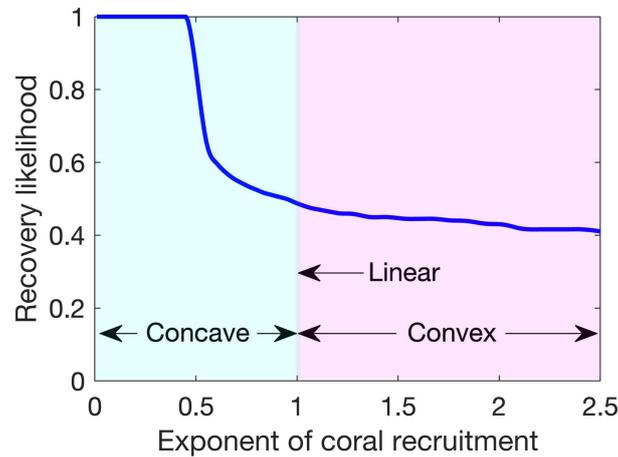


Figure 4. Variation in the likelihood of recovery of corals as a function of the type of recruitment density-dependence (as indicated by the exponent of coral recruitment (α)). The likelihood of recovery is defined as the fraction of the phase plane in which long-term trajectories lead to coral dominance. The exponent of coral recruitment spans from concave (cyan) to convex (magenta) density dependence, with linear forms occurring at the transition value. The other parameter values are listed in table 1.

The range of coral cover loss rates leading to exclusive coral dominance is minimal under the convex recruitment density-dependence form ($\alpha = 2.5$), higher under the linear form ($\alpha = 1$) and maximal under the concave form ($\alpha = 0.4$) (figure 5). However, the range of coral cover loss rates corresponding to alternative stable states shows a noticeable decreasing trend as we move from convex to linear and to concave forms. At a coral loss rate of 0.02 year^{-1} , the presence of alternative stable states in the convex and linear forms shows the existence of two distinct basins of attraction (figure 3a,b). Conversely, at the same coral loss rate, the exclusive coral-dominated state observed under the concave form confirms the presence of a single basin of attraction, as in figure 3c.

Due to the presence of alternative stable states, the system exhibits hysteresis, meaning that the coral–algae system follows different trajectories during the transient phase right after a disturbance and during a recovery. While a relatively small increase in the rate of live coral cover loss can trigger a transition from a coral to algal dominance, a return to coral dominance requires a substantial decrease in coral loss rate. Importantly, due to the decrease in the range of coral cover loss rate corresponding to alternative stable states, a return to the coral-dominated state becomes easier when shifting from convex to linear and to concave density-dependence forms.

3.3. Interactive effects of maximum local coral recruitment rate and coral loss rate

When the recruitment density-dependence follows a convex form ($\alpha = 2.5$), exclusive coral dominance occurs only at very low and within a narrow range of coral cover loss rates ($\delta_C < 0.008 \text{ year}^{-1}$) (figure 6a). However, the overall region of exclusive coral dominance increases in the linear case ($\alpha = 1$) (figure 6b) and reaches a maximum in the concave case ($\alpha = 0.4$) (figure 6c), while the regions corresponding to alternative stable states and exclusive low coral cover decrease along this gradient. An increase in the maximum local coral recruitment rate (r) raises the probability of exclusive coral dominance under the linear and concave density dependence forms, but has no effect under the convex form (figure 6). By contrast, the possibility of alternative stable states increases with higher maximum local coral recruitment rates in the convex form, while it decreases for the linear and concave forms. Therefore, post-disturbance coral dominance is regulated by the interactive effect of maximum local recruitment rates and the form of recruitment density-dependence.

3.4. Interactive effects of maximum local coral recruitment rate, coral loss rate and recruitment density-dependence

We find that the probability of exclusive coral dominance decreases (with a corresponding increase in the probability of alternative stable states) when shifting from concave ($\alpha < 1$) to convex ($\alpha > 1$) forms. Increasing coral loss rates (δ_C) drives a transition from exclusive coral dominance to exclusive low coral cover through alternative stable states (figure 7a). This trend occurs irrespective of the recruitment density-dependence form. Only the coral cover loss rate differs during the transition from one state to another for different values of α (figure 7b). Moreover, with coral populations characterised by very high α (convex form), the system can remain in alternative stable states, although the probability of coral recovery increases with increasing maximum local coral recruitment rate (r) (electronic supplementary material, figure S2). Therefore, a return to coral dominance following a disturbance strongly depends on the interaction among maximum local recruitment rate, coral cover loss rate and the form of recruitment density-dependence.

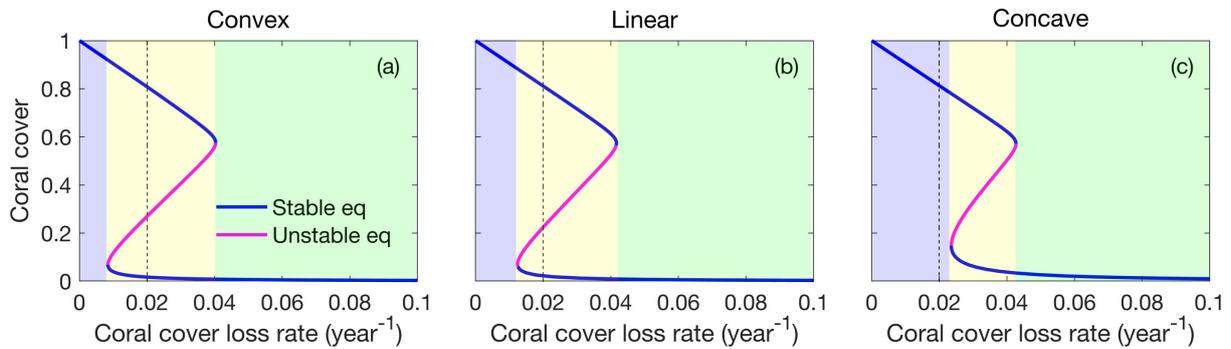


Figure 5. Coral cover at equilibrium under varying coral loss rates, δ_C , under different forms of recruitment density-dependence (convex, $\alpha = 2.5$; linear, $\alpha = 1$; concave, $\alpha = 0.4$). The blue lines represent fractional areas occupied by corals at stable equilibria, whereas the magenta lines represent coral cover at unstable equilibria. Blue-shaded regions represent coral-dominated states, yellow-shaded regions represent alternative stable states, and green-shaded regions represent low coral cover states. The dotted vertical line at $\delta_C = 0.02 \text{ year}^{-1}$ is the value of the coral cover loss rate used in figures 2 and 3. The other parameter values are listed in table 1.

4. Discussion

We presented a coral–algae competition model with local coral recruitment rates explicitly dependent on coral cover. In line with field observations, we considered three functional forms of density-dependent recruitment: linear, concave and convex. We found that coral species characterised by a concave density dependence show the highest probability of recovering following a disturbance. However, coral recovery also depends on the interactive effects of maximum local recruitment rate and the type of density-dependent recruitment.

Over the past few decades, accumulating evidence has documented phase shifts from corals to macroalgae, algal turfs [13], urchin barrens [45] or sponges [46]. Our results suggest that extensive coral mortality events could trigger swift transitions from coral-dominated to non-coral-dominated states, with low coral loss rates being a prerequisite for coral recovery. In natural systems, such extensive coral mortality can be attributed to one or more natural events, including storm surges, disease outbreaks and bleaching, which intensify over a short time span. Transitions from coral to seaweed (macroalgae) dominance, due to alternative basins of attraction, are widely reported [47–49]. Overfishing of herbivores [48,50] and/or nutrient enrichment [51] are potential drivers of phase shifts. Previous modelling studies explored phase shifts by examining the role of different ‘external’ stressors (e.g. sedimentation, eutrophication, overfishing and climate change, reviewed by [52]), and ‘internal’ factors (e.g. life stages) affecting the vulnerability of macroalgae to herbivory [37]. By contrast, our study focuses on coral mortality as the primary driver of phase shifts. With this we aim to reflect the effects of increasingly frequent mass bleaching events that could foster alternative stable states and trigger phase shifts in reef ecosystems.

The presence of alternative stable states and hysteresis has significant implications for the implementation of reef restoration strategies. Our model results suggest that even a small decline in coral cover can trigger a shift from a coral-dominated to an algal-dominated state. Once this shift occurs, simply reversing the stressor that caused the reduction of coral cover is not sufficient to switch back to the coral-dominated state due to hysteresis. Instead, the system stabilizes in an alternative state. In such cases, enhancing recruitment through restoration may not guarantee coral recovery unless the recruitment rate exceeds a critical threshold. Importantly, this threshold is influenced by various parameters, including species-specific traits and environmental conditions. Therefore, when alternative stable states exist, successful restoration requires a careful assessment of the threshold in the recruitment rate to overcome the system’s resistance to change.

Building on this, our modelling framework enables us to discern how different forms of recruitment density-dependence influence the post-disturbance trajectory of a reef. Specifically, we examined three forms of positive density dependence recruitment: concave, linear and convex, and compared the resulting coral recovery trajectories following a disturbance. Despite the limited number of studies addressing recruitment density-dependence in corals, there is empirical evidence supporting the occurrence of concave and linear forms in some coral species. For instance, concave density dependence has been observed in *Acropora* spp. in French Polynesia [9], while linear patterns have been reported in brooding species such as *Porites astreoides* [29]. Although convex density dependence is less commonly described, there is evidence suggesting that it may occur in nature. For instance, *Acropora* spp. from the Great Barrier Reef showed a disproportionate increase in larval recruitment as the proportion of gravid colonies approached 100% across large spatial scales [53]. The authors attributed this to enhanced gamete fertilisation success and predator satiation during mass spawning events. While recruitment would ultimately be constrained by space and competition, no saturation was observed within the empirical range studied in Hughes *et al.* [53]. Including all three forms in our numerical simulations provided a comprehensive view of how coral recovery trajectories might vary under different density-dependence regimes. Our results suggest that the likelihood of coral recovery declines progressively from concave to convex forms. Coral genera characterised by concave forms are more likely to re-establish dominance after a disturbance, as they tend to produce more recruits at low population densities, providing them a competitive advantage under stressful or degraded conditions. This idea is supported by the local recovery of *Acroporid* corals in French Polynesia, where survey data showed disproportionately large increases in recruitment as adult coral cover rose from very low to slightly higher levels—a pattern consistent with concave recruitment density-dependence—following two catastrophic disturbances [9].

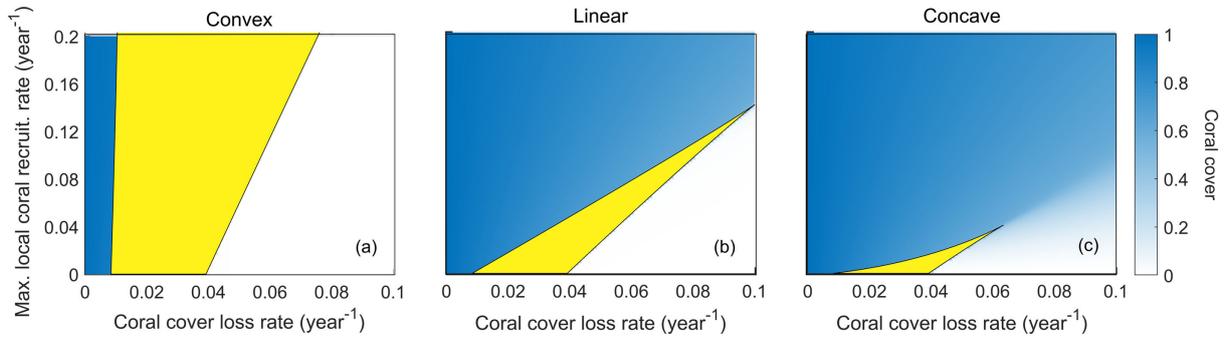


Figure 6. Steady-state regimes under varying maximum local coral recruitment rates (r) and rates of coral cover loss (δ_C). The blue colour represents different equilibrium states of coral cover. The yellow regions mark alternative stable states. The other parameter values are listed in table 1.

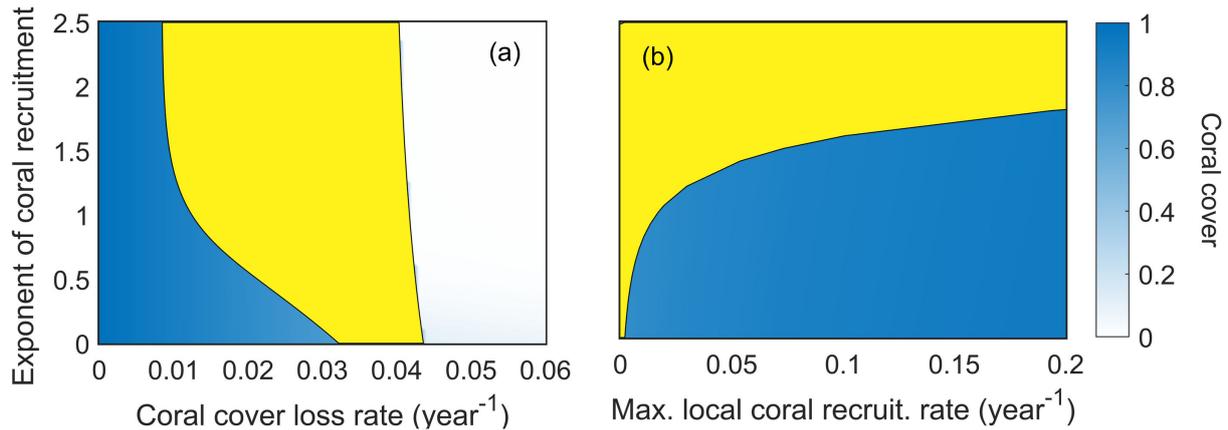


Figure 7. Steady-state regimes obtained by continuously varying α , the exponent of coral recruitment, which determines the type of recruitment density-dependence. The parameter α is set to vary with (a) coral cover loss rate (δ_C) and (b) maximum local coral recruitment rate (r). The blue colour represents different coral cover equilibrium states. Yellow regions mark areas with alternative stable states. The other parameter values are listed in table 1.

Additionally, our study suggests that coral genera exhibiting convex density dependence rely on high local recruitment rates for post-disturbance recovery, making these corals more vulnerable to collapse under persistent low-density conditions.

The relative importance of recruitment for coral reef recovery is system-specific. Life history strategies can affect the recovery of corals following disturbances, but recovery appears to be species-specific, with different coral species showing different types of recruitment density-dependence. Species with a fast turnover rate (e.g. *Pocillopora* spp.) can quickly recolonize recently disturbed habitats [54,55], whereas species with a low recruitment rate (e.g. *Acropora* spp. on coral reefs of Moorea [9]), which typically dominate environments favourable for reef growth and development (i.e. low nutrient levels), have slow recovery capacities [56]. However, the relationship between recruitment rate and coral recovery is not straightforward and depends on multiple factors [10]. For example, despite having low recruitment rates compared with other places [57], coral reefs in Moorea appear able to recover following massive and recurrent disturbances [58]. Interestingly, the particular resilient genus *Acropora* from Moorea exhibits an exceptionally low local recruitment rate but a concave recruitment density-dependence [9]. Our results demonstrate that the likelihood of coral recovery can be independent of the local recruitment rate when the dominant coral species follows a concave recruitment density-dependence. Therefore, we suggest that the form of recruitment density-dependence probably played a role in the recovery of *Acropora* spp. in Moorea.

While our study focuses on positive recruitment density-dependence, coral recruitment rates can also be negatively related to coral cover, e.g. negative power-law dependence, where the coral recruitment rate decreases with increasing coral cover [9]. Our results show that the possibility of recovery following a disturbance can increase if maximum local recruitment rates are high. Extending this idea, we propose that the recovery of species with a negative exponential or a negative power-law recruitment density-dependence requires very high maximum local recruitment rates to compensate for extensive losses of coral cover due to disturbances. The genus *Pocillopora* in Moorea recovered following massive and recurrent disturbances despite following the negative power-law or negative exponential forms of recruitment density-dependence [9]. Interestingly, *Pocillopora* spp. also showed an extremely high maximum recruitment rate [9], providing empirical support for our hypothesis. We conclude that successful coral recovery depends on the interplay between maximum local coral recruitment rate and the recruitment density-dependence form.

Our modelling framework also enables us to determine how different forms of recruitment density-dependence influence the post-disturbance trajectory of a reef. The existence of different nonlinear forms of recruitment density-dependence highlights the significance of species-specific recruitment events. Previous studies indicated that identifying the form of recruitment density-dependence most conducive for corals to re-establish dominance after a disturbance would make restoration efforts more effective [9,33,59]. Considering species-specific forms of recruitment density-dependence, recruitment rates, as well as genetic diversity, when investing in reef restoration is thus crucial to long-term ecosystem resilience and functionality of the

restored coral reefs [60,61]. Our study confirms that the local recruitment rate of a coral species is an important determinant of its post-disturbance trajectory. We propose to strategically consider both the form of recruitment density-dependence and the maximum local recruitment rate when selecting species for transplantation in disturbed areas. Species with concave density dependence, irrespective of maximum local recruitment rates, may recover more rapidly than those with convex or linear density dependence and low maximum local recruitment. Although focusing exclusively on these species could have unintended consequences for overall species richness and community structure, an initial emphasis on these species may help mitigate the most severe impacts and, thus, buy us time while developing programmes with a more comprehensive set of species. Moreover, considering the wide array of factors determining the post-settlement survival of small corals [62], environmental conditions and disturbance regime of the restored area will logically remain important factors in mitigation strategies.

In the context of the coral–algae competition model with external recruitment from neighbouring sites and different forms of recruitment density-dependence, the exploration of linear and power-law forms provides a significant step forward towards understanding the role of recruitment in coral recovery. However, our study also brings remaining knowledge gaps in sharp relief. For example, newly recruited individuals are more vulnerable to disturbances and predation than adults. Therefore, our model could be modified by incorporating life stages within coral populations with higher mortality for the newly recruited individuals. This will help to better understand coral recovery because recruitment alone does not ensure population growth if the mortality of newly recruited individuals is high (e.g. [63]). Future studies could also evaluate how prioritizing either fast recovering species (expressing linear and concave density dependence) or slow recovering species (expressing convex density dependence) affects overall reef recovery. Testing these different strategies may reveal the conditions that best promote long-term resilience and may help guiding targeted restoration efforts. Moreover, available empirical data suggest that recruitment in some corals exhibits negative density dependence [9,64]. Future modelling studies should consider more forms of recruitment density-dependence and include interspecific competition to investigate the full range of effects determining the post-disturbance fate of a reef. Although the exact shape of the concave functional form was determined based on field data [9], to enhance the explanatory capacity of models, we advocate for new laboratory experiments to empirically determine the precise forms of density dependence for different coral species as these functional forms are key to constrain models. Lastly, the time required for full coral recovery in our model (approx. 100–200 years) is unrealistically long, particularly given the expected increase in bleaching frequency [65,66]. While using parameters from previous studies allowed us to capture the general mechanisms of recovery under different forms of density dependence, including more realistic timescales would require laboratory experiments aiming at quantifying those rates that drive coral recovery dynamics. These knowledge gaps can be potentially bridged by combining models with more detailed descriptions of natural recovery rates and experimental studies that capture recovery within ecologically realistic time frames. Notwithstanding these limitations, our results shed new light on the ecological and physiological features that are most relevant to coral recovery and, as such, pave the way for designing knowledge-based conservation and restoration strategies.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The authors declare that the sources of all data supporting the findings of this study are available within the article. Matlab codes for figure 2 are available at [67].

Supplementary material is available online [68].

Declaration of AI use. Artificial intelligence (ChatGPT) was used solely to improve the readability and language of the manuscript. No content, analyses or scientific interpretations were generated by AI.

Authors' contributions. S.C.: conceptualization, investigation, methodology, software, visualization, writing—original draft, writing—review and editing; S.B.: conceptualization, writing—review and editing; B.K.: investigation, software, writing—review and editing; A.M.: conceptualization, resources, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. No funding has been received for this article.

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