

# Emergent Spatial Patterns Can Indicate Upcoming Regime Shifts in a Realistic Model of Coral Community

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**ABSTRACT:** Increased stress on coastal ecosystems, such as coral reefs, seagrasses, kelp forests, and other habitats, can make them shift toward degraded, often algae-dominated or barren communities. This has already occurred in many places around the world, calling for new approaches to identify where such regime shifts may be triggered. Theoretical work predicts that the spatial structure of habitat-forming species should exhibit changes prior to regime shifts, such as an increase in spatial autocorrelation. However, extending this theory to marine systems requires theoretical models connecting field-supported ecological mechanisms to data and spatial patterns at relevant scales. To do so, we built a spatially explicit model of subtropical coral communities based on experiments and long-term datasets from Rapa Nui (Easter Island, Chile), to test whether spatial indicators could signal upcoming regime shifts in coral communities. Spatial indicators anticipated degradation of coral communities following increases in frequency of bleaching events or coral mortality. However, they were generally unable to signal shifts that followed herbivore loss, a widespread and well-researched source of degradation, likely because herbivory, despite being critical for the maintenance of corals, had comparatively little effect on their self-organization. Informative trends were found under both equilibrium and nonequilibrium conditions but were determined by the type of direct neighbor interactions between corals, which remain relatively poorly documented. These inconsistencies show that while this approach is promising, its application to marine systems will require detailed information about the type of stressor and filling current gaps in our knowledge of interactions at play in coral communities.

**Keywords:** regime shifts, early-warning signals, alternative stable states, coral reefs, subtidal ecosystems, abrupt transitions.

## Introduction

While many ecosystems appear resilient to pulse perturbations and respond gradually and predictably to changes in environmental conditions, this is not always the case (Scheffer et al. 2001). Ecological systems can respond abruptly, even in the face of gradual external changes. These abrupt responses are different types of “regime shifts”—large and sometimes hard-to-reverse transitions in the state of an ecosystem. Identifying where and how shifts occur is essential if we are to anticipate (and prevent or mitigate) ecosystem degradation in the coming decades (Suding et al. 2004). Among the possible approaches for doing so is the development of indicators of abrupt transitions, or “early-warning signals,” which are spatial or temporal statistical signatures that arise in observations as a system is approaching a tipping point at which a regime shift occurs (Dakos et al. 2012; Kéfi et al. 2014). Spatial early-warning signals, in particular, make use of the fact that the ecological positive feedbacks that underpin regime shifts often have a spatial component. For example, spatial reconfiguration associated with regime shifts appear to arise in arid systems because vegetation establishment is greater around existing plants, by providing shade and concentrating water and nutrients (Rietkerk et al. 2002; Kéfi et al. 2007b). This feedback is local as it occurs at small spatial scales around a biogenic species, leading to self-organization of vegetation into characteristic spatial patterns. These patterns are altered

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with increasing stress levels in a predictable and measurable way, for example through increased spatial autocorrelation (Dakos et al. 2010), which makes them possible indicators of upcoming shifts.

Many of these indicators do not depend on the specific ecological mechanisms of interaction but only on the presence of local positive feedbacks leading to self-organization. As a result, this approach based on spatial patterns has been applied to a wide variety of terrestrial systems, such as arid systems (Kéfi et al. 2007a), tidal marshes (van Belzen et al. 2017), and forest/savanna transitions (Eby et al. 2017). Methods exist to compute them on remote-sensing data (Génin et al. 2018a), and statistical issues are being worked on to make the indicators derived from theoretical models more applicable to real situations (Nijp et al. 2019; Sankaran et al. 2019). However, while positive interactions are common, the strength of positive feedbacks can vary across ecosystems, or they can be dampened by negative feedbacks (Mayor et al. 2019), so they may not always be strong enough to lead to detectable signatures at the landscape scale. This can make indicator trends undetectable for all practical purposes or downright opposite of their theoretical expectations (Weerman et al. 2012; Génin et al. 2018b). Thus, extending this approach to new ecosystems requires first assessing whether and how indicators vary as stress increases and understanding how the self-organization of habitat-forming species relates to ecological interactions.

We aim here to extend and test the applicability of the indicator approach, primarily developed on terrestrial systems, to the study of regime shifts in coral communities, a paradigmatic (Hughes et al. 2017) central issue for the management and conservation of the typically high-diversity reefs (Dudgeon et al. 2010; Mumby et al. 2013). Identifying the conditions for the emergence of regime shifts and alternative stable states has been a long-standing, extensively discussed goal of marine ecology (Petraitis and Latham 1999; Petraitis and Dudgeon 2004). Many of those shifts have been shown to be tied, through observations and models, to the existence of strong positive feedbacks (Petraitis and Dudgeon 2004; Bramanti and Edmunds 2016; van de Leemput et al. 2016). Some of them are local, in which algae or corals can preferentially establish, survive, or grow faster closer to conspecifics, and are underpinned by a wide array of ecological mechanisms and interactions. Coral cover may increase faster around established colonies simply through the lateral expansion of existing colonies—a common inclusion in coral model dynamics (Langmead and Sheppard 2004; Fung et al. 2011; Muthukrishnan et al. 2016)—or because of a short dispersal distance of propagules (Johnson and Preece 1992; Carlon and Olson 1993). Corals can also provide structural complexity that supports a diverse herbivore community able to control algal growth and open bare space for coral recruitment (Hughes 1994; Graham et al. 2006). For algae,

similar spatial feedback mechanisms include higher nutrient availability around established algae (Muthukrishnan et al. 2016), reduced herbivory within algal beds (Hoey and Bellwood 2011), and direct lateral expansion of algae into adjacent areas (Mumby et al. 2006, 2007; Fung et al. 2011). Regardless of the particular ecological mechanisms, the effects of positive feedbacks on system dynamics are known: they will increase the probability of large regime shifts, possibly with alternative stable states when they are particularly strong (Muthukrishnan et al. 2016; van de Leemput et al. 2016).

Despite this well-known effect of spatial feedbacks on ecosystem dynamics, little information exists on whether changes in spatial patterns can be prognostic of regime shifts in coral systems (but see Fung et al. 2013). Spatial patterns indicative of local, spatially dependent positive interactions have been reported in corals, such as spatial aggregation (Carlon and Olson 1993), halos (Madin et al. 2022), and large-scale reticulate patterns (Schlager and Purkis 2015; van der Kaaden et al. 2020). While in principle these patterns could be used as indicators of regime shifts, they likely do not respond in the same way to different stressors and may not always produce their expected increasing trend in ecological settings that include both positive and negative feedbacks (Mayor et al. 2019). We examine here the behavior of three common indicators proposed in the published literature—autocorrelation (Dakos et al. 2010), variance (Guttal and Jayaprakash 2009), and patchiness (Kéfi et al. 2011)—with the expectation that all three exhibit positive trends along gradients of increasing stress for corals.

We base this work on a spatially explicit stochastic cellular automaton model for the subtropical coral communities of Rapa Nui (Easter Island) parametrized with experimental and monitoring observations. The model reproduces the main states in the coral/algae community, and we analyzed spatial indicators along gradients of increasing coral mortality (e.g., pollution), decreasing herbivore pressure, and increasing frequency of mortality events (e.g., bleaching). Three factors make Rapa Nui an ideal system to test and expand the theory of early-warning signals and to make available useful management tools. First, compared with other coral-dominated systems, coral communities at Rapa Nui comprise relatively few habitat-forming and consumer species (Wieters et al. 2014), which makes it easier to capture the critical interactions and players in the system. Second, experimental and monitoring studies over the past 15–20 years have allowed identification of strong ecological interactions and their spatial variability. These interactions, while tuned to the Rapa Nui system, are common to all or most coral communities. Third, the extreme clarity of ocean waters at Rapa Nui (Morel et al. 2007) permits characterization of spatial patterns at sufficient resolution and over unusually large spatial extents compared with other marine

ecosystems, allowing future evaluation of model predictions. We simulate a range of conditions and parameters that represent Rapa Nui and many other reefs, making our conclusions on early-warning indicators broadly applicable.

### Methods

We base our study on the shallow (<25 m) hard bottom communities of the hyperoligotrophic waters of Rapa Nui (Easter Island), in the eastern-central South Pacific (von Dassow and Collado Fabbri 2014). Here, subtidal seascapes are largely dominated by high cover (40%–80%) of corals, with the vast majority consisting of just two species; *Porites lobata* and *Pocillopora verrucosa* (Glynn et al. 2003; Wieters et al. 2014). Within and across these coasts, dominant coral habitats are patchily distributed, alternating spatially with open, bare rock or patches of fleshy macroalgal turfs composed mainly of foliose corticated algae, such as *Spatoglossum stipitatum* and *Lobophora variegata*. The main mobile benthic herbivore is the urchin *Diadema savignyi* (Wieters et al. 2014), which reaches higher density in coral-dominated patches.

### Model Description

Our model describes the changes in covers of coral, algae, and bare areas in a spatially explicit stochastic cellular automaton. The spatial domain of the model represents a homogeneous area equivalent to a site surveyed by a diver (a square of side 10 to 20 m). The model is implemented as a 2D lattice in which each cell of about 20 × 20 cm roughly matches the scale of field experiments and can be in only one of the three elementary states (coral, algae, or bare). At each time step, which represents 1 week, individual cells can switch from one state to another, with probabilities that capture the relative rates at which ecological processes occur. We used a four-way (Von Neumann) neighborhood; that is, cells are considered to be neighbors when they share an edge.

*Recruitment of Algae and Coral.* Increase in algal cover over space can result either from the successful establishment of propagules (spores) that settle from the water column or the lateral expansion of algae. These two processes result in (i) a homogeneous increase in cover over the landscape and (ii) increased algal cover near established algae. These two effects are reflected in the following probability of “bare” cells to become “algae” cells:

$$P(b \rightarrow a) = r_a(\alpha + (1 - \alpha)\rho_a) + l_a q_a,$$

where  $r_a$  is the rate at which algae grows from propagules (spores), which is multiplied by the amount of propagules

in the water column coming from two sources. One is the propagules produced by algae at the site and therefore depends on  $\rho_a$ , the proportion of cells in the algae state in the landscape. The other is the fraction of propagules that come from more distant sites, transported by currents to the local site and can be visualized as a relatively constant subsidy of spores. Thus,  $\alpha$  captures the “openness” of the modeled site; a high value of  $\alpha$  models the fact most propagules come from outside the site, whereas a low  $\alpha$  yields locally dependent algal growth in which the amount of propagules that settle is proportional to the site-wide abundance of algae. Because the species of algae at Rapa Nui are typically not taller than 20–30 cm and produce spores that can readily establish on the substrate, we considered here  $\alpha = 0.01$  (i.e., 1% of algal propagules come from outside the modeled site). The term  $l_a$  is multiplied by  $q_a$ , the proportion of cell neighbors in the algae state, and captures the effective increase of algal cover near existing algae, either through lateral expansion or the recruitment from propagules or fragments dispersed at a very short distance from the plant. This mechanism constitutes a local positive feedback, as it will increase the growth rate of algae around existing algae.

Increases in coral cover can result from the successful settlement and growth of larvae from the water column or the lateral expansion (growth) of existing coral colonies. At Rapa Nui, we found no dependence of the recruitment rate on the abundance of corals at a given site, nor increased recruitment near existing corals (A. Herreras, unpublished data). This is likely because the main coral species (*Pocillopora verrucosa* and *Porites lobata*) act there as broadcast spawners (Buck-Wiese et al. 2018), increasing the dispersal range of propagules. The probabilities of cells transitioning from the “bare” to the “coral” state is thus modeled as

$$P(b \rightarrow c) = r_c(1 + d_0 q_c),$$

where  $r_c$  is the rate at which space is colonized by coral colonies growing from coral propagules (planktonic larvae) that survive initial mortality, settle, and grow into an adult coral colony. The term  $r_c$  thus represents a net growth rate, as it includes the mortality due to consumption of coral recruits by urchins and other consumers. The term  $d_0$  quantifies how fast coral cover increases in the vicinity of existing corals, relative to the spatially homogeneous recruitment, and captures the net effect of one or more local ecological feedbacks. Cases in which coral cover increases faster around established colonies will be represented by a positive  $d_0$ , for example for species with important lateral expansion (e.g., reef building) or growth from fragments breaking off colonies, with very short dispersal. Coral species for which new colonies establish less around current adults (e.g., due to strong neighborhood competition) will have  $d_0 < 0$ .

### Mortality of Coral and Algae

At each time step, a cell in the coral state has the following probability of dying and switching to the bare state:

$$P(c \rightarrow b) = m_c + \delta_e m_e,$$

where  $m_c$  is the base mortality rate of adult corals and  $m_e$  is the mortality rate during an acute mortality event. At each time step,  $\delta_e$  has the probability  $p_e$  of being equal to 1 and is 0 otherwise. Setting  $m_e$  much higher than  $m_c$  allows mimicking acute pulse mortality events occurring at a single time step (e.g., a bleaching event). In this manner,  $p_e$  can be tuned to a given frequency of disturbances or return times of a Poisson process, such as storms or heat waves.

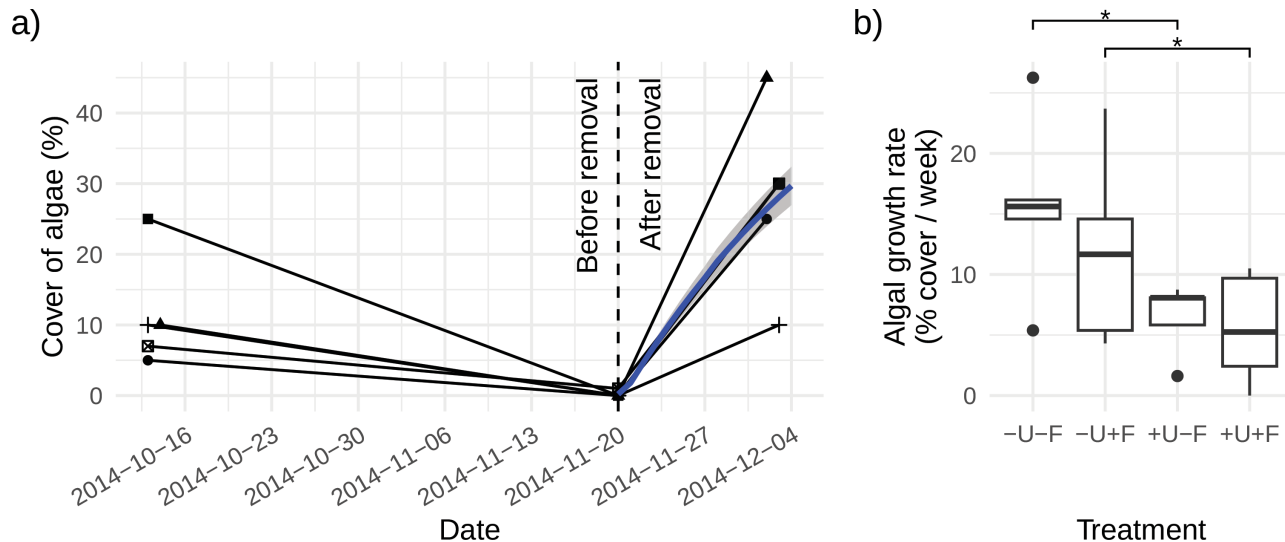
The probability of a patch to change from the algae to bare state is

$$P(a \rightarrow b) = m_a + h_u g(\theta_c q_c + \theta_b q_b),$$

where  $m_a$  is the mortality rate of algae in the absence of grazing,  $h_u$  is the biomass of urchins per area ( $\text{kg m}^{-2}$ ), and  $g$  is the mass-specific grazing rate of urchins (in cover removed per weight of urchin;  $\text{m}^2 \text{kg}^{-1}$ ). The terms  $\theta_c$  and  $\theta_b$  are unitless ratios of the density of urchins in coral and bare areas relative to the general density in the landscape. We note that this formulation assumes that grazing occurs only at the edges of algal patches since urchins are effectively foraging only in cells with bare or coral neighbors (i.e., with nonzero  $q_c$  and  $q_b$ ). This matches particularly well the ecosystems of Rapa Nui, where our experimental results show

that herbivory is mostly driven by urchins (fig. 1), which avoid entering established algal patches but will graze on their edges. However, this formulation would need to be adapted for ecosystems where herbivory is mainly driven by fish with high mobility and low microhabitat preference. Many coral models include overgrowth of corals by macroalgae (e.g., Mumby et al. 2006; Fung et al. 2011). Because this is something we rarely observed at Rapa Nui, we left it out for simplicity.

We ran model simulations using a  $100 \times 100$  grid size, which allowed us to examine the emergent spatial patterns. We considered five levels of spatial feedbacks that produced a diverse range of model behaviors. First, we considered a light negative feedback of  $d_0 = -0.5$ , representing antagonistic neighborhood effects slowing recruitment and growth near the edges (Evensen and Edmunds 2016). Second, we considered strong negative feedback ( $d_0 = -1$ ), which although somewhat unrealistic was useful to illustrate model behavior. Third, a situation without local feedbacks ( $d_0 = 0$ ) was considered, in which corals expand little laterally and recruits are dispersed homogeneously in the seascape. Finally, we considered situations with positive feedbacks, either small ( $d_0 = 0.5$ ) or large ( $d_0 = 8$ ) in magnitude, which would correspond to a faster increase in coral cover near existing colonies resulting from a short-range dispersal of coral propagules, a major role of lateral expansion of existing coral colonies, or a combination of such effects (for more information about these values, see supplement 1; supplements 1–4 are available online).



**Figure 1:** *a*, Observed algal cover before and after the clearing of five quadrats (black lines), in the absence of urchins (*Diadema savignyi*) and fish (–U–F). The shape of the points indicates the experimental replicate, the blue trend the model average prediction (blue line) and its standard error (gray ribbon). *b*, Observed increase in algal cover after removal, under different combinations of herbivore exclusion (presence/absence of urchins [+U/–U] or presence/absence of fish [+F/–F]). Overbars indicate significant differences between treatments based on a Mann-Whitney *U*-test ( $P < .1$ ).

Model parameter values were based on fitting the model predictions to experimental results and observations made at Rapa Nui over the past 20 years (table 1; detailed information about the approach is provided in supplement 1). Growth rates of algae and corals ( $r_a$ ,  $r_c$ ) and herbivory ( $g$ ) were based on a clearing and exclusion experiment, in

which  $20 \times 20$ -cm surfaces were cleared and the subsequent regrowth of algae and coral was measured, in both the presence and absence of grazers (urchins and fish; fig. 1). The rate of lateral expansion of established algae,  $l_a$ , was obtained by monitoring the regrowth of algae in experimentally created gaps in an established algal bed (predominantly

**Table 1:** Model parameter definitions, values, and experiments or rationale used to set their values

Model parameter	Description	Value used in model simulations	Source of parametrization <sup>a</sup>	Note
$r_a$	Reproduction of algae from propagules emitted at the modeled site	1.81 week <sup>-1</sup>	Estimated from in situ exclusion experiments	...
$l_a$	Lateral growth speed of algae	.030 week <sup>-1</sup>	Estimated from lateral regrowth of algae after making a small clearing in an established patch	...
$\alpha$	Proportion of algae propagules from outside the modeled site	.01	Set to a small value reflecting a propagule shadow mostly dependent on the local abundance of algae	...
$r_c$	Base reproduction rate of corals	$1.31 \times 10^{-3}$ week <sup>-1</sup>	Estimated from increase in coral cover after removal	...
$d_0$	Lateral local effect of corals	-1, -.5, 0, .5, or 8	Various values were used to represent different dominant modes of coral reproduction	...
$m_a$	Base mortality of algae	.079 week <sup>-1</sup>	Estimated from the loss of tagged blades of <i>Lobophora variegata</i> (de Ruyter van Steveninck and Breeman 1987)	...
$h_u$	Herbivore density at the site (kg m <sup>-2</sup> )	Ranging from 0 to 2.2 kg m <sup>-2</sup> or fixed to 2.0 kg m <sup>-2</sup>	Within the observed range of measured urchin densities at Rapa Nui (0 to 4.61 kg m <sup>-2</sup> ; estimated average .23 kg m <sup>-2</sup> over 1999–2013)	Variable in the “decreasing urchin density” degradation scenario, fixed otherwise
$g$	Mass-specific grazing rate of herbivores	.19 m <sup>2</sup> kg <sup>-1</sup>	Estimated from exclusion experiments and urchin surveys	...
$\theta_b, \theta_c$	Preference of herbivores for bare and coral patches (unitless)	$\theta_b = 1.03, \theta_c = .96$	Estimated from urchin surveys documenting microhabitat preferences	...
$m_c$	Base mortality rate of corals	Ranging from $10^{-4}$ to $10^{-2.25}$ week <sup>-1</sup> or fixed to $10^{-4}, 10^{-3.75},$ or $10^{-3}$ (fig. 2a1–2e1)	...	Variable in the “increasing base coral mortality” degradation scenario
$m_e$	Mortality rate of corals during a mortality event	.095 week <sup>-1</sup>	Set to reflect mortality from the last mass bleaching event at Rapa Nui (March 2000; on average 61% coral mortality in 10 weeks)	...
$p_e$	Probability of a mass mortality event occurring in a given time step	Ranging from $1/(20 \times 52)$ to $1/(2 \times 52)$ or fixed to zero	Set to reflect the range of return rates of mass bleaching events (Hughes et al. 2018)	Variable in the “increasing frequency of bleaching events” degradation scenario, zero otherwise

<sup>a</sup> See also supplement 1.

*Spatoglossum stipitatum*). Urchin microhabitat use ( $\theta_b$ ,  $\theta_c$ ) was estimated using surveys measuring densities in different microhabitats (coral, algae, or bare areas).

#### *Degradation Scenarios and Computation of Indicators*

Community degradation and trends in temporal and spatial indicators were considered along several scenarios of coral community degradation for which we ran different sets of model simulations.

First, we simulated the common condition of slow but smoothly increasing (press) perturbation due to anthropogenic impacts, such as increased pollution, sediment loadings, and frequent but small and localized disturbances. This may affect various stages of the coral life cycle but was simplified into a gradient of increasing coral base mortality ( $m_c$  between  $10^{-4}$  and  $10^{-2.25}$ ). The model was run until equilibrium was reached.

Second, we simulated a decreasing grazing pressure, which may also occur as a result of persistent anthropogenic stressors (press perturbation). Both pollution and direct exploitation of commercial species can slowly reduce urchin stocks, a situation modeled here as a decrease in  $h_u$  between 2.2 and 0 kg m<sup>-2</sup>, and letting the system reach equilibrium at each parameter value. Coral mortality rate was fixed for a given  $d_0$  value but variable across values of  $d_0$  to allow starting from high cover of corals (table 1).

Third, we modeled the effect of acute environmental stressors that occur over a short period of time but cause significant mortality over the entire seascape (pulse-type perturbations), such as unusually high seawater temperatures or river runoffs causing extended coral bleaching. This scenario was modeled as a gradient of increasing frequency of these mortality events ( $p_e$  between  $1/(2 \times 52)$  and  $1/(20 \times 52)$ ; i.e., two expected mortality event per year to one every 20 years). In this situation, the system never reaches equilibrium (corals are permanently recovering from disturbance events), but we ran it for a similar number of iterations than in the equilibrium case to make sure there was no influence of starting conditions.

For all simulations, we identified the stressor value ( $m_c$ ,  $h_u$ , or  $p_e$ ) at which the transition from a coral-dominated to an algae-dominated seascape occurred or, if no sharp transition occurred, the value at which coral cover decreased by one-third of its total reduction along the gradient. This is a rule of thumb, and the results presented here would not change as long as the threshold is within the range of stress values immediately preceding the sharp decrease in coral cover. For simulations run to equilibrium (first two scenarios), we identified alternative stable states when the final coral cover depended on initial conditions (at least 5% cover difference). The computation of spatial indicators was done on simulations starting from high coral cover (99%) in

order to observe the degradation of a seemingly healthy coral-dominated community, as is observed at Rapa Nui.

To compute spatial indicators, we extracted from each simulation run binary matrices, which contained ones where the cell was in the focal state (coral or algae) and zero otherwise. On these matrices, we quantified the spatial self-organization of algae and coral areas based on three common indicators used in the literature. The first is spatial variability using the spatial variance, which is expected to increase as a result of critical slowing down (Guttal and Jayaprakash 2009). Spatial variance statistics were calculated after “coarse graining” the matrix (Sankaran et al. 2018), which involves dividing an original matrix of size  $S \times S$  into nonoverlapping submatrices of size  $n \times n$ . The average of each submatrix is then taken to obtain a final coarse-grained matrix of size  $S/n \times S/n$  (in this work,  $n = 5$ ). The second is spatial autocorrelation using Moran’s  $I$  statistic at lag 1, that is, between neighboring cells (Dakos et al. 2010). The third is average patch size, which is expected to arise from local feedbacks producing aggregation into patches at the scale of the landscape (Kéfi et al. 2007a; Sankaran et al. 2019). We calculated the base-10 log of the average patch size (contiguous sets of cells) and investigated how it deviated from what would be expected given a homogeneous cover using the null model we describe further down.

Theory predicts changes in the spatial structure of algal and coral areas as stress increases. However, the covers of each interacting state will change at the same time and affect indicator trends (Sankaran et al. 2018; Nijp et al. 2019). Moreover, because all share the same 2D space, indicators computed on algae and coral areas are not independent. To remove these effects, we compared the observed indicator values to randomized versions of the seascape, which removed the effect of cover (but not always completely; see caveats in supplement 2). This allowed us to construct null expected indicator values that reflect the fact that corals or algae can establish anywhere there is a bare area in a seascape but not where the other state is already present. We report in the main text the difference (Moran’s  $I$ , average patch size) or the relative difference to this null expectation (variance) as appropriate.

We used R software (ver. 4.2.0), along with the package *spatialwarnings* (ver. 3.0.3; Génin et al. 2018a) and custom scripts, to implement the model, run the simulations, and compute the indicators. To reduce noise in trends due to the stochastic nature of the model, we computed the average indicator value for each simulation based on 128 seascapes taken 10,000 iterations apart from each other. Five such simulations were run for each parameter combination, then averaged (32 for simulations with mortality events, as stochasticity was higher for those). Because of residual noise in indicator values, we used the significance of

a Kendall's  $\tau$  correlation test as a criterion to consider that an indicator had an increasing trend or not along the stress gradient. Specifically, we considered that an indicator had a negative or positive trend when the  $P$  value of the test was below .01.

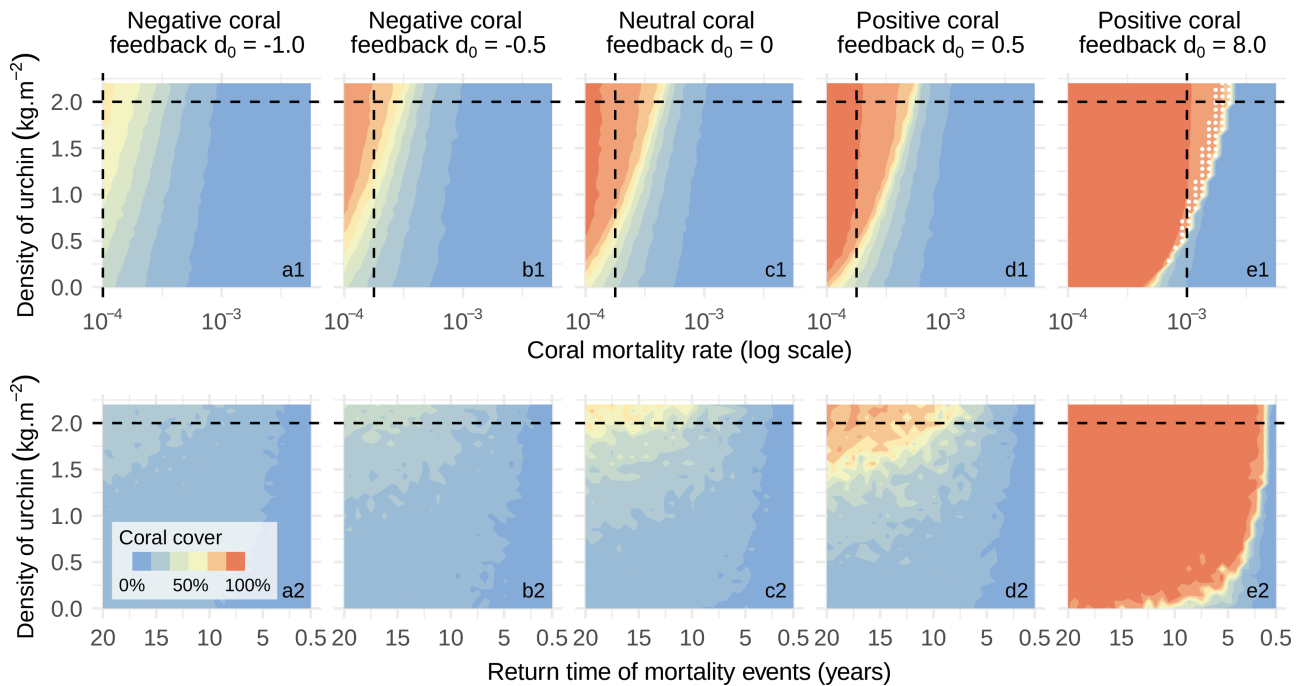
### Results

The model predicted contrasting states at equilibrium. Depending on the stress gradient, either coral or algae dominated the system (red and blue, respectively, in fig. 2a1–2e1). Going from a negative to a neutral and then to a positive local effect of coral colonies on themselves allowed the coral cover to be higher for similar basal coral mortality rates or herbivore pressure. Negative and neutral local feedbacks produced smooth transitions (e.g., fig. 2a1–2c1), whereas positive local coral feedbacks produced comparatively sharper responses, in which the coral cover maintained itself at high levels and then rapidly dropped past a given threshold stress level (e.g., fig. 2d1, 2e1). When positive feedbacks were strong ( $d_0 = 8$ ), such sharp responses were associated with alternative stable states over a range of parameter values whose span increased with herbivore pressure (fig. 2e1). In this range, equilibrium covers could

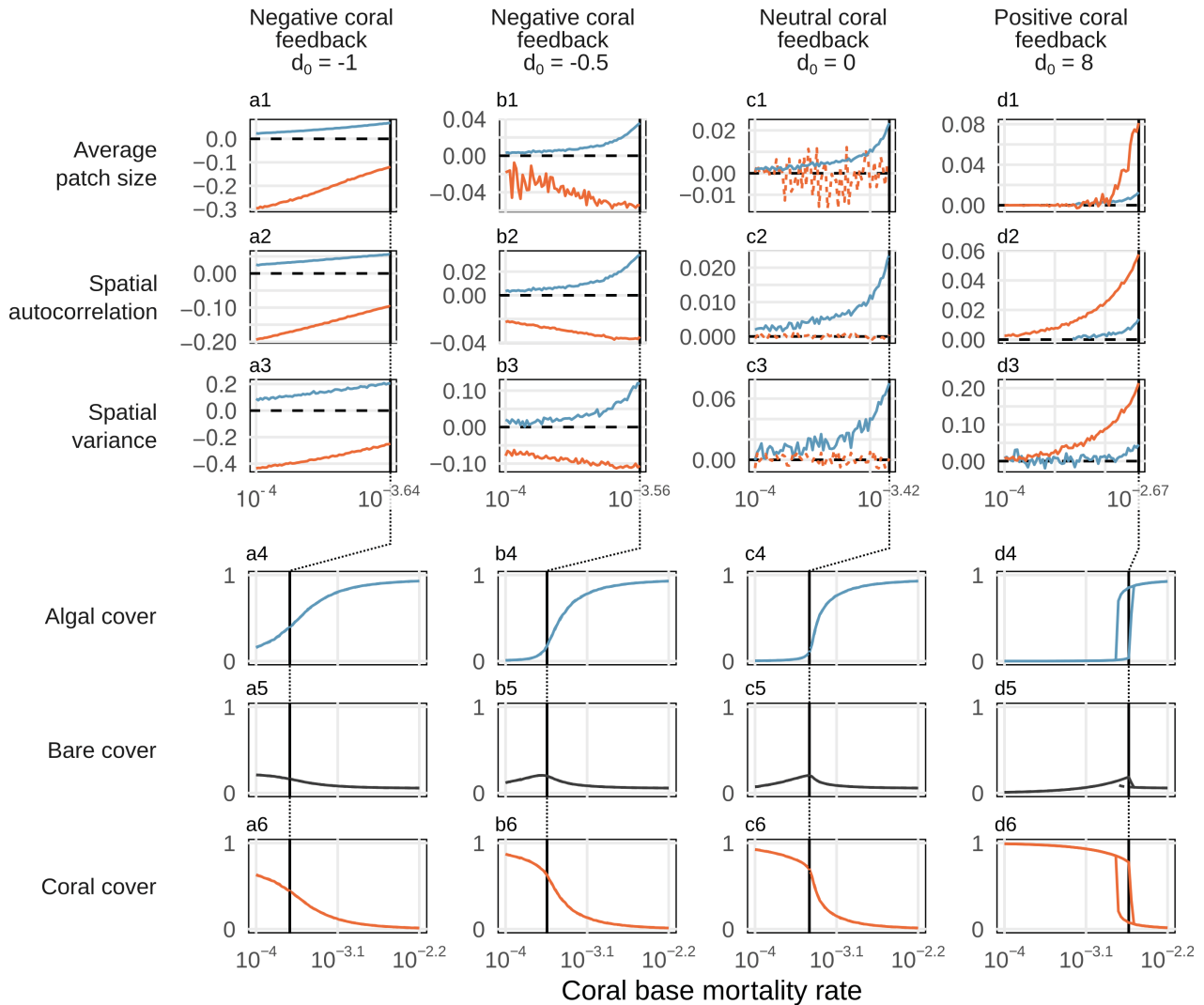
be algae or coral dominated depending on whether the initial conditions were algae or coral dominated, respectively. Qualitatively similar patterns were observed when the system was permanently out of equilibrium due to frequent pulse disturbances (fig. 2a2–2e2). The coral-algae coexistence space was smoother and more beneficial to algae under negative local coral interactions and sharper when neutral or especially when positive local coral interactions were considered.

#### *Spatial Indicators along a Stress Gradient Affecting Coral Mortality*

Alternative stable states were observed only when corals produced a strong positive local feedback ( $d_0 = 8$ ). In those cases, the decrease in coral cover was relatively minor as coral mortality increased (less than 25%), until a tipping point was reached at which coral cover collapsed almost entirely (fig. 3d6), and algae invaded the landscape (fig. 3d4). Before this regime shift, the cover of algae was very low (<1%). For strongly negative local feedbacks on coral cover ( $d_0 = -1$ ), no such shift was observed and the transition was smoother, with stable coexistence of algae and coral at all levels of coral mortality (fig. 3a4,



**Figure 2:** Equilibrium (a1–e1) or average (a2–e2) predicted coral cover, as a function the type of coral local feedback ( $d_0$ ), the density of urchins ( $h_u$ ), the base coral mortality ( $m_c$ ), or the return rate of mortality events. The dashed lines indicate the trajectories along  $h_u$ ,  $m_c$ , and the return time of mortality events ( $1/(52p_c)$ ) considered for indicator trends in figures 3–5. The dotted region indicates the parameter space with alternative stable states (present only in e1).



**Figure 3:** Algae, bare, and coral covers at equilibrium (bottom panels, *a4–d6*) and indicator values (upper panels, *a1–d3*) along an increase in coral baseline mortality ( $m_c$ ), for different types of coral local feedback  $d_0$  and indicators computed on the cover of either coral (red) or algae (blue). Dotted lines in indicator trends (*a1–d3*) indicate nonsignificant trends (correlation test,  $P > .01$ ). The black vertical line indicates the point up to which indicator trends are considered. For conciseness, results for  $d_0 = 0.5$  are not shown (for full results, see supplement 4, fig. S4.1).

3a6). Intermediate values of coral feedback produced an intermediate pattern, with sharper changes in coral abundance (fig. 3b6, 3c6) but without alternative stable states.

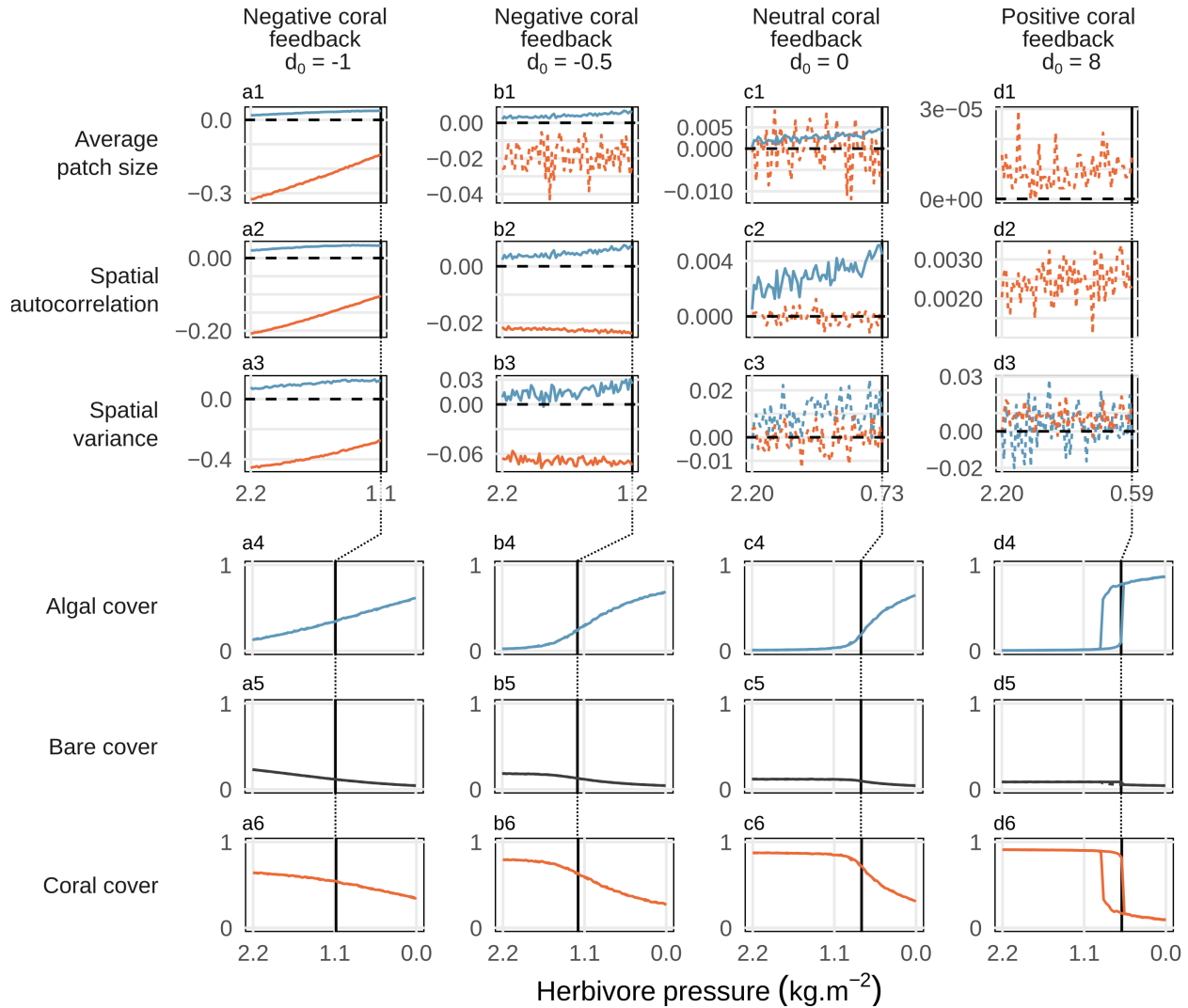
Trends in spatial indicators computed on algal patches were always significant and positive, regardless of the type of coral feedback  $d_0$  (see fig. 3a1–3d3 and summary of trends in fig. 6), whereas trends in coral-based indicators depended on the type of coral local feedback  $d_0$ . Positive values in coral indicators produced increasing trends as coral mortality increased (fig. 3d1–3d3; summary in fig. 6), no trends when  $d_0$  was zero (fig. 3c1–3c3), and negative trends when  $d_0$  was  $-0.5$  (fig. 3b1–3b3). However, under conditions of strong

negative local coral feedback ( $d_0 = -1$ ), the trend in coral spatial indicators was reversed back to an increasing trend (fig. 3a1–3a3).

#### *Spatial Indicators along a Stress Gradient Affecting Herbivore Abundance*

When herbivore pressure decreased, the system exhibited alternative stable states only when coral local feedbacks were positive (fig. 4a6–4d6). This time, we found little change in coral cover before the regime shift (<15%), while it decreased by 70% after the regime shift (fig. 4d6), along





**Figure 4:** Algae, bare, and coral covers at equilibrium (*bottom panels, a4–d6*) and indicator values (*upper panels, a1–d3*) along a decrease in herbivore pressure ( $h_n$ ), for different types of coral local feedback  $d_0$  and indicators computed on the cover of either coral (red) or algae (blue). Dotted lines in indicator trends (*a1–d3*) indicate nonsignificant trends (correlation test,  $P > .01$ ). The black vertical line indicates the point up to which indicator trends are considered. For conciseness, results for  $d_0 = 0.5$  are not shown (for full results, see supplement 4, fig. S4.2).

with the opposite trend in algal cover (fig. 4d4). When coral local feedbacks were neutral or negative, no regime shift was observed, and coral cover was gradually replaced by algae as herbivore pressure decreased (fig. 4a6–c6, 4a4–c4).

Spatial indicators computed on algal cover increased when the local coral feedback  $d_0$  was negative or neutral (fig. 4a1–4a3, 4b1–4b3, 4c1–4c3; summary in fig. 6), although in this latter case the increase in spatial variance was not significant for our chosen threshold. When  $d_0$  was strongly positive, the cover of algae was too low for autocorrelation and average patch size to be computed (fig. 4d1, 4d2), and the trend in spatial variance was nonsignificant (fig. 4d3).

Indicators computed on coral cover had inconsistent behavior as herbivory decreased, with either no detectable trend at all for zero or positive  $d_0$  (fig. 4c1–4c3, 4d1–4d3; summary in fig. 6) or only the autocorrelation and variance showing a decreasing trend for  $d_0 = -0.5$  (fig. 4b1–4b3). However, all indicators had clear positive trends when  $d_0$  was strongly negative (fig. 4a1–4a3).

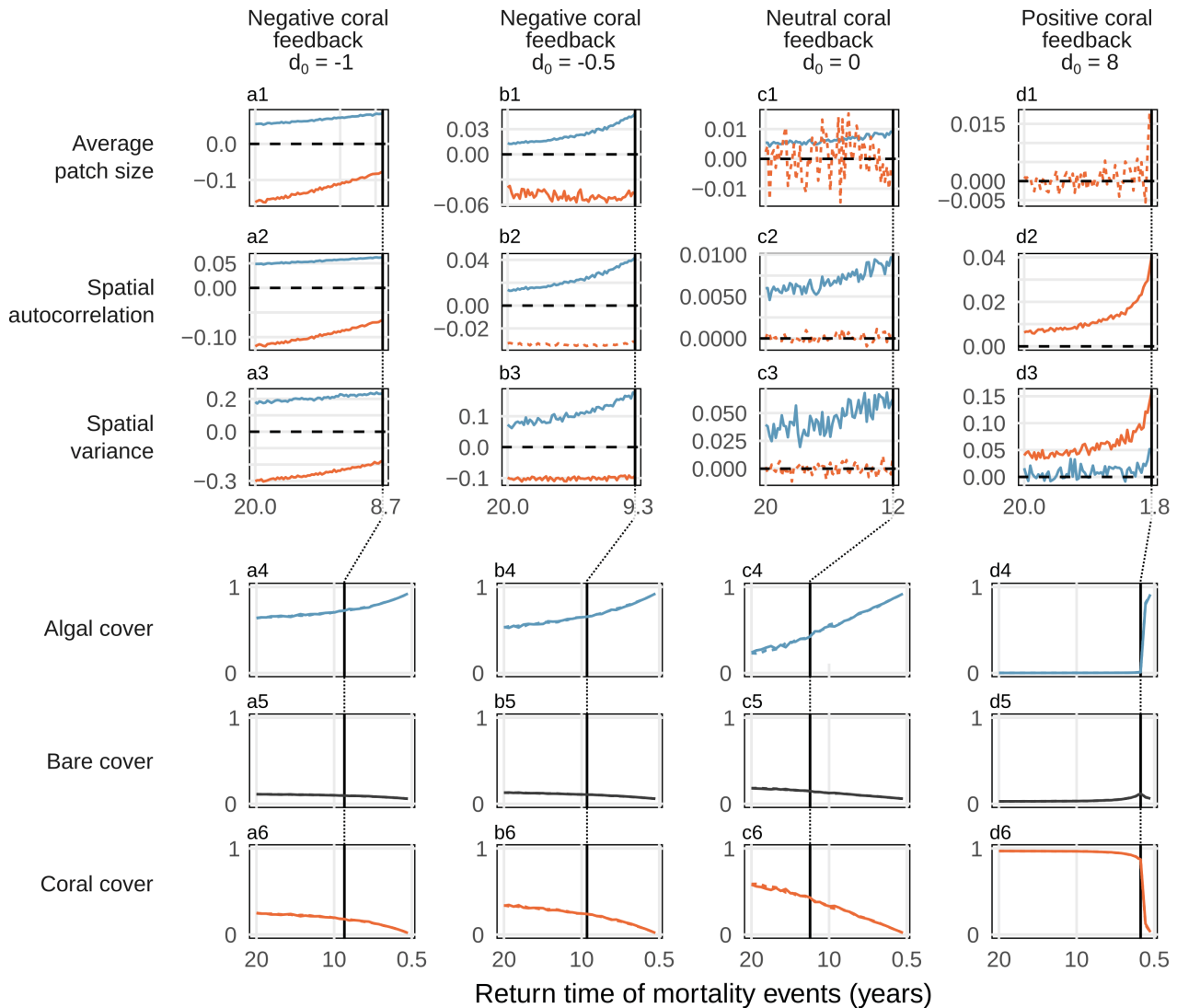
#### *Spatial Indicators along a Gradient of Disturbance Events*

As the frequency of pulse disturbances increased, we observed again sharper changes in coral and algal covers when

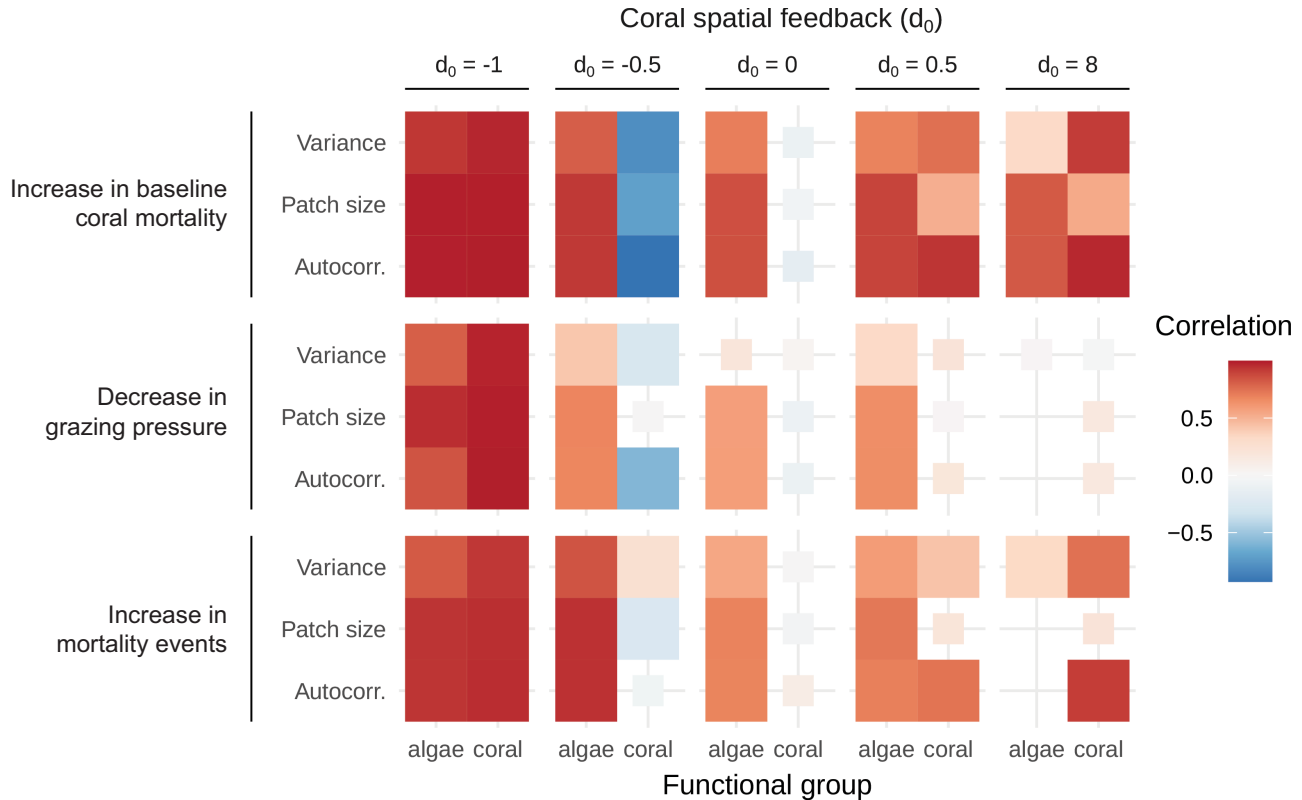
the neighbor effects of corals were positive (fig. 5d4–5d6). In this latter case, a minor decrease in coral cover was observed as the frequency of mortality events increased (<15%), up to a point past which the coral cover decreased rapidly and became replaced by algae. Comparatively smoother changes in covers were observed when coral effects were negative or neutral. In this case, coral cover remained low at all times (<50%) and smoothly decreased as the frequency of pulse disturbance events increased (fig. 5a6–5c6).

Indicators computed on algal cover always had an increasing trend as the frequency of pulse disturbance increased (fig. 5; summary in fig. 6), except for the average

patch size and autocorrelation when  $d_0$  was positive, for which algal cover was too low to compute indicators (fig. 5d1, 5d2). When the local effects of corals were strongly negative ( $d_0 = -1$ ), coral-based indicators always showed increasing trends (fig. 5a1–5a3), but their behavior in other cases was inconsistent. In the case of a small, negative coral feedback, only a slight increase in variance (fig. 5b3; summary in fig. 6) and decrease in patch size (fig. 5b1) was observed, with no trend in autocorrelation (fig. 5b2). When the coral had no local effect on itself, indicators based on coral covers were insensitive ( $d_0 = 0$ ; fig. 5c1–5c3). When the feedback was positive, indicators



**Figure 5:** Average cover of algae, bare, and coral covers (*bottom panels, a4–d6*) and indicator values (*upper panels, a1–d3*) along an increase in return time of mortality events ( $1/(52p_e)$ ), for different types of local coral feedback  $d_0$  and indicators computed on the cover of either coral (red) or algae (blue). Dotted lines in indicator trends (*a1–d3*) indicate nonsignificant trends (correlation test,  $P > .01$ ). The black vertical line indicates the point up to which indicator trends are considered. For conciseness, results for  $d_0 = 0.5$  are not shown (for full results, see supplement 4, fig. S4.3).



**Figure 6:** Summary of correlations between the degradation gradient and indicator values. Tile colors indicate the correlation between the indicator value and increasing degradation. A positive correlation corresponds to an increase in indicator value with stress. When nonsignificant ( $P > .01$ ) the tile is reduced, and it is missing when the indicators could not be computed (e.g., because of the absence of the relevant state).

had increasing trends with stress, although only the auto-correlation and variance were significant (fig. 5d2, 5d3). The average patch size of corals spiked only right before the tipping point, which resulted in a nonsignificant correlation (fig. 5d1).

### Discussion

Regime shifts, at which a sharp decrease in coral cover occurs past a tipping point in stress, have been well documented in many tropical and subtropical systems. As expected from previous theoretical work, in our model these shifts were tightly connected to the existence of strong positive local feedbacks within coral beds. In their absence, algae and corals coexisted and replaced each other more gradually across common stress gradients. Under many but not all modeled conditions, the emerging spatial structure captured by early-warning indicators showed the expected changes in spatial patterns as conditions worsened for corals and approached collapse (i.e., they signaled the regime shift). This depended on the type of local feedbacks (negative, neutral, or positive) and the type of stressor:

increases in coral natural mortality were more suitable to develop spatial indicators than changes in herbivory.

#### *Type, Strength of Feedbacks, and Indicator Trends*

Local spatial feedbacks in coral models can be the result of various ecological mechanisms, whose relative strength ultimately determines whether regime shifts with alternative stable states arise. While only the strength of positive feedbacks determines whether alternative stable states are present in a given reef system (van de Leemput et al. 2016), our work shows that the type of positive feedback will determine which spatial patterns (i.e., early-warning indicators) can be indicative of a shift. This is best illustrated from our results by comparing the direct local positive feedback of corals (when  $d_0 > 0$ ) and the indirect positive effect of herbivory, which opens up space by reducing algal cover near existing corals and whose strength is determined by  $h_{i,c}$ . Increasing the strength of both mechanisms expands the parameter space over which alternative stable states occur. Yet their effects on spatial patterns differ in important ways. The intensity of coral neighborhood effects

( $d_0$ ), relative to base mortality and reproduction ( $m_c$  and  $r_c$ ), determines the intensity of spatial self-organization of corals. As coral mortality  $m_c$  is increased, the relative rate of these processes changes, which produces the observed changes in spatial patterns. However, herbivore-mediated feedbacks have a different mechanism: they open up space for corals but have no effect on their self-organization in the seascape. The decrease in herbivore density (decreasing  $h_u$ ) thus reduces overall coral cover, but it does not alter the way corals self-organize in the space available to them. As a result, there is little to no change in coral spatial patterns. While these two mechanisms may have similar effects on the appearance and magnitude of regime shifts, it is essential to know which type of positive mechanisms is at play to interpret trends in indicators. Much of the modeling effort in coral systems has emphasized the feedback of herbivores balancing the competition for space between corals and algae (e.g., Mumby et al. 2007; Fung et al. 2011), but we show here that while essential for coexistence, it may be less relevant in the context of finding spatial indicators compared with processes directly affecting the self-organization of coral cover, such as lateral growth. Informed application of indicators to coral communities will thus require understanding whether feedbacks affect coral spatial structure directly or indirectly.

Beyond the type of feedbacks, our simulations show that it is also essential to quantify their strength. This is exemplified by the cases where the local effect of corals  $d_0$  is negative. When corals have a relatively weak negative effect on their neighborhood, indicators show a decreasing trend as coral mortality increases. However, this trend is reversed when neighbor effects are sufficiently strong to significantly limit coral cover ( $d_0 = -1$ ). The very strong negative neighbor effectively limits the spatial clustering of corals by imposing a checkerboard-like pattern of coral cells that strongly lowers spatial autocorrelation. As stress increases and coral cover reaches lower densities, this effect decreases, which leads to indicator values increasing toward their null expectation.

The dominant feedbacks and their strength in coral beds is likely to be species specific. Reef-building species will usually have strong positive effects, since they grow faster into adjacent space than at a distance away. However, for many other species, neighborhood effects are more complex and likely context dependent. Experimental work remains the most convincing approach to infer the type of such local interactions and our model highlights the importance of focusing research efforts in this aspect of coral ecology, but it may not be practical to run such experiments at the relevant spatial and temporal scales. Our results suggest that spatial metrics could be used to identify the type of local interactions. For instance, along an increase in stress gradient, negative local coral interactions will always generate negative autocorrelation values (i.e., spa-

tial segregation between coral colonies). Conversely, positive autocorrelation values are indicative of positive coral interactions leading to aggregation of colonies. Inferring such interactions from the spatial structure may thus be a way to know which type of coral-coral interaction are dominant or most common (Lewis 1970; Bradbury and Young 1983) and thus help interpreting trends in spatial indicators. However, such an approach does come with its own set of methodological challenges (Blanchet et al. 2020), and corals may have both negative and positive effects on their neighborhood, depending on the distance at which neighbors are located (Schlager and Purkis 2015; van der Kaaden et al. 2020).

Our model included a single coral “species” in the sense that neighborhood effects were the same for all modeled corals. In natural settings, however, coral cover is made of several species, possibly with different intraspecific interactions with their neighbors. Taking the two abundant species of Rapa Nui as examples, *Porites lobata* is often considered a stronger competitor and may have a negative effect on neighbors, while *Pocillopora verrucosa* may be considered more opportunistic and may have comparatively little neighborhood effect. In such a context, the cover of *Porites* may show changes in spatial structure along a degradation gradient, while *Pocillopora* may not. The analysis of spatial patterns may have to be done considering each species separately or grouping them depending on their neighborhood effect, instead of lumping coral cover.

#### *Indicators and Nonequilibrium Dynamics*

The vast majority of studies of indicators of regime shifts investigate changes in spatial patterns at equilibrium (e.g., Guichard et al. 2003; Kéfi et al. 2007a). This assumes ecosystems with fast responses, so that the observed covers and spatial patterns are at all times close to their equilibrium for the stress level being applied to the system (Petraitis 2013). Coral ecosystems have response times that are probably too slow to fit such an assumption (Hughes et al. 2013), as changing environmental parameters, such as temperature, do so over timescales that are similar to the response of coral communities, and pulse rather than press perturbations such as bleaching events are commonplace. A complete understanding of the behavior of spatial indicators under such nonequilibrium conditions is a large endeavor beyond the scope of this study. However, our results suggest that even under such disturbed conditions, spatial patterns produce similar trends to the equilibrium situation. This arises because the mortality of corals is applied homogeneously over the landscape, so the self-organization of corals and algae is dampened but does not disappear. Disturbance introduces noise in the simulations, but taking the average indicator values recovers the increasing

trends in indicators, although our limited number of simulations was not always able to do so (e.g., in the case of the variance and patch size under light negative feedback conditions). It is important to note that the average trend shown here does not represent well the very large spread in indicator values along the gradient (supplement 3, fig. S3.1). For example, when  $d_0 = 8$ , the average spatial variance observed at the shift is higher than under lower return times in only half of the simulations. Under real-world scenarios, when pulse disturbances are important, many of such trends in indicator values may be undetectable, and sampling effort should therefore be substantially increased.

*Conclusions: Simple Predictions from the Spatial Structure of Coral Beds*

While abrupt shifts are a type of response of coral systems to pressing stress, they are most likely not present everywhere, leading to debates as to how widespread they can be and whether they are associated with alternative stable states (Dudgeon et al. 2010; Mumby et al. 2013). Because experiments cannot always be set up at the relevant spatial and temporal scales (Petraitis and Latham 1999), using the indirect approach provided by the analysis of spatial structure in conjunction with auxiliary experimental work may thus be an interesting research avenue to contribute to this debate, as well as a practical tool for managers. A spatial model can be used to identify the most critical ecological information to be gathered (e.g., intracoral interactions) and the conditions under which emergent spatial structure can be used as indicators. Sites that are approaching a tipping point over time may show increasing autocorrelation, spatial variance, or patch size as stress levels increase, depending on the strength and sign of local feedbacks. However—and perhaps more realistically given the scarcity of marine spatiotemporal data—indicators may be used to rank a set of local sites in terms of proximity to tipping points. Clearly, interpreting trends in spatial indicators requires a good knowledge of the ecological context, and future empirical studies in different communities will enrich spatial indicators and delimit conditions for their application.

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### Statement of Authorship

A.G.: funding acquisition, methods development, data collection, data analysis, software development, model analysis, coding simulation; S.A.N.: supervision, methods development/experimental design, writing—original draft, writing—review and editing; A.G.-M.: supervision, methods development/experimental design, writing—original draft, writing—review and editing; E.A.W.: funding acquisition, methods development/experimental design, data collection, provision of resources, supervision, writing—original draft, writing—review and editing.

### Data and Code Availability

Data and code for this work are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.n5tb2rbzw>; Génin et al. 2023).

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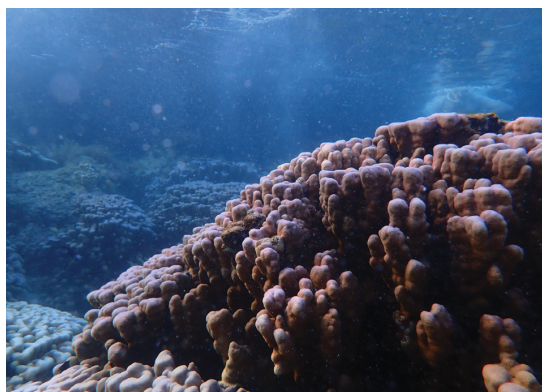
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A *Porites lobata* coral colony, the species making most of coral cover at Rapa Nui. This mounding coral is present from subtidal depths as well as in some intertidal rock pools, as seen here. Photo credit: B. Salgado Murillo.