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Geometric analysis of regime shifts in coral reef communities

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Abstract. Coral reefs are among the many communities believed to exhibit regime shifts between alternative stable states, single-species dominance, and coexistence. Proposed drivers of regime shifts include changes in grazing, spatial clustering, and ocean temperature. Here, we distill the dynamic regimes of coral–macroalgal interaction into a three-dimensional geometry based on stability, akin to thermodynamic phase diagrams of state transitions, to facilitate analysis. Specific regime-shifting forces can be understood as trajectories through the cubic regime geometry. This geometric perspective allows us to understand multiple forces simultaneously in terms of the stability and persistence of interacting species. For example, in a coral–macroalgal community, grazing on macroalgae leads to alternative stable states when there is no spatial clustering (e.g., high habitat connectivity), while warming decreases coexistence. However, with spatial clustering, grazing promotes coexistence because of elevated local intraspecific competition. The geometry of regime shifts provides a general framework to analyze two-species communities and can help conservation efforts navigate complexity and abrupt environmental changes.

Key words: alternative stable states; bifurcation; coexistence; competition; coral reef; geometry; grazing; macroalgae; origami; regime shift; spatial clustering; warming.

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INTRODUCTION

Regime shifts and alternative stable states have been implicated in many communities, including coral reefs (Hughes et al. 2017), shallow lakes (Scheffer et al. 1993), kelp beds (Ling et al. 2014), and terrestrial forests (Hirota et al. 2011). Discontinuous shifts in community dynamics due to gradual environmental changes imply that conservation and management may have to anticipate and confront historical legacy traps (Tekwa et al. 2019*a*). The potential for regime shifts is a pressing concern in the Anthropocene, as exemplified by recent heatwaves driving coral reefs to a depauperate state (Hughes et al. 2019). Coral reefs have been intensely studied and share general features with a wide range of other communities suggested to exhibit regime shifts, particularly those that feature two species whose interactions are selectively mediated by grazers, nutrients, fire, or temperature (Mumby et al. 2007, Staver and Levin 2012, Graham et al. 2015, Schmitt et al. 2019). However, there remains disagreement about the evidence for regime shifts and alternative stable states among coral reefs (Bruno et al. 2009, Dudgeon et al. 2010, Mumby et al. 2013) and other communities (Schröder et al. 2005). One possible explanation for this disagreement is that there are different mechanisms leading to regime shifts even within one ecosystem type such as coral reefs (van de Leemput et al. 2016), such that empirical examinations of one mechanism will yield negative results across sites.

In the coral literature, multiple regime shift mechanisms have been modeled separately, including interspecific competition among coral species, interspecific competition between coral and macroalgae, predator–prey interactions, and grazer-mediated interactions (Knowlton 1992, Mumby et al. 2007, Petraitis and Hoffman 2010, van de Leemput et al. 2016). These mechanisms hinge on space being a limiting resource for benthic coral reef communities (McCook et al. 2001, Sandin and McNamara 2012), as is evident by the common use of coral cover (maximum of 100%) in the literature (Jokiel et al. 2015). However, models that track coral cover often treat space as if it were any other limiting nonspatial resource, without explicitly incorporating spatial dynamics (Elmhirst et al. 2009, Anthony et al. 2011, Blackwood et al. 2011, Baskett et al. 2014, Fabina et al. 2015, McManus et al. 2019). However, we know from the broader ecological literature that spatial clustering, arising from low habitat connectivity or limited dispersal, can strongly determine species stability in communities even with linear interaction responses (Bolker and Pacala 1999, Chesson 2000). There is therefore a need to synthesize the variety of spatial and nonspatial mechanisms of coral reef regime shifts in general ecological terms.

Here, we propose simple modifications to a bilinear mathematical model (Volterra 1926, Lotka 1978, Neuhauser and Pacala 1999) so as to use generic community ecological terms to synthesize spatial, temperature, and grazing effects on coral–macroalgal interactions. This model reveals basic ingredients that lead to alternative stable states or coexistence of corals and macroalgae on coral reefs, as well as what these species stability outcomes mean for the community. We then distill the model to three parameters that completely define the possible dynamic regimes and that can be visualized as a cubic volume. We show how previously suggested bifurcating factors—such as grazing, spatial clustering, and warming—are vectors traversing this volume. The ultimate goal of this formalism is to let scientists and conservation managers generate and test regime shift hypotheses, without restriction to a single mechanism, using a generic model that is more widely applicable than existing system-specific models.

METHODS

We first present the Lotka-Volterra competition model as a foundation for two-species interactions, and then, we show that a coral–macroalgal model can be analyzed as a special case of this framework. We then incorporate spatial clustering to obtain a general spatial Lotka-Volterra formulation of dynamic regimes, representing a more general two-species model than existing coral models. Finally, we add temperature-dependent growth. The specific spatial and temperature dependence introduced for coral–macroalgal interactions allows us to subsequently explore how grazing, spatial clustering, and warming affect coral reef communities' dynamic regimes.

Lotka-Volterra competition model

We first restate the classic two-species Lotka-Volterra competition equations and their well-known implications for bistability and coexistence (Volterra 1926, Gause 1934, Lotka 1978, Kingsland 2015). The species in these equations can represent coral and macroalgae. The Lotka-Volterra model assumes that each species has growth (r_i) and mortality (m_i) that make up the intrinsic rate of increase ($r_i - m_i$). In addition, competition between species i and j results in linear per capita growth rate changes ($-r_i a_{ij}$, including when $j \neq i$, indicating interspecific rate, and when $j = i$, indicating intraspecific rate). The dynamic equation is then

$$\frac{dN_i}{N_i dt} = r_i(1 - a_{ii}N_i - a_{ij}N_j) - m_i. \quad (1)$$

Table 1 summarizes the coefficients, and Table 2 shows symbol definitions for this and subsequent models for comparison. There are three nontrivial equilibria sets, including species 1 dominance, species 2 dominance, and coexistence

Table 1. Model equations. The dynamic equations are given in the form of $dN_i/(N_idt)=\sum(\text{coefficient} \times \text{state})$. Subscript i refers to the focal species and $j \neq i$. Symbols are defined in Table 2.

Model	Species (i)	Density changes	Intrinsic rate ($\times 1$)	Intraspecific interaction ($\times N_i$)	Interspecific interaction ($\times N_j$)	Higher-order interspecific interaction ($\times(N_j^2 + N_j^3 + \ldots)$)
Lotka-Volterra	1	$dN_1/N_1dt = \Sigma$	$r_1 - m_1$	$-r_1a_{11}$	$-r_1a_{12}$	0
	2	$dN_2/N_2dt = \Sigma$	$r_2 - m_2$	$-r_2a_{22}$	$-r_2a_{21}$	0
Mumby model	1 coral	$dN_1/N_1dt = \Sigma$	$r - d$	$-r$	$-(r + a)$	0
	2 algae	$dN_2/N_2dt = \Sigma$	$\gamma - g$	$-\gamma$	$-(\gamma + g - a)$	$-g$
Spatial Lotka-Volterra	1	$dN_1/N_1dt = \Sigma$	$r_1 - m_1$	$-r_1a_{11}C_{11}$	$-r_1a_{12}C_{12}$	0
	2	$dN_2/N_2dt = \Sigma$	$r_2 - m_2$	$-r_2a_{22}C_{22}$	$-r_2a_{21}C_{12}$	0

Table 2. Symbol definitions. Parameter values are for Figs. 2–4.

Definition	Species 1 (coral) parameter values	Species 2 (macroalgae) parameter values
Coral–macroalgal model (without spatial + temperature dependence)		
Macroalgal overgrowth on coral		$a = 1.1$
Coral mortality	$d = 0.5$	
Grazing rate		$g = [0.55–0.85]$
Birth rate	$r = 1$	$\gamma = 1.1$
Lotka-Volterra equivalent (with spatial + temperature dependence)		
Intraspecific interaction effect	$a_{11} = C_{11}$	$a_{22} = C_{22}$
Interspecific interaction effect	$a_{12} = (r_1 + a)C_{12}/r_1$	$a_{21} = (r_2 + g - a)C_{12}/r_2$
Relative (intra-to-inter) clustering	$C_{11}/C_{12} = [1, 2, 4]$	$C_{22}/C_{21} = [1, 2, 4]$
Intraspecific clustering	$C_{11} = [1,1.19,1.41]$	$C_{22} = [1,1.19,1.41]$
Mortality	$m_1 = d$	$m_2 = g$
Density or cover	$0 \leq N_1 \leq 1$	$0 \leq N_2 \leq 1$
Intrinsic growth rate	$r \cdot \exp(-\Delta T^2/(2\sigma_1^2))$	$\gamma \cdot \exp(-\Delta T^2/(2\sigma_2^2))$
Thermal tolerance	$\sigma_1 = 1$	$\sigma_2 = \sqrt{2}$
Actual optimal temperature	$\Delta T = [0, 1]$	$\Delta T = [0, 1]$

(Appendix S1: Table S1). Stability analysis (Appendix S1) shows that the single-species equilibrium for species i is stable if:

$$\frac{a_{ji}}{a_{ii}} > \left(\frac{r_j - m_j}{r_j}\right) / \left(\frac{r_i - m_i}{r_i}\right). \tag{2}$$

That is, if the ratio of interspecific competition (of species j on i, a_{ji}) over intraspecific competition (of i, a_{ii}) is greater than the ratio of species j's isolated equilibrium density ($(r_j - m_j)/r_j$) over species i's isolated equilibrium density ($(r_i - m_i)/r_i$) (when intraspecific competitions are equal, $a_{11} = a_{22}$), then the dominance of species i (with j locally extirpated) is stable. If the condition (2) is true for only $i = 1$ but not $i = 2$, then species 1 competitively excludes species 2 deterministically and vice versa for species 2 competitively excluding species 1. If the condition is false for both species, then coexistence is stable. However, if (2) is true for $i = 1$ and for $i = 2$, then coexistence is unstable and alternative stable states occur, with either species dominating depending on initial conditions.

Coral–macroalgal model

We next show that the Lotka-Volterra formulation can help understand competitive exclusion, bistability, and coexistence conditions in prominent coral–macroalgal models. The Mumby model (Mumby et al. 2007) and related models (Li et al. 2014) consider coral (N_1) and macroalgal (N_2) cover. These models exhibit bistability when an implicit herbivore's grazing rate on macroalgae (g) is at an intermediate value. The Mumby model can be rewritten in Lotka-Volterra form, with terms arranged according to the intrinsic rate of increase, and intraspecific and interspecific interactions (Table 1, Appendix S2). For coral and macroalgae, respectively, the intrinsic growth rates are $r - d$ and $\gamma - g$, where r and γ are birth rates and d is the coral mortality rate. The intraspecific competition rates are $-r$ and $-(\gamma + g - a)$, where a is the rate at which macroalgae overgrows coral. The interspecific competition rates are $-(r + a)$ and $-\gamma$. Parameter values were chosen (Table 2) such that coral cover would attain realistic levels (Darling et al. 2019), and macroalgal competitiveness relative to corals would be sensitive to a range of realistic grazing rates that lead to bifurcations (Mumby et al. 2007). The dynamic equations are

$$\frac{dN_1}{N_1 dt} = r - d - rN_1 - (r + a)N_2 \tag{3a}$$

$$\frac{dN_2}{N_2 dt} = \gamma - g - (\gamma + g - a)N_1 - \gamma N_2 - g(N_1^2 + N_1^3 + \cdots) \tag{3b}$$

With this formulation, it becomes clear that the Mumby model is a particular specification of the Lotka-Volterra model in which grazing reduces the intrinsic growth rate of macroalgae and increases the interspecific competitive effect of corals on macroalgae. This formulation also reveals the implicit assumptions about competition in the model, namely that interspecific competition is greater than intraspecific competition for corals under any grazing rate. Interspecific competition is also greater than intraspecific competition for macroalgae when grazing rate is sufficiently high (Appendix S2; Table 1). Thus, the alternative stable states observed in the model can be understood in terms of the Lotka-Volterra terminology of interspecific vs. intraspecific competition.

In addition, the Mumby model features a negative grazing effect on macroalgae that increases in magnitude geometrically with coral cover ($N_1^2 + N_1^3 + \ldots + N_1^\infty$) (Appendix S2, Table 1). Dropping these higher-order interactions shrinks but does not eliminate the bistable region, and in fact, the alternative stable states remain identical (Appendix S2; see Table 2 for parameter values). Therefore, the Lotka-Volterra model appears sufficiently nuanced to represent alternative stable state dynamics between coral and macroalgae.

We note that Lotka-Volterra-based models traditionally define species state (N_i) as density (biomass or abundance per area), while the coral literature tracks proportion of habitat covered by biomass (maximum fractional cover of one or 100%) (Jokiel et al. 2015). By scaling density with the appropriate unit area, it can be capped at 1 and thus becomes interchangeable with percent cover for the subsequent results.

Having established the connection between the Lotka-Volterra model and the Mumby model, we now proceed to incorporate space into the Lotka-Volterra model.

Spatial Lotka-Volterra model

Spatial competition is an implicit assumption in the coral–macroalgal interaction literature (McCook et al. 2001, Sandin and McNamara 2012). Here, we explicitly consider how spatial dynamics affect coral and macroalgae using the Lotka-Volterra formulation. The Lotka-Volterra model can be changed into a spatial version using the spatial moment framework (Durrett and Levin 1994, Bolker and Pacala 1999, Lion and Baalen 2008, Tekwa et al. 2015). According to the spatial moment framework, interaction neighbor densities for a focal species i in a non-spatial model (N_j) can be replaced by the local density N_{ij} or $C_{ij}N_j$ (related to the second spatial moment, see Appendix S3), where C_{ij} is a continuous-space clustering coefficient. The intraspecific and interspecific interaction rates are the same as for the Lotka-Volterra competition model 1, except they are multiplied by C_{ii} and C_{ij}, respectively. These clustering coefficients are relevant across a variety of ways of thinking about space, including continuous space (with neighbors weighted by distance through interaction kernels), discrete space such as habitat networks or metacommunities (with neighbors being within a patch), or social networks (with neighbors being connected nodes) (Lion and Baalen 2008, Tekwa et al. 2015). N_{ij} or $C_{ij}N_j$ expresses the average number of species j neighbors that an individual of species i interacts with per area per time, and can be different from N_j, the average number of neighbors that an individual would interact with if all were randomly distributed or if the interaction neighborhood were the entire community. In a continuous-space perspective, N_{ij} is the average number of j individuals within

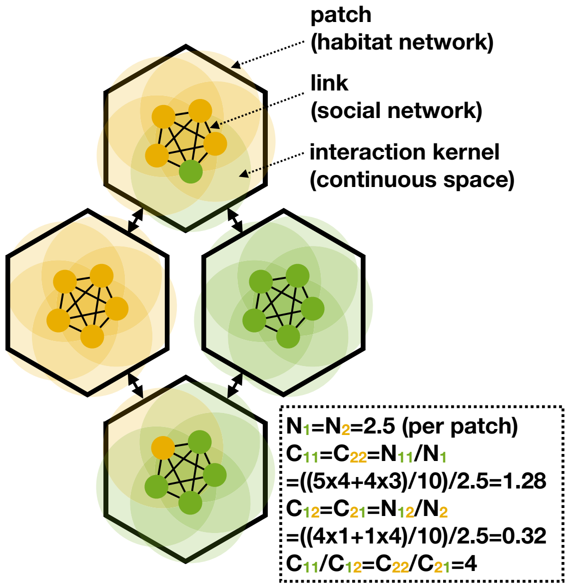

Fig. 1. Descriptions of spatial clustering. The spatial clustering of individuals (circles) of two species can be conceptualized in three different ways. First, patches (hexagons) in a habitat network can delimit which individuals are interaction neighbors. Double arrow links indicate migration, which does not directly enter the clustering computation but can dynamically affect where individuals end up spatially. Second, links (thin lines) in a social network can specify which pair of individuals interact at a given time. Third, interaction kernels (circular shades) can weigh individuals within a certain distance as neighbors. The spatial clustering discussed in the main text can be described under any of these three frameworks with clustering coefficients C_{ij}. These coefficients can be tallied in terms of the average number of neighbors (or node degree) j that i experiences (N_{ij}) and the global average number of individuals i per area or patch (N_i). Sample calculations of N_i, N_{ij}, C_{ij}, and relative clustering (C_{ii}/C_{ij}) are obtained by taking averages and ratios of individual and neighbor counts (see box).

an i individual's interaction kernel (circular shades in Fig. 1). In social network terminology with two species, N_{ii} is the average node degree in the within-species network, whereas N_{ij} ($i \neq j$) is the average node degree in the bipartite network (where the links are between species, Fig. 1). In habitat network terminology, N_{ij} is the average number of j individuals within a patch that contains at least one i individual, and links between patches describe the individual migration rates that determine N_{ii} (patches in Fig. 1). The three perspectives on spatial configurations may have different underlying spatial dynamics, but they can all be described at any given time using N_{ij} (and hence also C_{ij}).

The clustering coefficient is convenient because it captures spatial clustering effects as a single multiplicative factor, indicating how many more (when $C_{ij} > 1$) or fewer (when $C_{ij} < 1$) times an individual of species i encounters an individual of species j than the global density of j. The higher the value of C_{ij}, the more clustered j is around i. This also allows one to write an interaction effect on population growth rate (dN_i/N_idt) as $a_{ij}C_{ij}N_j$. In this form, it is clear that the dynamic equations are the same as the nonspatial Lotka-Volterra equations, with interaction coefficients a_{ij} replaced by $a_{ij}C_{ij}$. That is, spatial clustering scales up the effective interaction effects. By definition, $C_{ij} = C_{ji}$ (Tekwa et al. 2015). Spatial clustering can be due to either endogenous (low dispersal and pattern formation) or exogenous (habitat connectivity and matrix constraint) processes. In particular, low dispersal leads to C_{ij} being greater than one within species ($C_{ii} > 1$) and less than one between species ($C_{ij} < 1$) because offspring tend to be near parents (Bolker and Pacala 1999, Lion and Baalen 2008, Tekwa et al. 2019*b*). Here, we assume that clustering is constant through time and ignore possible dependencies on N_i or higher moments (Bolker and Pacala 1999). Among species or morphs that are very similar, as in an incremental evolutionary process without population size dynamics, it has been shown that relative clustering (C_{ii}/C_{ij}) is constant (Nathanson et al. 2009, Tarnita et al. 2009, Tekwa et al. 2015). In the more general ecological case where species can be very different, more habitat connectivity or higher movement rates are still expected to create less relative clustering (approaching one with the highest connectivity or movement rates) (Bolker and Pacala 1999, Tarnita et al. 2009, Tekwa et al. 2019*b*). However, in some systems, a bifurcation is associated with dramatic changes in spatial clustering (Kéfi et al. 2013, Nijp et al. 2019), which may produce quantitatively different coupled dynamics. Thus, the constant clustering assumption is an approximation that roughly captures spatial effects on regime dynamics, but real spatially driven bifurcations may be more complex.

Spatial clustering affects coral and macroalgal competition terms under the spatial Lotka-Volterra framework. By matching terms in the spatial Lotka-Volterra model and the coral–macroalgal model (Table 1), we find that intraspecific competition a_{ii} is 1 without spatial clustering (compare [1] and [3]), and increases with within-species clustering (C_{ii}; Table 2). Interspecific competition effects a_{ij}, on the other hand, are moderated by space and other parameters (C_{ij}, r, g, and a; Table 2).

With spatial considerations, the stability criterion for species i dominance is given as:

$$\frac{c_{ij}a_{ji}}{c_{ii}a_{ii}} > \left(\frac{r_j - m_j}{r_j}\right) \Big/ \left(\frac{r_i - m_i}{r_i}\right). \tag{4}$$

This inequality is hard to attain when relative clustering (C_{ii}/C_{ij}) is high. Thus, clustering promotes global coexistence, even when there tends to be one species dominating locally. This matches the well-known hypothesis that spatial variation promotes coexistence (Chesson 2000).

Temperature dependence

Warming is recognized as one of the most dramatic factors affecting coral reefs (Hughes et al. 2019). As a simple and analytically tractable way to consider temperature, we assume that intrinsic growth rates r_i are maximal when temperature matches the historical temperature (equivalent to r for corals and γ for macroalgae in the Mumby et al. (2007) model) and that growth rates decrease when temperature deviates from these optima according to (nonstandardized) Gaussian functions. A species' thermal tolerance is the standard deviation of each of these Gaussian functions. Further, we assume that macroalgae has a wider thermal tolerance (σ_1) than corals (σ_2, Table 2), at values that would respond strongly to a 1°C increase in temperature. Mortality rates are assumed to be constant in temperature for corals (d) and for macroalgae (g).

RESULTS

We use stability criteria in the spatial Lotka-Volterra model to show how dynamic regimes in two-species (e.g., coral–macroalgal) communities can be generically described using simple geometry with only three parameters for competition and growth. We then show how the effects of grazing, spatial clustering, and warming translate to changes in these three competition and growth parameters to affect dynamic outcomes in the coral–macroalgal system. We aim to show that diverse mechanisms of community regime shifts can be synthesized under a common, low-dimensional geometric framework.

Geometry of dynamic regimes

The community dynamic regimes of a two-species spatial Lotka-Volterra model are determined by two inequalities involving three parameters. From Eq. 4, the three parameters are (1) the local species 1 intra-to-interspecific cross-competition ratio $\alpha_1 = C_{11}a_{11}/(C_{21}a_{21})$; (2) the local species 2 intra-to-interspecific cross-competition ratio $\alpha_2 = C_{22}a_{22}/(C_{12}a_{12})$; and (3) the intrinsic growth inequality ratio between species 2 and 1, $f_{21}=(1 - m_2/r_2)/(1 - m_1/r_1)$ (see Table 3). The competition ratios are called "cross-competition," because they are ratios of the intraspecific competition effect on the focal species relative to the interspecific competition effect on the other species. Competition ratios also encapsulate the positive and multiplicative effects of spatial clustering. Table 3 shows that the possible combinations of inequalities produce the four dynamic regimes of alternative stable states, species 1 only, species 2 only, and coexistence. The

Table 3. Conditions for each community dynamic regime. The variables that determine dynamic regimes are (1) intra-to-interspecific cross-competition ratio $\alpha_1 = C_{11}a_{11}/(C_{21}a_{21})$, (2) intra-to-interspecific cross-competition ratio $\alpha_2 = C_{22}a_{22}/(C_{12}a_{12})$, and (3) intrinsic growth inequality f_{21}=(1-m_2/r_2)/(1-m_1/r_1).

Conditions	Community dynamic regimes
$1/\alpha_1 > f_{21} > \alpha_2$	Alternative stable states
$1/\alpha_1 > f_{21} < \alpha_2$	Species 1 only
$1/\alpha_1 < f_{21} > \alpha_2$	Species 2 only
$1/\alpha_1 < f_{21} < \alpha_2$	Coexistence

"quadruple points" ($1/\alpha_1 = \alpha_2 = f_{21}$, e.g., $\alpha_1 = \alpha_2 = f_{21} = 1$) are where the four dynamic regimes collide (named after the triple point in the thermodynamic transition between solid, liquid, and gas) (Maxwell and Harman 1990). Some illustrative calculations made in terms of these three parameters demonstrate that increases in grazing shift the dynamics from "species 2 (i.e., macroalgae) only" to "alternative stable states" to "species 1 (i.e., coral) only" (Appendix S2: Table S1), while increases in relative clustering shift the dynamics from "alternative stable states" to "species 2 only" and eventually to "coexistence" (Appendix S3: Table S1).

The three parameters constitute the coordinates in which the stability of each species can change. The planes $1/\alpha_1 = f_{21}$ and $f_{21} = \alpha_2$ bisect, respectively, regions where species 1 and species 2 dominance are marginally stable. In particular, in log-space these planes are flat (because all dimensions are ratios; Fig. 2A). Using these planes, we can construct a volume with the three dimensions as axes and dynamic regimes as categorical outcomes coded by color (Fig. 2B). This cube completely describes all possible dynamic regimes and their relationships with parameters in the spatial Lotka-Volterra model. For pedagogical purpose, the regime geometry (Fig. 2A) can be constructed using origami paper as shown in Fig. 3.

The dynamic regime geometry distills the spatial Lotka-Volterra model into three bifurcation dimensions that summarize competition and intrinsic growth properties (α_1, α_2, f_{21}). This is a drastic dimensionality reduction from the original spatial Lotka-Volterra model (11 dimensions: a_{11}, a_{12}, a_{21}, a_{22}, C_{11}, C_{12}, C_{22}, m_1, m_2, r_1, and r_2) and the linearized coral–macroalgal model (5 dimensions: a, d, g, γ, and r) (Tables 1 and 2). The dimensionality reduction also means that there are multiple ways (multiple combinatorial changes in the original parameters) to achieve the same bifurcations. For example, equal changes to either relative clustering C_{11}/C_{21} or the local competition ratio a_{11}/a_{21} result in the same change in α_1 and therefore the same sequence of regime shifts—either from coexistence to species 1 only, or from species 2 only to alternative stable states depending on f_{21} (Fig. 2 B).

We focused here on coral–macroalgal competition, but the results in this section apply to any two species by virtue of the generic spatial Lotka-Volterra formulation.

System-specific outcomes

The categorization of dynamic regimes and dimensional reduction allows one to take a geometric approach to reasoning. Here, we illustrate the utility and limitation of geometric reasoning by comparing it against species-level outcomes for a particular set of parameters. In this system, we explore how changes in grazing (Mumby et al. 2007), spatial clustering (Bolker and Pacala 1999), and warming (Hughes et al. 2019) affect dynamic regimes—quantities that should be obtainable from geometric reasoning alone. We also explore the effects on coral and macroalgal covers or densities—quantities that are related to but are more specific than categorical regimes (see Appendix S3: Table S2 for parameter values and numerical outcomes from this example).

First, we show how parameter changes can be represented as trajectories or "bifurcation vectors" corresponding to the geometric coordinates of α_1, α_2, and f_{21} (series of circles in Fig. 2B). As grazing increases, it decreases the relative growth of macroalgae vs. coral (f_{21}) and decreases the cross-competition ratio (relative intraspecific competition) for macroalgae (α_1). A major effect of relatively high grazing is to drive the system toward the lower part of Fig. 2B. In contrast, increases in spatial clustering increase the cross-competition ratios for both species (α_1, α_2), driving the system toward the front left corner of Fig. 2B.

The effects of warming are more complicated. Warming decreases the cross-competition ratios (α_1, α_2) independently of clustering and grazing.

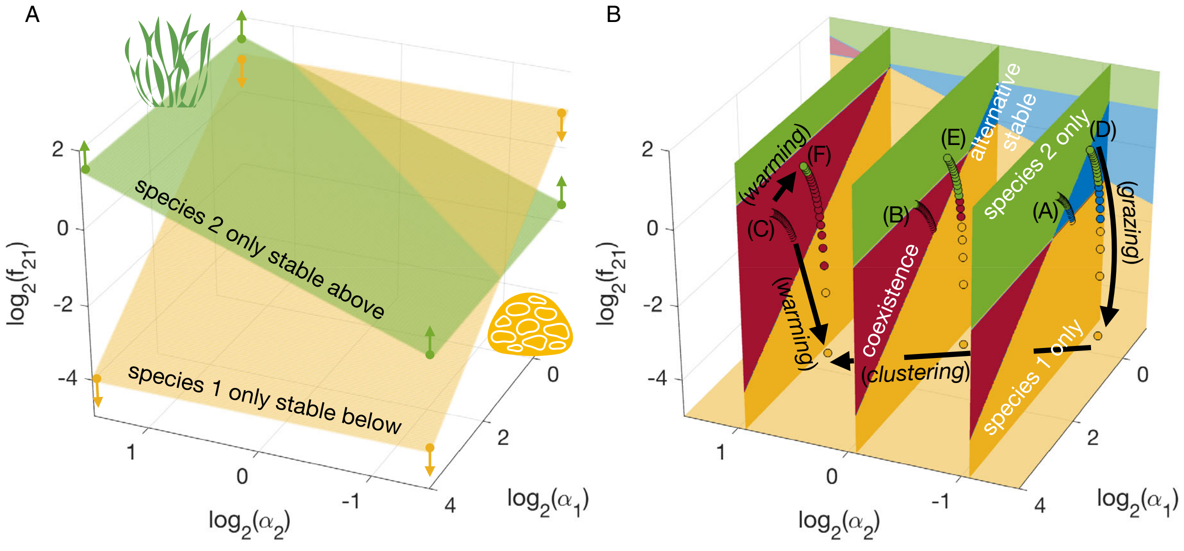

Fig. 2. Geometric representation of the relationship between Lotka-Volterra parameters and the four possible dynamic regimes. The dimensions are the species 1 intra-to-interspecific cross-competition log-ratio ($\log_2(\alpha_1)$), the species 2 cross-competition log-ratio ($\log_2(\alpha_2)$), and the intrinsic growth log-inequality of species 2 over species 1 ($\log_2(f_{21})$). (A) The two-species spatial Lotka-Volterra model's dynamic regimes are separated by two planes that define the marginal stability of each species' dominance. These planes bisect each other and create four dynamic regimes (B), which are illustrated using three two-dimensional cross-sections (colored regimes with white text). Bifurcation vectors (black arrows and text) show the effects of grazing, warming, and spatial clustering. Letters A-F corresponding to subplots in Figure 4. Series of circles colored by regimes represent how equidistant increments in grazing in a coral–macroalgal model traverse the regime geometry. The series start at three different and fixed spatial clustering and two warming levels.

Less intuitively, warming increases the growth inequality (f_{21}) at low grazing due to macroalgae's wider thermal tolerance, but decreases the growth inequality at high grazing where even a slight drop in γ pushes macroalgae closer to zero growth (see Table 1). The result is an expanded range of f_{21} values traversed by grazing variation when combined with warming, which for instance leads to transitions from coexistence to species 1 only that would otherwise not occur.

We next compare coral and macroalgal cover changes (Fig. 4) to corresponding regime shifts from the geometric perspective (Fig. 2). Under no warming and no spatial clustering, increases in grazing transition the community from macroalgal dominance to alternative stable states to coral dominance (Fig. 4A). With more clustering, macroalgal dominance is only realized at low grazing, while coexistence becomes more likely at high grazing (Fig. 4B, C). With warming, the grazing parameter ranges that lead to macroalgae (at low grazing) or coral dominance (at high grazing) increase, while the grazing ranges that lead to coexistence or alternative stable states decrease (Fig. 4D-F) when compared to the case with baseline temperatures (Fig. 4A-C). The geometrically predicted alternative stable states and coexistence regimes, corresponding to cases in Figure 4A, F, are confirmed with phase diagrams where transient trajectories with different initial conditions converge on the expected number of stable equilibria (Fig. 5).

In summary, the outcomes for the specifically parameterized coral–macroalgal system illustrate the levels of dynamic precision that cannot be gleaned from geometric reasoning alone; but the dynamic regime predictions from geometry remain accurate. The most detailed features of a dynamic system—transient trajectories (Fig. 5)—are only partly captured by equilibrium

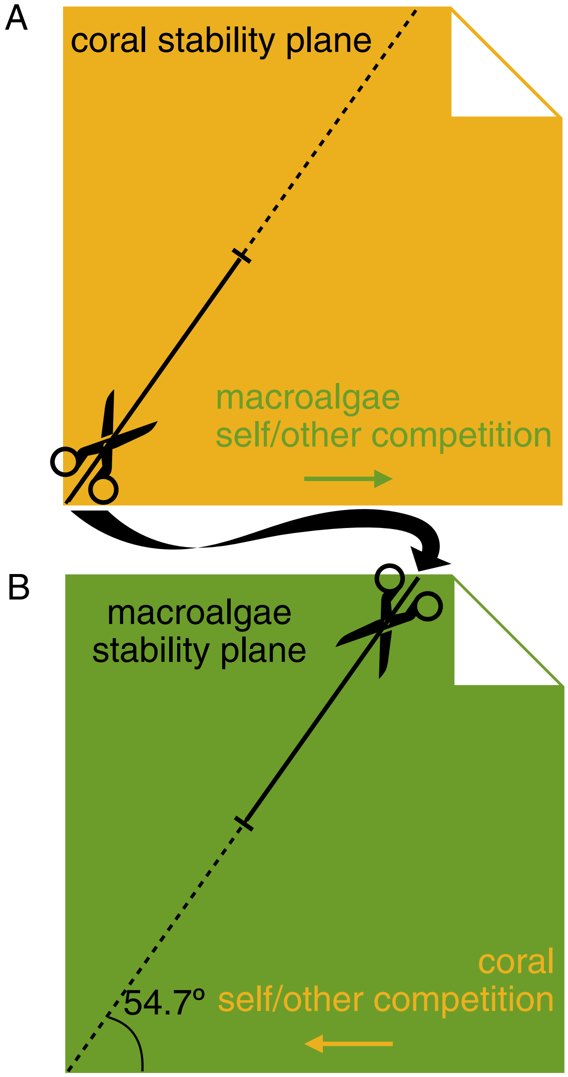

Fig. 3. Regime shift origami. The community stability of (A) coral (yellow) vs. (B) macroalgae (green) can be constructed using two pieces of single-sided color paper representing species stability planes (zero maximum eigenvalue), with the colored side indicating negative maximum eigenvalues and stable single-species existence. The result is a pyramid-like structure as in Fig. 2A, with the *x*- and *y*-axes labeled as illustrated (α_1 and α_2), and the *z*-axis indicating f_{21}.

analyses (Fig. 4). Equilibria, or expected coral and macroalgal densities, are in turn not captured by regime geometry (Fig. 2). Nevertheless, with only three coordinates α_1, α_2, and f_{21} (Fig. 2 vectors and matching color codes in Fig. 4 and Appendix S3: Table S2), regime shifts caused by multiple bifurcating forces including grazing, warming, and spatial clustering can be inferred using geometric reasoning alone (series of circles in Fig. 4B).

DISCUSSION

Regime shifts have been a focus of conservation in an era of change (Steffen et al. 2015), and coral reefs have served both as a model for understanding such shifts and as an important biome that is a focus of substantial conservation efforts (Bellwood et al. 2004, Hughes et al. 2017). Conservation efforts are, however, confounded in part by the diverse and disparate proposals for

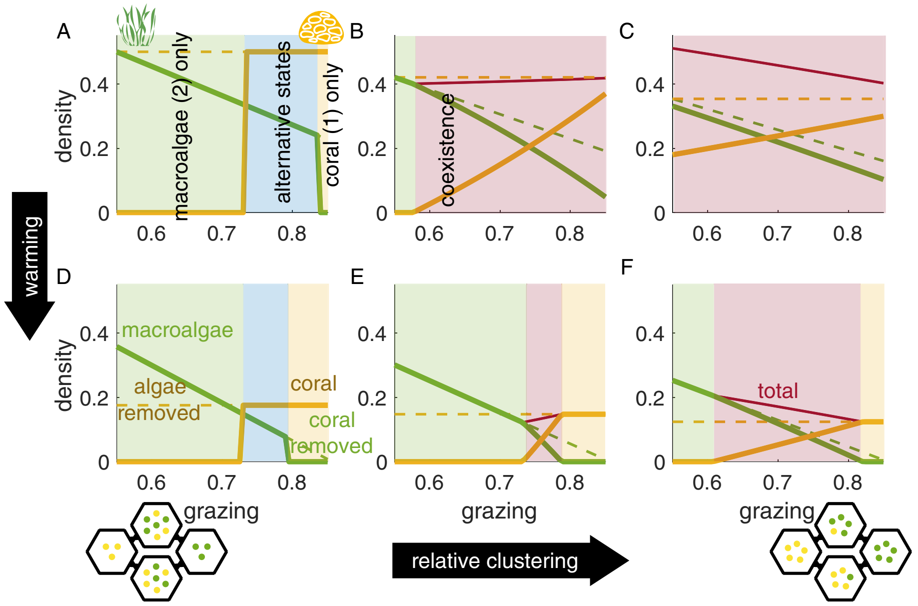

Fig. 4. Regime shifts and coral–macroalgal density changes driven by changes in grazing. Results are from the spatial Lotka-Volterra model (see Table 2 for parameterization). Plots show macroalgal cover or density (green line), coral cover (yellow line), macroalgae or coral with the other artificially removed (dotted lines, to contrast with coexistence effects), and total cover of both taxa during coexistence (maroon line). (A-C) Baseline temperatures, with relative clustering (C_{ii}/C_{ij}) at 1, 2, or 4 (from left to right). (D-F) 1 °C warming, with relative clustering being 1, 2, and 4. The shades indicate the regimes of macroalgal dominance (green), alternative stable states (blue), coral dominance (yellow), and coexistence (red). Yellow and green dots in patch diagrams at the bottom illustrate cases of low (left) vs. high (right) relative clustering.

mechanisms that drive regime shifts in coral reefs (Mumby et al. 2013, van de Leemput et al. 2016, Hughes et al. 2019). Here, we provided a theoretical synthesis that captures the essential dynamics within coral reefs and other competitive communities. Further, we found that the dynamic regimes of alternative stable states, single-species dominance, and coexistence can be fully determined by only three synthetic parameters. The reduced parameter set summarizes intraspecific vs. interspecific spatial competition effects (α_1, α_2), as well as intrinsic growth differences between species (f_{21}). The three parameters form a cubic volume that allows for a geometric analysis of regime shifts. Ecologically realistic bifurcations or regime-shifting forces, such as grazing, spatial clustering changes, and warming, can be visualized as vectors through the dynamic regime cube. These results were derived for well-known systems with simple linear Lotka-Volterra effects to illustrate the novel geometric method. A similar approach of obtaining geometry from marginal stability could yield analogous insights for nonlinear effects such as predation and parasitism (Holling 1959, Rosenzweig and MacArthur 1963).

The regime perspective produces conservation-relevant insights despite ignoring species-specific outcomes. In a coral–macroalgal system, we showed that grazing decreases the intrinsic growth difference f_{21} and moves the system away from macroalgal dominance. With warming, the regime geometry distance traversed by a unit change in grazing rate increases, thereby increasing the likelihood of either coral or macroalgae dominating. Spatial clustering on the other hand moves the system toward higher intraspecific competition relative to interspecific competition (α_1 and α_2), which promotes coexistence and reduces the effectiveness of grazing for inducing coral dominance. This geometric reasoning suggests that the protection of grazers

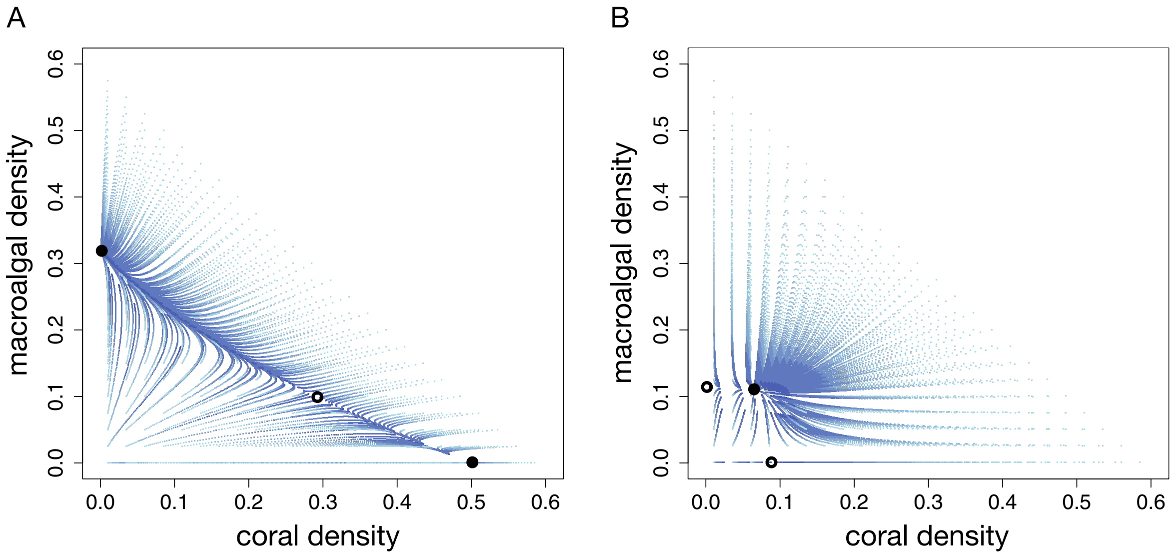

Fig. 5. Phase diagrams of Lotka-Volterra coral-macroalgal dynamics. Trajectories (blue) are shown for 100 time steps starting at evenly spaced initial densities, with darker color indicating densities at later times. Filled circles are analytically derived stable equilibria, while open circles are unstable equilibria. (A) Trajectories corresponding to baseline temperatures, no spatial clustering, and a grazing rate of 0.75 showing alternative stable states (scenario in Fig. 3A). (B) Trajectories corresponding to an increased temperature, high spatial clustering, and a grazing rate of 0.75 showing coexistence (scenario in Fig. 3F).

will have an enhanced positive effect on coral conservation under warming in conjunction with low spatial clustering (such as by maintaining habitat connectivity between reefs). In contrast, if grazer protection fails in the face of fishing pressure (Costello et al. 2016, Tekwa et al. 2019*a*), then high clustering through low habitat connectivity (e.g., greater distance between protected areas) may actually enhance coral persistence through spatial coexistence mechanisms (Chesson 2000), although at much lower levels than if both grazers and habitat connectivity are protected. These geometric results illustrate that multiple management tools, such as controls on grazing and connectivity, can interact to produce alternative routes to achieve conservation goals.

The geometry of regime shifts resembles other uses of graphical reasoning such as population growth isoclines (Tilman 1980, Knowlton 1992, McCann and Yodzis 1995) and grazing or economic phase diagrams (Gordon 1954, Noy-Meir 1975). The novelty of our approach lies in its basis in stability criteria, rather than flows, that directly provide intuition regarding community outcomes. Our approach also focuses on how dynamic regimes shift with all possible parameter changes, in contrast with traditional Lotka-Volterra studies that often explored transient dynamics and equilibria at fixed parameterizations or variations along one parameter (Bomze 1983, Neuhauser and Pacala 1999). Regime geometry is most analogous to phase diagrams of thermodynamic states, such as the *p-v-T* (pressure–volume–temperature) diagram of a substance's transitions between solid, liquid, and gas states (Maxwell and Harman 1990). If regime geometry and thermodynamic phase diagrams are truly analogous, then dynamics deviating from the spatial Lotka-Volterra model (nonlinear terms) could appear as modified marginal planes and regime volumes in the competition-growth space. The success of thermodynamic phase diagrams for different substances has facilitated engineering advances such as the motor and refrigeration, suggesting that regime geometry can provide a boost for conservation and ecosystem engineering by moving theoretical reasoning from mathematics to a more intuitive visualization.

The ability to geometrically represent system-specific bifurcations in generic ecological terms allows for a synthetic understanding of a wide variety of ecological communities. Regime shifts in lakes (Scheffer et al. 1993), kelp forests (Ling et al. 2014), and terrestrial forests (Hirota et al. 2011) share both similarities and differences with coral reefs, but can all be placed within the same geometry defined by the dimensions of competition and growth. The spatial Lotka-Volterra model that the geometry represents is also testable using data from these diverse ecosystems, because it makes specific predictions about when and what kinds of shifts should occur as competition and growth ratios vary. Such a cross-system empirical synthesis can potentially facilitate the exchange of diverse conservation experiences. Moreover, the geometry highlights that regime shifts (Scheffer and Carpenter 2003) should be considered more broadly to include transitions between coexistence and single-species dominance, rather than being solely associated with alternative stable states. Coral reefs (Hughes et al. 2017, Darling et al. 2019) and other ecosystems (Waters et al. 2016) face multiple stressors and perturbations simultaneously in the Anthropocene, resulting in conservation challenges that seem impossibly complex unless ecological theory sheds light on their commonalities and interactions. The geometric perspective on stability is one potential tool to distill complexity to an accessible form, avoid simplistic explanations, and open multiple management options for conservation success.

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LITERATURE CITED

Anthony, K. R. N., J. A. Maynard, G. Diaz-Pulido, P. J. Mumby, P. A. Marshall, L. Cao, and O. Hoegh-Guldberg. 2011. Ocean acidification and warming will lower coral reef resilience: CO2 and coral reef resilience. Global Change Biology 17:1798–1808.

Baskett, M. L., N. S. Fabina, and K. Gross. 2014. Response diversity can increase ecological resilience to disturbance in coral reefs. American Naturalist 184:E16–E31.

Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. Nature 429:827–833.

Blackwood, J. C., A. Hastings, and P. J. Mumby. 2011. A model-based approach to determine the long-term effects of multiple interacting stressors on coral reefs. Ecological Applications 21:2722–2733.

Bolker, B. M., and S. W. Pacala. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. American Naturalist 153:575–602.

Bomze, I. M. 1983. Lotka-Volterra equation and replicator dynamics: a two-dimensional classification. Biological Cybernetics 48:201–211.

Bruno, J. F., H. Sweatman, W. F. Precht, E. R. Selig, and V. G. W. Schutte. 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology 90:1478–1484.

Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology 58:211–237.

Costello, C., et al. 2016. Global fishery prospects under contrasting management regimes. Proceedings of the National Academy of Sciences of the United States of America 113:5125–5129.

Darling, E. S., et al. 2019. Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. Nature Ecology & Evolution 3: 1341–1350.

Dudgeon, S., R. Aronson, J. Bruno, and W. Precht. 2010. Phase shifts and stable states on coral reefs. Marine Ecology Progress Series 413:201–216.

Durrett, R., and S. Levin. 1994. The importance of being discrete (and spatial). Theoretical Population Biology 46:363–394.

Elmhirst, T., S. R. Connolly, and T. P. Hughes. 2009. Connectivity, regime shifts and the resilience of coral reefs. Coral Reefs 28:949–957.

Fabina, N. S., M. L. Baskett, and K. Gross. 2015. The differential effects of increasing frequency and magnitude of extreme events on coral populations. Ecological Applications 25:1534–1545.

Gause, G. F. 1934. The struggle for existence. Williams & Wilkins, Baltimore, Maryland, USA.

Gordon, H. S. 1954. The economic theory of a common-property resource: the fishery. Journal of Political Economy 62:124–142.

Graham, N. A. J., S. Jennings, M. A. MacNeil, D. Mouillot, and S. K. Wilson. 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97.

Hirota, M., M. Holmgren, E. H. Van Nes, and M. Scheffer. 2011. Global resilience of tropical forest and savanna to critical transitions. Science 334:232–235.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91:385–398.

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

Hughes, T. P., et al. 2019. Ecological memory modifies the cumulative impact of recurrent climate extremes. Nature Climate Change 9:40–43.

Jokiel, P. L., K. S. Rodgers, E. K. Brown, J. C. Kenyon, G. Aeby, W. R. Smith, and F. Farrell. 2015. Comparison of methods used to estimate coral cover in the Hawaiian Islands. PeerJ 3:e954.

Kéfi, S., V. Dakos, M. Scheffer, E. H. Van Nes, and M. Rietkerk. 2013. Early warning signals also precede non-catastrophic transitions. Oikos 122:641–648.

Kingsland, S. 2015. Alfred J. Lotka and the origins of theoretical population ecology. Proceedings of the National Academy of Sciences of the United States of America 112:9493–9495.

Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. American Zoologist 32:674–682.

Li, X., H. Wang, Z. Zhang, and A. Hastings. 2014. Mathematical analysis of coral reef models. Journal of Mathematical Analysis and Applications 416: 352–373.

Ling, S. D., et al. 2014. Global regime shift dynamics of catastrophic sea urchin overgrazing. Philosophical Transactions of the Royal Society B 370:20130269.

Lion, S., and M. van Baalen. 2008. Self-structuring in spatial evolutionary ecology. Ecology Letters 11:277–295.

Lotka, A. J. 1978. The growth of mixed populations: two species competing for a common food supply. Pages 274–286 *in* The golden age of theoretical ecology: 1923–1940. Springer, Berlin, Germany.

Maxwell, J. C., and P. M. Harman. 1990. The scientific letters and papers of James Clerk Maxwell. Cambridge University Press, Cambridge, UK.

McCann, K., and P. Yodzis. 1995. Bifurcation structure of a three-species food-chain model. Theoretical Population Biology 48:93–125.

McCook, L., J. Jompa, and G. Diaz-Pulido. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19:400–417.

McManus, L. C., J. R. Watson, V. V. Vasconcelos, and S. A. Levin. 2019. Stability and recovery of coral-algae systems: the importance of recruitment seasonality and grazing influence. Theoretical Ecology 12:61–72.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98–101.

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

Nathanson, C. G., C. E. Tarnita, and M. A. Nowak. 2009. Calculating evolutionary dynamics in structured populations. PLoS Computational Biology 5: e1000615.

Neuhauser, C., and S. W. Pacala. 1999. An explicitly spatial version of the Lotka-Volterra model with interspecific competition. Annals of Applied Probability 9:1226–1259.

Nijp, J. J., A. J. A. M. Temme, G. A. K. Voorn, L. Kooistra, G. M. Hengeveld, M. B. Soons, A. J. Teuling, and J. Wallinga. 2019. Spatial early warning signals for impending regime shifts: a practical framework for application in real-world landscapes. Global Change Biology 25:1905–1921.

Noy-Meir, I. 1975. Stability of grazing systems: an application of predator-prey graphs. Journal of Ecology 63:459.

Petraitis, P., and C. Hoffman. 2010. Multiple stable states and relationship between thresholds in processes and states. Marine Ecology Progress Series 413:189–200.

Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. American Naturalist 97:209–223.

Sandin, S. A., and D. E. McNamara. 2012. Spatial dynamics of benthic competition on coral reefs. Oecologia 168:1079–1090.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology & Evolution 18:648–656.

Scheffer, M., S. H. Hosper, M.-L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends in Ecology & Evolution 8:275–279.

Schmitt, R. J., S. J. Holbrook, S. L. Davis, A. J. Brooks, and T. C. Adam. 2019. Experimental support for alternative attractors on coral reefs. Proceedings of the National Academy of Sciences of the United States of America 116:4372–4381.

Schröder, A., L. Persson, and A. M. De Roos. 2005. Direct experimental evidence for alternative stable states: a review. Oikos 110:3–19.

Staver, A. C., and S. A. Levin. 2012. Integrating theoretical climate and fire effects on savanna and forest systems. American Naturalist 180:211–224.

Steffen, W., et al. 2015. Planetary boundaries: guiding human development on a changing planet. Science 347:1259855.

Tarnita, C. E., H. Ohtsuki, T. Antal, F. Fu, and M. A. Nowak. 2009. Strategy selection in structured populations. Journal of Theoretical Biology 259:570–581.

Tekwa, E. W., E. P. Fenichel, S. A. Levin, and M. L. Pinsky. 2019*a*. Path-dependent institutions drive alternative stable states in conservation. Proceedings of the National Academy of Sciences of the United States of America 116:689–694.

Tekwa, E. W., A. Gonzalez, and M. Loreau. 2019*b*. Spatial evolutionary dynamics produce a negative cooperation–population size relationship. Theoretical Population Biology 125:94–101.

Tekwa, E. W., A. Gonzalez, and M. Loreau. 2015. Local densities connect spatial ecology to game, multilevel selection and inclusive fitness theories of cooperation. Journal of Theoretical Biology 380: 414–425.

Tilman, D. 1980. Resources: a graphical-mechanistic approach to competition and predation. American Naturalist 116:362–393.

van de Leemput, I. A., T. P. Hughes, E. H. van Nes, and M. Scheffer. 2016. Multiple feedbacks and the prevalence of alternate stable states on coral reefs. Coral Reefs 35:857–865.

Volterra, V. 1926. Variations and fluctuations of the number of individuals in animal species living together. Animal Ecology 409–448.

Waters, C. N., et al. 2016. The Anthropocene is functionally and stratigraphically distinct from the Holocene. Science 351:aad2622.

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