

Dynamic excitability underlies molluscan shell pigmentation

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Pigmentation in mollusc shells exhibits an exceedingly diverse range of patterns that raises questions on the mechanisms underlying such diversity. This work introduces a new class of excitable systems, which extends the well-known FitzHugh-Nagumo model to allow for dynamic variation of the phase space. The phenomenon emerging from such a dynamic variation of the underlying excitable system is termed *dynamic excitability*. It is shown that the essential features of several classes of pigmentation patterns can be described through this unified framework of dynamic excitability, and that many of the patterns can be understood as the underlying excitable system dynamically switching between different unsteady states. A fast switch between two dynamic states is responsible for the emergence of some of the more complex pigmentation patterns observed in molluscan shells. The modeling suggests that dynamic excitability could be a universal mechanism underlying the large diversity of molluscan shell pigmentation patterns.

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I. INTRODUCTION

Molluscs exhibit a fascinatingly diverse array of pigmentation patterns on their shells, which has naturally prompted questions on the functionality and mechanisms of shell color and pigmentation. Despite numerous studies, there appears to be no real consensus on these questions [1]. Nevertheless, various attempts have been made to model the pigmentation patterns themselves as a dynamical process. Underlying the vast diversity of shell pigmentation is the homologous organ, the mantle, which sits in contact with the shell, folding around the shell's outer edge [2]. The mantle is responsible for the growth of the shell, adding new material layer-by-layer on this growing outer edge of the shell, with pigmentation typically also being deposited in this new layer. Each new layer of the shell (along with its pigmentation) represents an instantaneous snapshot of the developmental process. Molluscan shells therefore have a unique feature that each shell represents the entire historical record of its developmental process [1–3]. Such a growth process has naturally prompted the modeling of pigmentation patterns to be performed considering a system dynamically evolving in time and in one spatial dimension. Early attempts include computer simulations performed by Waddington and Cowe [4] for the generation of wedgelike patterns. The work of Meinhardt and Klingler [5–7] proposes several different reaction-diffusion systems for modeling varying patterns observed in shells. The underlying idea of the models is based on the activator-inhibitor type systems, which are also identified with local activation and

lateral inhibition (LALI) type models in developmental biology [8,9]. The various reaction-diffusion models for shell pigmentation are covered in detail in Ref. [10]. Pigmentation models based on neural network type mathematical models have been proposed in the work of Ermentrout and co-workers [3,11], which is based on the idea that shell patterns may represent a recording of the nervous activity of the organism. The LALI ideas also underlie the proposed neural models and the approach has also been successful in modeling a wide range of observed pigmentation patterns. An alternate approach has been to utilize models based on cellular automata [12], which specify rules for updating the system state for the generation of pigmentation patterns, which have also found some success in simulating patterns observed in molluscan shells [13,14].

While the previous modeling efforts have been successful in reproducing many of the individual patterns, they often suffer when it comes to the interpretation of several classes of patterns together. The work of Meinhardt in Ref. [10], for example, presents several different reaction-diffusion models for the varying classes of patterns; it does not, however, present a unifying model from which the individual classes of models may be derived. The unsaid interpretation of such lack of unification is that there may be several different underlying biological mechanisms that eventually lead to the diversity of patterns that are observed. Similarly, cellular-automata models can reproduce many of the individual patterns based on individual rules but offer no insight into what leads to the selection of these rules or how a particular organism may switch between rules. The work of Boettiger *et al.* [11] does provide a single neural network model for several pigmentation patterns; however, the model is nonlocal in time, effectively requiring the previous time history of the pigmentation production for the evolution of the pattern. Not only does this make the model hard to analyze, but it also imposes rather stringent requirements on the biological mechanism that would be responsible for pigmentation production, since the organism would also need a mechanism to sense

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the position of pigmentation through preexisting layers of the shell.

In the current work, we take a different perspective to the problem of shell pigmentation patterning. We take the reaction-diffusion approach to model the underlying system as has been done by Meinhardt [10]; however, it is recognized that much of the dynamical information is in fact contained in the “reaction” term. This allows us to analyze the system locally by dropping the diffusion term and infer the dynamics in phase space. This approach is of course not new; Barkley in modeling transition pipe flows has referred to the local part of the model as the “heart of the model” [15], and neural excitability is often understood through this local phase-space picture [16,17]. However, such a phase-space-based approach appears to be lacking in previous modeling efforts of Meinhardt and Klingler [5,7,10]. Taking this approach allows one to connect the patterns observed in the spatially extended domain to the local phase space, thereby illuminating intimate connections between the various classes of observed patterns.

The local phase space is then endowed with an excitable structure of the prototypical FitzHugh-Nagumo model. A hint of such underlying excitable dynamics comes from a particular pigmentation pattern that seems to be very commonly observed, which is of localized pigmentation regions that propagate through space. This particular pattern has been given various names such as traveling waves, wedgelike patterns, or oblique lines, and the earliest numerical simulations of Ref. [4] in fact focused on reproducing such patterns. Such localized propagating structures are observed in other pattern-forming systems as well and subsequent theoretical work has shown this to be one of the defining features of excitable systems in spatially extended domains [16–20]. The role of excitability in the generation of such traveling waves was recognized in the extensive reporting of pigmentation patterns in Ref. [10]; however, excitable dynamics form just one of the many proposed mechanisms for the generation of pigmentation patterns.

In the current modeling effort, excitable dynamics takes center stage, and we introduce a new class of excitable systems that we refer to as *dynamic excitability*. This is an extension of the FitzHugh-Nagumo model with an additional (possibly global) variable that primarily acts to dynamically modify the phase-space structure of the underlying (FitzHugh-Nagumo) system. It is shown that this new system generates the essential features of several classes of the pigmentation patterns observed in molluscan shells. The focus, however, is not just on the reproduction of patterns, but on the dynamics behind the emergence of the patterns. Two ideas are key to understanding the evolution of the distinct classes of patterns that are discussed in the later sections. The first is that the local phase-space structure determines the distinct spatial patterns that emerge from the system evolution, and variations of the phase space lead to predictable transitions between these patterns. The second is that the phase-space dynamics can be connected to spatial dynamics through the understanding of front propagation. In particular, the dynamic variations in phase space leads to dynamic variations in front velocities, and it is these transient effects that lead to the many distinct patterns observed in molluscan shells. These aspects are explained in significant more detail in subsequent

sections in the article. It is the understanding of these dynamic variations in phase space that allows us to make deeper connections across many different classes of patterns. The diversity of patterns in molluscan shells is immense, and the goal of the modeling here is not to reproduce every aspect of observed pigmentation patterns in molluscan shells but rather to capture the most essential properties of the various patterns. Given the enormous diversity of observed patterns, it is likely that a single model will prove insufficient to describe all the existing patterns if one attempts to incorporate every fine detail; nevertheless, the proposed model based on dynamic excitability does present a unified framework to explain a number of (previously disparate) classes of pigmentation patterns. The unified framework also allows us to elucidate how the different patterns relate to each other from a dynamics point of view, which is of particular relevance since multiple patterns can often be observed to coexist within a single shell. Such coexistence of patterns necessarily implies that the same underlying system must be responsible for the different patterns. The unifying point of view then has obvious biological implications in that there might indeed be universal aspects to the a great variety of the molluscan pigmentation patterns.

The subsequent sections are structured as follows. The essential structure of excitability is described in Sec. II, along with the description of various patterns (and their dynamics) obtained through a limited variation of the parameters. This is done without allowing for dynamic changes of the phase space. The observed pigmentation patterns in shells corresponding to the numerically simulated model solutions are highlighted. The excitable model is then extended in Sec. III to allow for dynamic variation of the phase space, and it is shown how several more complex patterns naturally emerge due to the extension. A discussion of the results is done in Sec. IV and concluding remarks are made in Sec. V.

II. EXCITABLE STRUCTURE

A. Essential underlying structure

The essential structure of the model is based on the dynamics of excitable systems, similar to the FitzHugh-Nagumo model of nerve conduction [16,21,22]. The model consists of two variables (herein denoted as A and B) that are governed by the evolution equations of the type

$$\frac{\partial A}{\partial t} = \frac{1}{\epsilon} f(A, B) + \epsilon D_A \nabla^2 A, \quad (1a)$$

$$\frac{\partial B}{\partial t} = g(A, B) + \epsilon^2 D_B \nabla^2 B. \quad (1b)$$

Here, ϵ is a small parameter that imparts a “slow-fast” structure to the system such that A typically evolves much faster than B [unless $f(A, B) \approx 0$]. We borrow the terminology of Ref. [10] and refer to A as the activator and to B as the inhibitor, although the mapping of the variables and their literal meaning should be considered only approximate and the dynamics are more appropriately viewed from the perspective of “slow” and “fast” variables. Nevertheless, the activator-inhibitor terminology is retained here and large values of the activator are identified here with the deposition of the pigment on the shell surface. ∇^2 is the Laplacian operator, which, in the current context, is the one-dimensional Laplacian. D_A and

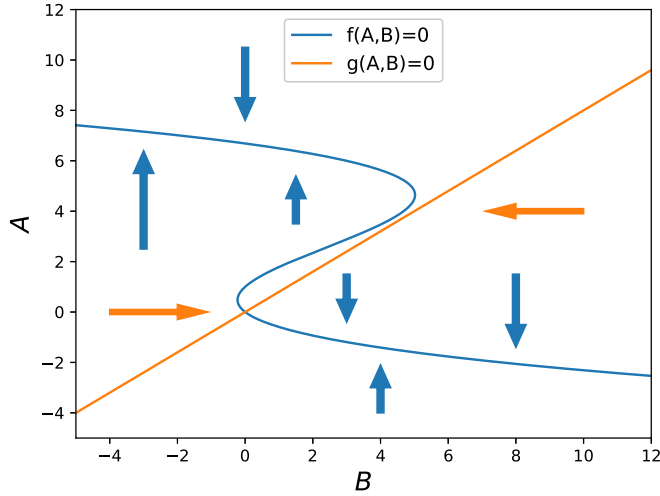


FIG. 1. Qualitative phase flow of a typical (local) excitable system along with the nullclines. The blue arrows indicate the direction of activator (A) flow in different parts of the phase space, while the orange arrows indicate direction of inhibitor (B) flow.

D_B are diffusion coefficients for A and B , respectively. From the modeling point of view, the physical length scale of the system can always be rescaled such that $x \mapsto \sqrt{D_B}x$, so that $D_A \mapsto D_A/D_B$ and $D_B \mapsto 1$, in the rescaled system. We follow this scaling in the current work and D_B is always set to one. The functions $f(A, B)$ and $g(A, B)$ provide the local evolution rates of the two variables and dictate the essential dynamics of the system. The two evolution functions are of the type

$$f(A, B) = \alpha_1 A(A - 1)(A - \alpha_2) + \alpha_3 B, \quad (2a)$$

$$g(A, B) = \beta_0 + R(\cos(\phi)A + \sin(\phi)B),$$

$$R = \sqrt{(\beta_1)^2 + (\beta_2)^2},$$

$$\phi = \arctan(\beta_2/\beta_1), \quad (2b)$$

where $\alpha_1, \alpha_2, \alpha_3, \beta_0, \beta_1, \beta_2$ are system parameters. A local model of the system is obtained by dropping the Laplacian terms in Eq. (1), which removes the spatial coupling of the evolution operators. The action of the evolution operators is best understood through the nullclines of the system, which are the loci of the points in the (A, B) phase space where $f(A, B)$ and $g(A, B)$ individually vanish. The nullclines for a typical system are shown in Fig. 1, with the solid blue line representing the nullcline of the activator [$f(A, B) = 0$], and the solid orange line representing inhibitor nullcline [$g(A, B) = 0$]. The parameters of the particular system can be found in Table I. The nullclines form a skeletal structure of the phase space such that the qualitative evolution of the system in different regions of phase space may be understood by simply knowing the direction of motion (i.e., the sign of the time derivative) of the individual variables A and B in the particular region. The blue arrows in Fig. 1 mark the direction of motion of A , while the orange arrows mark the direction of motion of B in the different regions. The cubic nature of $f(A, B)$ creates two distinct attracting branches of the activator, referred to as the upper and the lower branch, and one repelling branch that connects these two attracting branches. The inhibitor nullcline is uniformly attracting in

all regions of space. When the system is close to the upper branch of the activator nullcline, it corresponds to large values of the activator and therefore the upper branch is identified as states of pigmentation whereas when the state is close to the lower branch it refers to the state of “no pigmentation.” The inhibitor system parameters β_1 and β_2 are expressed in an alternate form using the derived parameters R and ϕ . The choice of representing the coefficients of $g(A, B)$ using R and ϕ may first appear as an unnecessary complication; however, this is done in anticipation of the modification of these equations introduced later in Sec. III, wherein the coefficients of A and B in the function $g(A, B)$ are dynamically varying. The interpretation of the dynamic variation is significantly simplified in the $R - \phi$ representation, since ϕ represents the angle of the inhibitor nullcline and is fundamentally responsible for determining the fixed point(s) of the system. The intersection of the two nullclines represents a fixed point, and the system depicted in Fig. 1 only has one stable fixed point that lies on the lower branch. However, as the parameters are varied, the system may exhibit an unstable fixed point or even multiple fixed points.

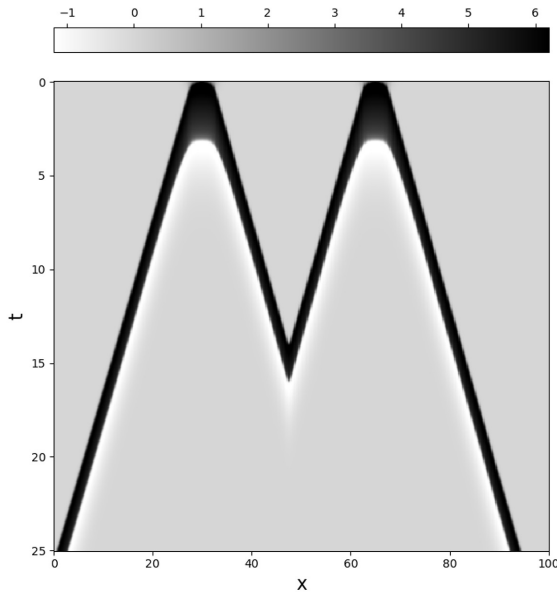
In the extensive reporting on shell patterns in Ref. [10], the observed patterns are categorized into several classes based on their essential features (albeit there are some that defy classification). In the subsequent sections, we explore how several of those classes of patterns emerge due to the variation of the fixed points of the underlying excitable structure of the system. Later, allowing for dynamic variation of fixed points generates more complex patterns, the dynamics of which may be understood in relation to the structures from their static counterparts. Unless specified otherwise, all numerical simulations reported hereafter are performed for a spatial domain of $x \in [0, 100]$ with periodic boundary conditions at the edges. The initial conditions for the simulations vary depending on the case and are reported individually, along with the nullclines of the system. The parameter values for all the individual cases are reported in the Appendix.

B. Traveling waves and wedge patterns

Bidirectional waves or wedge-shaped patterns are observed in several shells as shown in Fig. 2(a) and were the first pigmentation patterns that were investigated numerically by Waddington and Cowe [4]. Such patterns have a few characteristic features. When originating spontaneously in an unpigmented region, one obtains two localized regions of pigmentation that travel in opposite directions from the origin point. They are identified as oblique lines or traveling waves in Ref. [10], and these waves travel essentially symmetrically from their point of origin so that the wave speeds for the forward and backward waves have the same magnitude. Additionally, when two such waves collide, they annihilate so that the pigmentation disappears after annihilation. These properties are very typical of excitable systems, and the FitzHugh-Nagumo model is the prototypical model used to understand such phenomena [18–20]. These localized traveling solutions are simply referred to as pulses in the context of excitable systems and have been identified with propagating electrical pulses in nerve fibers. Similar modeling based on the excitable system idea is performed in fluids to



(a)



(b)

FIG. 2. Wedge patterns: (a) Bidirectional pigmentation waves observed in *Cymbiola nobilis* [23]. (b) Space-time plot of the system depicting bidirectional wave generation and annihilation.

model transition in pipe flow, where such localized traveling solutions are referred to as puffs [15,24] and are identified with the localized convecting turbulence. For the bidirectional waves in shells, the symmetry of the forward and backward moving waves is due to the reflection symmetry of the system, so that under the transformation, $x \mapsto -x$, Eq. (1) remains invariant. This is generally referred to as parity symmetry in the theoretical physics literature.

The nullclines of the system for the generation of such traveling waves are depicted in Fig. 3. The system is numerically solved with two localized Gaussian impulses (with amplitude $A = 6.0$ and standard deviation $\sigma = 2.0$) as initial conditions and the resulting space-time plot is depicted in Fig. 2(b). Here, the vertical axis represents the time dimension, while the horizontal axis represents the physical space. The dark regions represent large activator values (upper branch), identified as

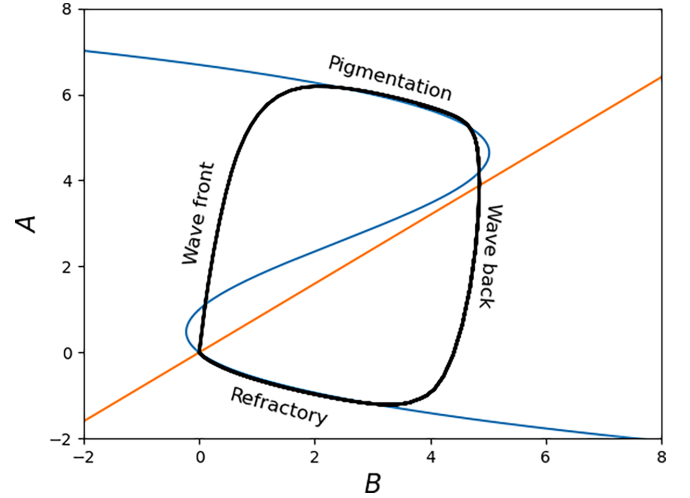


FIG. 3. Nullclines of the system for the generation of localized traveling pulses. The black line represents the local phase of the solution at each spatial point in the domain.

pigmented regions, while the gray (and white) regions depict small activator values (lower branch), identified with a lack of pigmentation. The color scale of the space-time plot is indicated by the colorbar on top of the figure, and henceforth the same color scale is used all subsequent space-time plots. The generation of bidirectional waves from the initial localized impulses as well as the annihilation of two of the waves upon collision is clearly evident.

The local phase of the solution for each point in the domain [at $t = 22$] is shown in Fig. 3 with a black line. This is the representation of the two pulse solutions in phase space. Both the forward and backward moving pulses have the same representation. The two lines joining the lower and the upper branch of the activator nullclines are the front solutions (sometimes referred to as shocks), where the system varies rapidly. These represent the sharp interfaces between the nonpigmented background (lower branch) and the pigmented (upper branch) traveling waves. Typically, the interface facing the direction of propagation of the localized solution is referred to as the wave front, while the opposite interface is referred to as wave back. In this case, the front solution connecting the upper branch to the stable fixed point forms the wave front, while the second front solution that connects the upper and lower branches (but not at the fixed point) is the wave back. The dynamics of the two front solutions evolve independent of each other and depend on the system parameters so that when the two front solutions have the same velocity (and direction) one obtains localized structures (a pulse) that propagate uniformly through the domain. The part of the solution lying on the upper branch in Fig. 3 is effectively the excited state and is responsible for the pigmented region in our case. The part of the solution lying on the lower branch forms the nonpigmented region. In the nonpigmented region, the part of the solution that lies further away from the fixed point forms what is referred to as a refractory region, in which it is very difficult to push the system back in to the excited state. In the space-time plot, this may be identified with the small white color just behind the pigmented traveling

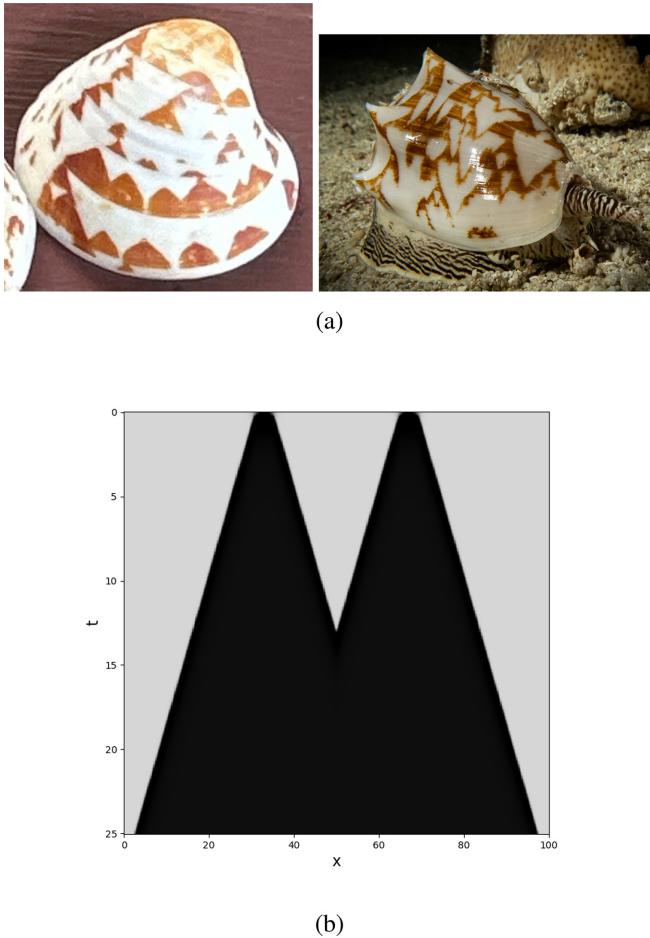


FIG. 4. Slug patterns: (a) Dense triangular pigmentation observed in (left) *Liocncha hieroglyphica* [25] and (right) *Cymbiola vespertilio* [26]. (b) Space-time plot of the system depicting the generation of dense pigmentation patterns, referred to as pigmentation slugs.

wave. The key regions—wave front, wave back, pigmentation, and refractory region—are indicated in the phase plot in Fig. 3. As a final note, we mention that a propagating pulse does not always form. Depending on the system parameters, the dynamics may be such that even though an initial excitation causes the formation of a pulse, it rapidly collapses and the system returns back to the stationary state. One may find the details for the criteria for stable propagation of pulses in Ref. [18].

C. Dense triangular pigmentation

For some parameters, the wave back fails to form, and instead of two pulse solutions moving in opposite directions one obtains a single expanding structure. This leads to patterns where the system lies close to the upper branch for extended regions in space, with the boundaries of such regions expanding in time. Instead of traveling waves of pigmentation, this manifests as dense regions of pigmentation that expands over time. Such pigmentation patterns can be observed in Fig. 4(a). In contrast to the case of traveling waves, one may observe that the collision of such expanding regions of pigmentation

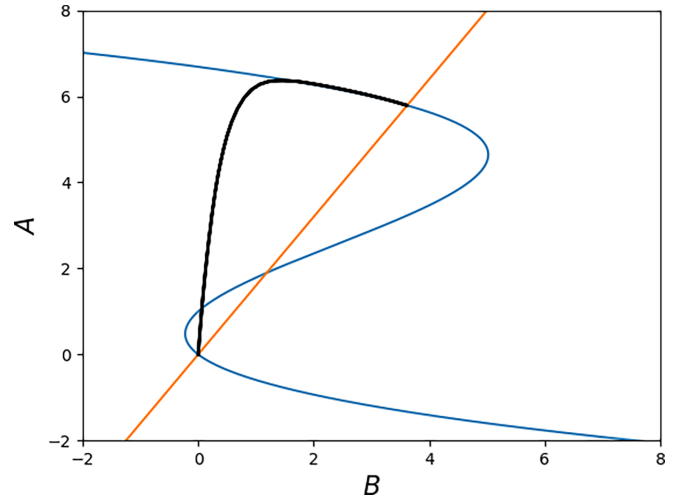


FIG. 5. Nullclines for the generation of pigmentation slugs. The black line represents the local phase of the solution.

does not lead to the annihilation of the pigmentation pattern but rather they merge into a single region of dense pigmentation. Systems with such characteristics are generally not the focus of investigations in studies of excitation in nerve fibres; however, such expanding structures find application in hydrodynamic modeling of pipe flow transition where expanding regions of localized turbulence are indeed observed [15,24]. In the hydrodynamic literature, such expanding regions of turbulence have been referred to as slugs, and we will borrow the terminology to refer to expanding regions of pigmentation as pigmentation slugs and the system to be in a slug state.

The phase plot and nullclines for such a system are shown in Fig. 5. In this particular case, the inhibitor nullcline intersects all the three branches of activator system leading to two stable fixed points on the attracting branches and an unstable fixed point on the repelling branch. The space-time plot for a numerical simulation initiated with two localized Gaussian impulses (with amplitude $A = 6.0$ and standard deviation $\sigma = 2.0$) is shown in Fig. 4(b). The initial impulses continuously expand to form dense regions of high activator concentration. The regions merge into one another upon collision. The phase portrait of the system is shown with a black line in Fig. 5 and only one front solution is formed, which is the same for both the left and the right interfaces.

D. Striped patterns

Patterns with parallel pigmentation bands that run perpendicular to the growing edge can be observed in Fig. 6(a). This suggests that locally the system lies on either the upper or the lower branch and that the state does not vary over time. This suggests the existence of a fixed point on each of the attracting branches. One corresponding to nonpigmented region implying a fixed point located on the lower branch, and one lying on the upper branch corresponding to the pigmented region of the shell. As mentioned earlier, diffusion is responsible for providing the system with coupling in physical space so that the thickness of the bands varies with the diffusion coefficient of the activator. The nullclines for such a system are depicted in

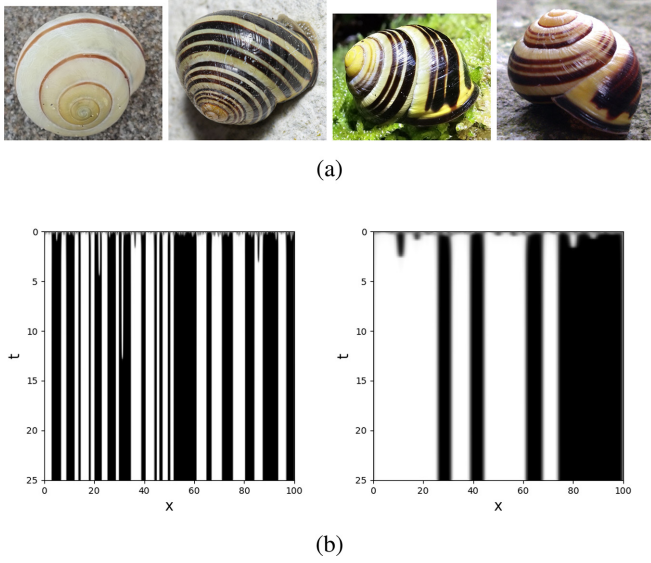


FIG. 6. Striped patterns: (a) Parallel pigmentation bands observed in *Cepaea nemoralis* [27–30]. (b) Striped patterns obtained in simulations using two different diffusion coefficients, (left) $D = 2$ and (right) $D = 40$.

Fig. 7, which shows fixed points located on both the attracting branches. There is an additional fixed point on the repelling branch however this fixed point is unstable. This is similar to the system that generates pigmentation slugs; however, in this case, the orientation of the inhibitor nullcline is different from that in Fig. 5, which generated the slug patterns. The system parameters may be found in the Appendix. The system was solved numerically using two different diffusion coefficients, $D_A = 2$ and $D_A = 40$, with a random initial condition (in space) about the unstable fixed point. Locally, the system evolves toward one of the two stable fixed points. Figure 6(b) shows the space-time plot of the solution. Black striped bands that come to an abrupt end signify points in phase space, which start close to the upper branch but eventually end up at the lower branch fixed point. The converse is true for white

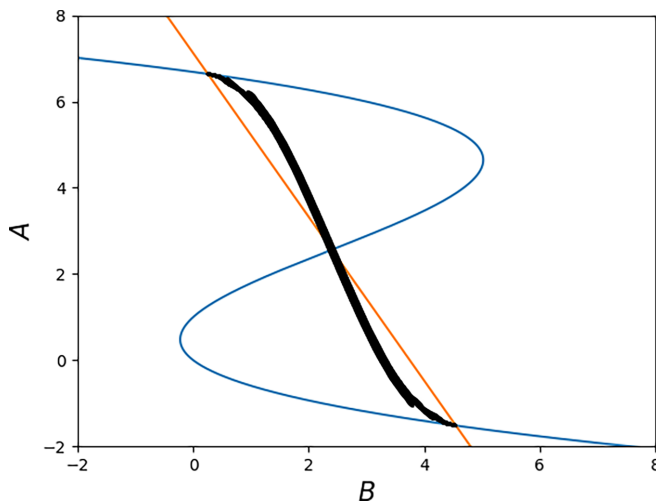


FIG. 7. Nullclines of the system for the generation of stationary parallel bands.

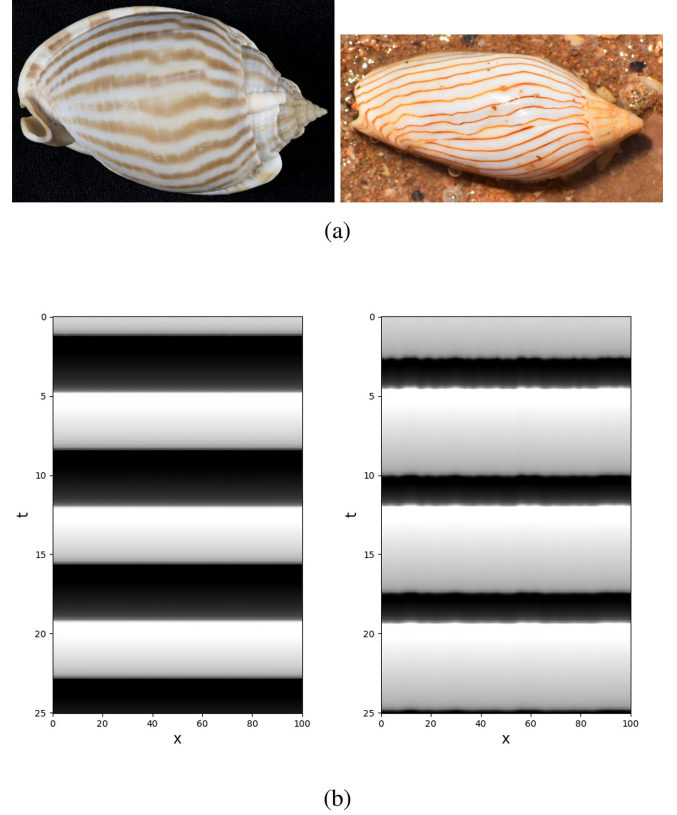


FIG. 8. Oscillatory patterns: (a) Alternating pigmentation patterns parallel to the growing edge in (left) *Phalium strigatum* [31] and (right) *Amoria ellioti* [32]. (b) Space-time plots of simulations using two different inhibitor systems with (left) a symmetric and (right) an asymmetric limit-cycle oscillation.

stripes that eventually disappear. Depending on the parameters, it is possible that one fixed point may dominate over the other such that the system state across the entire domain may end up at one or the other fixed point. In that case, the striped pattern could be seen as a transient solution. However, the timescale over which such an asymptotic state is reached could be very long, such that the transient state is indiscernible from a steady state.

E. Oscillatory patterns

Patterns with alternating bands of pigmentation and no pigmentation are observed as shown in Fig. 8(a), with the pigmentation bands running parallel to the growing edge of the shell. This suggests that the system along the whole spatial domain oscillates between the upper and lower branches of the activator nullcline, suggesting an unstable fixed point of the system and no stable fixed points leading to a limit-cycle oscillation (LCO). The thickness of the pigmentation bands depends on the relative time that the system spends near the upper branch as compared to the lower branch. When the branches are symmetrically located relative to the fixed point, the time spent near the two branches is roughly equal and one obtains bands of nearly equal width for pigmented and nonpigmented regions. On the other hand, if the time spent in the two branches is unequal then the pigmented and

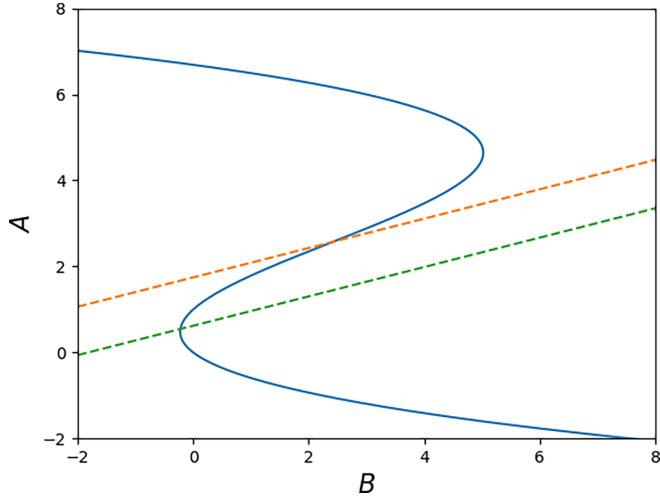
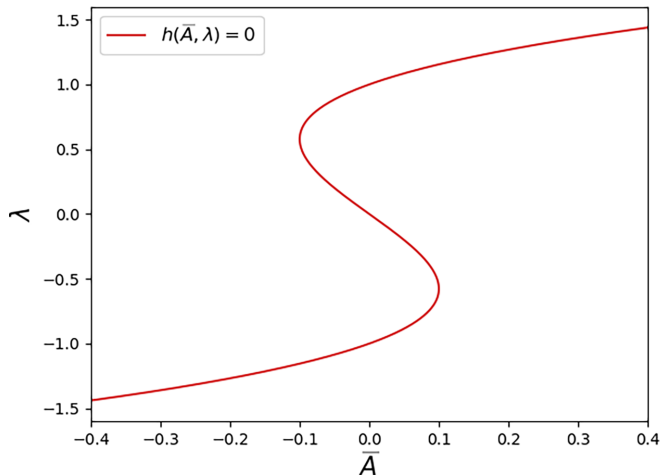
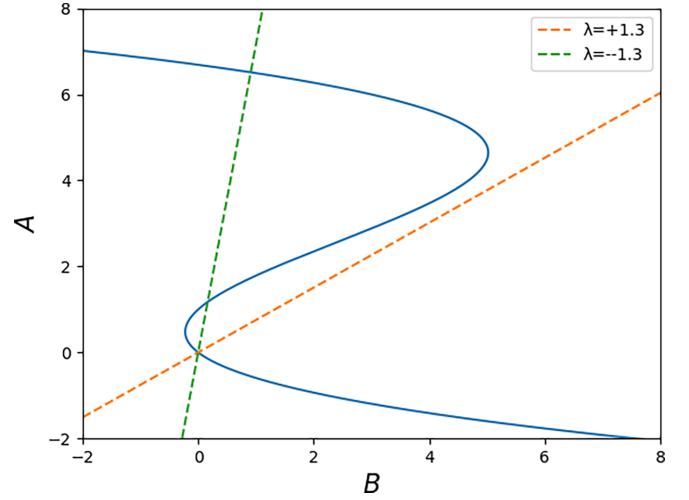


FIG. 9. Nullclines for oscillatory patterns.

nonpigmented regions differ in width. Figure 9 shows the nullclines of the system that leads to limit-cycle oscillations. The nullclines of two different inhibitor systems are plotted—one in which the branches are equidistant from the fixed point and one in which the fixed point is located close to the lower branch. The space-time plots for the two systems are depicted in Fig. 8(b). The alternating bands are of equal width for the symmetric LCO, where the branches are equidistant from the fixed point. On the other hand, unequal bands are obtained for asymmetric LCOs. The converse case is not depicted; however, it is easy to see that if the fixed point is located close to the upper branch one would obtain thicker pigmented bands relative to the nonpigmented ones. It is important to note that the real measure of band thickness is the relative time spent in the vicinity of each of the branches and not the relative position of the fixed points. One can have a more complicated dynamical system in which the branches may be asymmetrically located with respect to the unstable fixed point; however, the system nonetheless spends nearly equal time close to the two branches.

FIG. 10. Nullcline of $h(\bar{A}, \lambda)$ that characterizes the evolution of λ . The parameter defining $h(\bar{A}, \lambda)$ is $\gamma_1 = 3.849$.FIG. 11. Nullclines of a dynamic excitable model with varying λ parameter.

III. DYNAMIC EXCITABILITY

A. Dynamic variation of phase space

While the excitable structure of the system is able to reproduce the essential dynamics of many of the patterns observed in shell pigmentations, there are aspects of pigmentation patterns that are not reproduced by this basic structure. A commonly observed pattern is that of wave branching, wherein a new traveling wave emerges from preexisting traveling waves and then moves in the opposite direction. Such behavior can be seen in Fig. 12(a). Another example is the case of traveling waves that pass through each other [Fig. 13(a)] rather than the usual collision and annihilation behavior expected in excitable systems. Neither of these characteristics occurs in the basic excitable system model, and they require that the underlying system undergoes changes for such properties to emerge. Such effects can be incorporated if we consider the following modified system:

$$\frac{\partial A}{\partial t} = \frac{1}{\epsilon} f(A, B) + \epsilon D \nabla^2 A, \quad (3a)$$

$$\frac{\partial B}{\partial t} = g(A, B, \lambda) + \epsilon^2 \nabla^2 B, \quad (3b)$$

$$\frac{d\lambda}{dt} = \frac{1}{v} h(\bar{A}, \lambda), \quad (3c)$$

$$\bar{A} = \frac{1}{\delta_1 L} \int_L A dx - A_{\text{eq}}, \quad (3d)$$

where L is a specified length scale of integration and δ_1 determines the sensitivity of the term. In the current work, L is taken to be the length of the entire domain, so that $\bar{A}$ has no spatial variations. A_{eq} can be considered as some equilibrium value of the average activator concentration in the domain. $\bar{A}$ then represents the deviation from the equilibrium activator concentration and is in effect a measure of the global state of the system. We will refer to $\bar{A}$ simply as the average activator concentration. Similarly, for the case where $\bar{A}$ is spatially independent, λ also has no spatial dependence and acts as a global variable for the function $g(A, B, \lambda)$. The global nature of λ is introduced here due to previous observations of

globally synchronized evolution events in the patterns, such as simultaneous branching events in traveling wave patterns [10], which can only be explained through some level of global synchronization taking place in the system. Further comments are made in Sec. IV regarding the global nature of λ and its possible variations. The variable ν is again a small parameter that gives λ a fast-variable-like structure so that it undergoes rapid evolution unless $h(\bar{A}, \lambda) \approx 0$. The functions f , g , h are defined as

$$f(A, B) = \alpha_1 A(A - 1)(A - \alpha_2) + \alpha_3 B, \quad (4a)$$

$$g(A, B, \lambda) = \beta_0 + R(\cos(\phi)A + \sin(\phi)B) + \beta_3 \lambda, \quad (4b)$$

$$h(\bar{A}, \lambda) = \gamma_1 \bar{A} - \lambda(\lambda - 1)(\lambda + 1),$$

$$R = \sqrt{(\beta_1)^2 + (\beta_2)^2},$$

$$\phi = \arctan(\beta_2/\beta_1) - \lambda \Delta\phi, \quad (4c)$$

with β_3 , ν , $\Delta\phi$, and γ_1 being additional parameters of the expanded system. Note that some parameters here can be made redundant, for example, λ can be rescaled so that $\Delta\phi = 1$. However, the current form of the equations allows for easier interpretation and variation of the system. Clearly, the new system defined by Eqs. (3) and (4) has the same underlying excitable structure as defined by Eqs. (1) and (2). If λ is held constant at $\lambda = 0$, then one obtains the original excitable system.

The essential role of the newly introduced variable λ is to dynamically determine the local structure of the f and g nullclines in the $A - B$ phase plane. The activator system remains unchanged while in the inhibitor system the slope of the nullcline now has a dependence on the newly introduced variable λ (which itself is dependent on the average activator concentration in the domain). The variable λ then dictates whether the underlying $A - B$ excitable system exhibits pulslike, sluglike, or oscillatory dynamics. If β_3 is nonzero, then the location of the original fixed point of the activator-inhibitor system also varies. The evolution of λ is again best understood through the system nullcline in the $(\bar{A}, \lambda)$ phase space depicted in Fig. 10. The λ system has two branches—upper and lower branch. For $\bar{A} > 0.1$, λ evolves toward the upper branch, while for $\bar{A} < -0.1$ λ evolves toward the lower branch. For $-0.1 < \bar{A} < 0.1$, the system exhibits a region of metastability where it may evolve toward either branch depending on the value of λ .

The functional form of $h(\bar{A}, \lambda)$ is determined by the requirement that the underlying $A - B$ excitable system can exhibit both pulslike and sluglike dynamics. Hence, h must have two distinct branches, where λ is at or near equilibrium. The cubic function is the simplest function that allows for evolution dynamics with two distinct attracting branches and hence the cubic dependence on λ of h . Similarly, the linear dependence on $\bar{A}$ allows for the simplest coupling of the λ variable to the $A - B$ system evolution. This functional form of h is of course not unique and other functional forms can be used that generate the essential characteristics of two distinct λ branches along with coupling with the $A - B$ excitable system. An alternative form of h can be used with piecewise linear variations; however, this would introduce discontinuous gradients in the flow of λ . Higher-order terms could also be added without changing the essential nature of the λ sys-

tem; however, they are unnecessary to elucidate the essential dynamics of the overall model of dynamic excitability. The cubic dependence on λ along with a linear cross-coupling then corresponds to one of the simplest representations for the required dynamics without introducing unnecessary degeneracies or higher-order terms. Despite the simplicity of h , the dynamics of λ are fairly robust, and small variations in the functional form of h do not alter the qualitative evolution of the overall system.

The effect of λ on the underlying excitable system for typical values considered here is shown in Fig. 11. The system parameters can be found in Table II. The nullcline for $\lambda = +1.3$ (with $\Delta\phi = -0.3023$) effectively creates a system similar to the one depicted in Fig. 3, which would generate propagating pulses. While for $\lambda = -1.3$, the system is similar to the one depicted in Fig. 5, i.e., in a slug state. One may thus interpret the upper and lower branches of λ as representing, respectively, the pulslike and sluglike states of the underlying excitable system, with transitions occurring between these two states. For $\nu \ll 1$, λ has a fast-variable structure and, thus the transitions between states occur on a fast timescale.

We refer to the dynamics of the system described by Eqs. (3) and (4) as *dynamic excitability*. The word “dynamic” here referring not to the unsteady nature of the solutions, but rather to the dynamic nature of the basic excitable system that underpins the evolution. In the subsequent subsections, we show how such dynamic excitability leads to many of the complex shell pigmentation patterns. We keep the function $h(\bar{A}, \lambda)$ the same across all cases, and differences in the system is achieved primarily through the variation of $\Delta\phi$, ϕ , δ_1 , A_{eq} , β_3 , and ν .

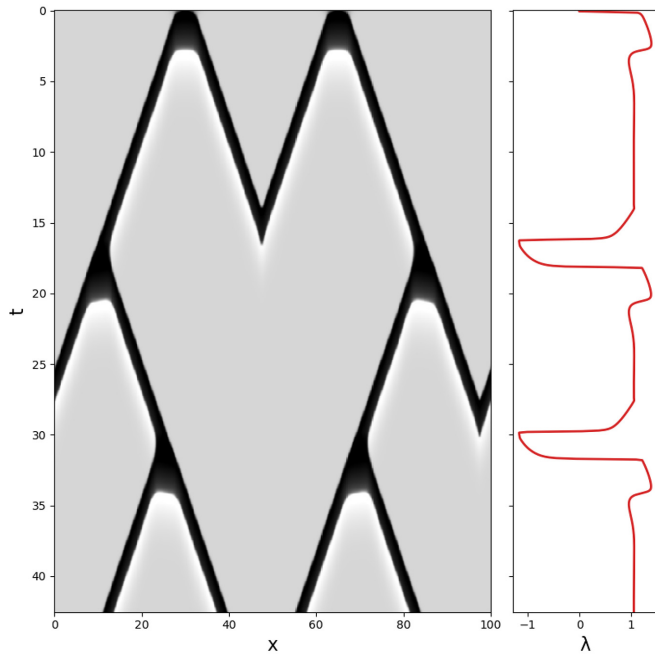
B. Branching waves

As depicted in Fig. 12(a), traveling waves may generate waves that branch off from an existing traveling wave and propagate in the opposite direction. We use the system described earlier for dynamic excitability to simulate such patterns. The λ -dependent nullclines of the system are the same as the ones shown in Fig. 11, and the parameters may be found in Table II. The system is initialized with two localized Gaussian impulses (with amplitude $A = 6.0$ and standard deviation $\sigma = 2.0$) and integrated over time numerically. The space-time plot of the resulting solution is depicted in Fig. 12(b), which shows the spontaneous branching off of a wave from an existing propagating pulse.

It is instructive to understand the pattern from a dynamics point of view. As the system is impulsively started, the system rapidly moves to the pulslike state (λ upper branch) and two pairs of bidirectional waves are generated. As mentioned in Sec. IIB, the wave front and wave back of each pulse propagate in the same direction; however, the structure of the front and back solutions is not identical. In this state, the system is in dynamic equilibrium and λ does not significantly vary. As two of the propagating pulses collide and annihilate, $\bar{A}$ in the domain suddenly reduces and the excitable system quickly transitions to the slug state (λ lower branch) as is seen from the rapid change in λ . In the slug state, the wave front is not significantly affected and it continues propagating relatively unchanged. However, the system no longer supports



(a)



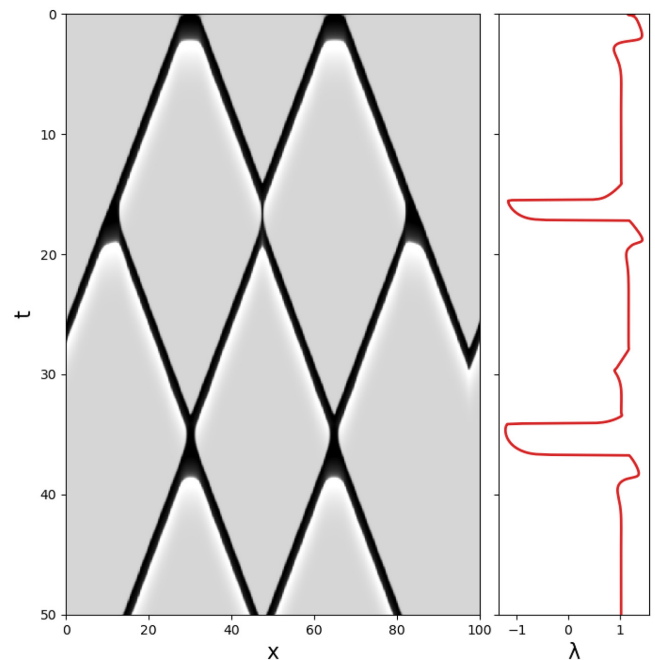
(b)

FIG. 12. Branching waves: (a) Shell pigmentation depicting branching waves in *Oliva porphyria* [33]. (b) Space-time plot of the system depicting such branching waves, along with the variation of λ .

the wave back solution as seen earlier in Fig. 5. The wave back therefore transforms to a wave front. This is a process of velocity reversal of the front solution, wherein the speed of the wave back reduces as it transforms to a wave front, eventually reaching zero and then changing sign. This is the origin of the branching off process and, since the underlying system changed globally, it takes place in all existing waves. The front continues to evolve until the transformation to a wave front is complete and an incipient slug is formed. In the new slug state, $\bar{A}$ is constantly increasing and the system quickly reaches the point where it transitions back to the pulse state, again through a fast λ variation. This causes the incipient pigmentation slug to rapidly collapse and a new pulse is generated instead. This completes the branching off process. The system is again back to the state of dynamic equilibrium with two pairs of propagating pulses. The process repeats at the next wave collision.



(a)



(b)

FIG. 13. Crossing waves: (a) Shell pigmentation depicting wave crossings, annihilation, and branching patterns in *Tapes literatus* [34]. (b) Space-time plot of the system the simulating such behavior of waves, along with the variation of λ .

C. Wave crossings

Again somewhat contrary to expectation, pigmentation patterns in some shells seem to exhibit traveling waves that pass through each other upon collision, as can be seen in Fig. 13(a). The usual behavior of colliding pulses in excitable systems is to annihilate and return the system to the stationary state. Small changes are made to the system simulated in the previous subsection to show how such crossing waves may be generated. The nullclines of the system are depicted in Fig. 14. As is evident from the nullclines and from the comparison of

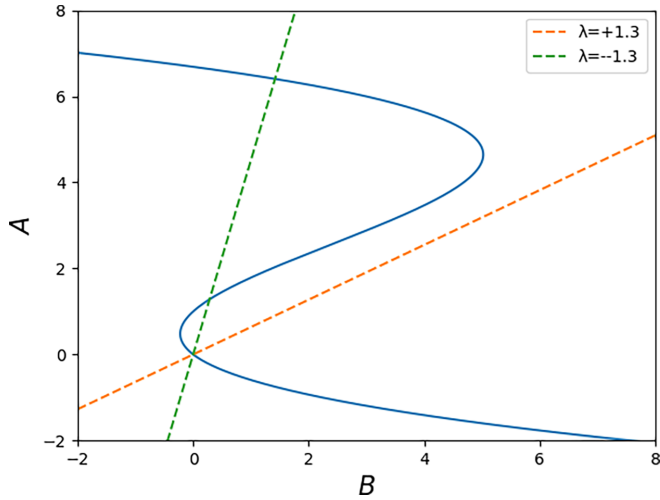


FIG. 14. Nullclines of the dynamically excitable system for the traveling waves with crossings.

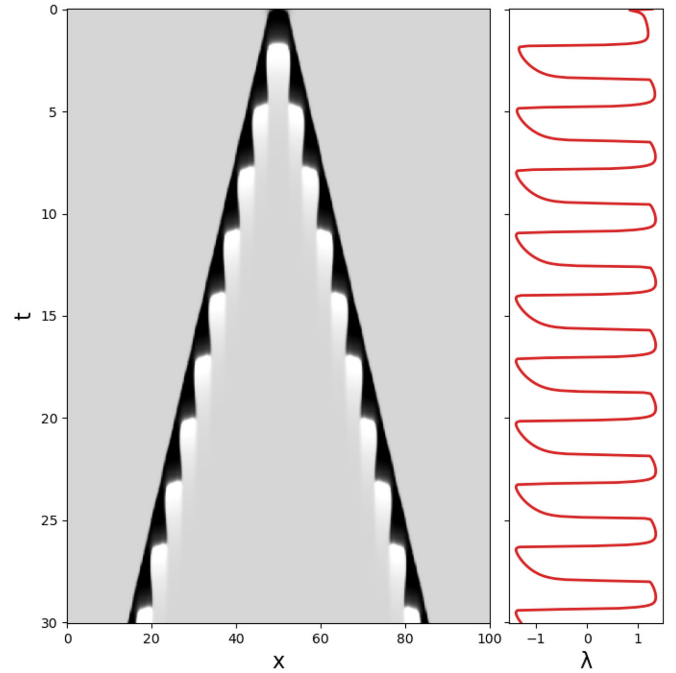
values in Table II, the parameters are only slightly different from the case of branching waves. Nonetheless, such small differences are enough to induce seemingly opposing behavior in the dynamics. The key differences being that both δ_1 and ν are now smaller than in the case for branching waves, leading to increased sensitivity to changes in activator concentration as well as a faster timescale of branch switching in λ . The space-time plot from the solution of the system, initiated with two localized Gaussian impulses (as for the previous case of branching waves), is depicted in Fig. 13(b). The crossing of waves upon collision can be clearly observed.

The dynamics of the process are similar to the case of branching waves. Initially, the system reaches the dynamic equilibrium state of two pairs of propagating pulses. Upon collision of two pulses, the process of annihilation initiates; however, the system is more sensitive to a reduction of $\bar{A}$. Hence, even before the annihilation is complete, the system switches to the slug state. This causes the branching off process (described in Sec. III B) in the two noncolliding waves in the domain. For the two waves in state of incomplete annihilation, the wave back of each of the colliding waves has not completely collapsed, and these are regenerated to create wave fronts moving in opposite directions, and an incipient pigmentation slug is generated. Again, as the amount of activator increases in the domain, the system shifts back to the pulse state and the incipient slug that arose from the partially annihilated waves also collapses, resulting in another pair of propagating pulses. The system now is again in dynamic equilibrium, although the total number of pulses in the system has increased to six. After some time, another wave-pair collision takes place. This time, however, due to the increased number of waves, $\bar{A}$ does not reduce significantly enough to induce a transition to the slug state. The wave collision therefore results in annihilation of the two waves. Now, the domain has four propagating pulses, and the next wave collision results in “wave crossing” instead of annihilation.

An important point to note in the process is that wave branching, wave crossing, and wave annihilation are all generated within the same system. This can also be observed in the image of shell pigmentation in Fig. 13(a), which displays



(a)



(b)

FIG. 15. Branching triangles: (a) Shell pigmentation depicting branching triangles in *Lioconcha castrensis* [35]. (b) Space-time plot of the system depicting such branching triangles from the wave back of a propagating pulse, along with the λ variation of the system.

all the three attributes within a single shell. Additionally, the process of wave branching and wave crossing is intimately connected with the triangular pigmentation patterns (slugs). The two patterns are in fact generated through the mediation of an incipient slug state, which quickly collapses, resulting in the formation of new propagating waves.

D. Branching triangles

The switching of the excitable system between pulse and slug states also appears to underlie the generation of bidirectional waves of triangles as shown in Fig. 15(a). The nullclines for the system that generates such structures are plotted in Fig. 16, and the corresponding space-time plot is shown in

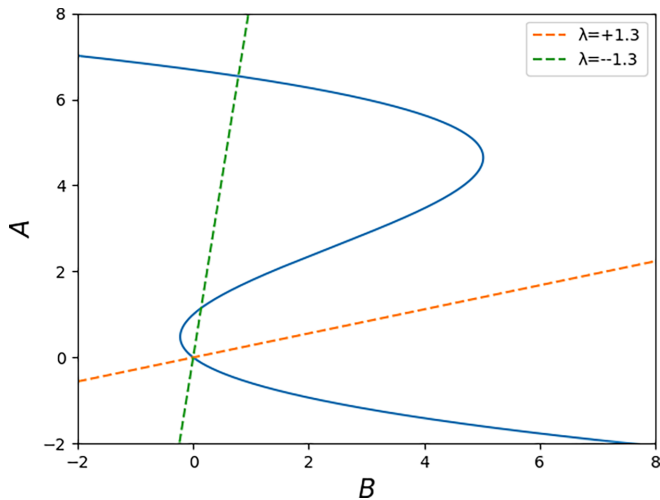


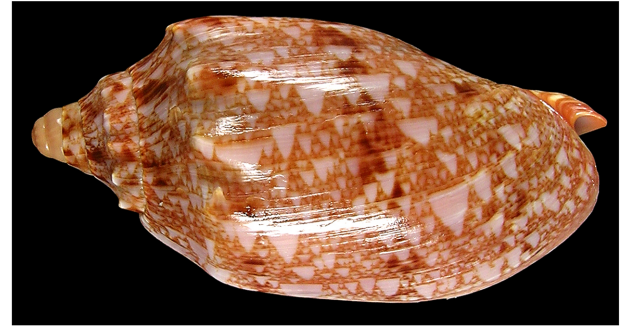
FIG. 16. Nullclines of the dynamically excitable system for branching triangles.

Fig. 15(b). In this particular case, two propagating pulses are already out of dynamic equilibrium and the system switches to the slug state. However, the sensitivity induced by the system parameters is such that the incipiently forming slug quickly pushes the system back to the pulse state. The result is that the slug collapses too quickly and the wave back does not have enough time to transform into a wave front moving in the opposite direction. As is evident, the wave back does indeed change direction but has not fully transformed into a wave front before the system switches back to pulse state. The wave back thus returns to its original state. Since the system remains out of dynamic equilibrium in the two pulse state, the process continuously repeats and a series of branching trianglelike features are formed behind a propagating pulse.

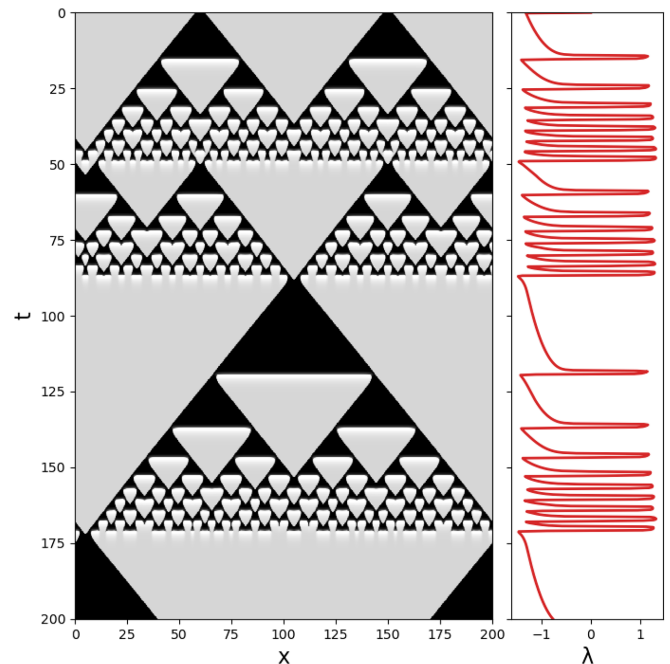
E. Sierpiński triangles

The lack of dynamic equilibrium can lead to more fascinating pigmentation patterns that resemble a fractal structure. Figure 17(a) depicts one particular shell pigmentation pattern that resembles Sierpiński triangles. The nullclines for the generation of such patterns are shown in Fig. 18, and the space-time plot of the solution initiated with two localized impulses is shown in Fig. 17(b). In this case, the system is solved in a larger domain with $x \in [0, 200]$. The similarity between the pigmentation patterns and the space-time plot is clearly visible.

The evolution of the solution can also be easily understood in the framework of dynamic excitability with the dense black triangles representing the system in the slug state. As the slug expands, the average activator in the system, $\bar{A}$, increases to the point that the system switches to the pulse state. This causes the slug to collapse and transform into two incipient pulses at each wave front. The pulse state, however, is short lived and the system quickly returns back to the slug state, and the incipient pulse transforms into a slug. This cycle, slug $\rightarrow$ pulse $\rightarrow$ slug, effectively doubles the number of slugs in the domain. The increase in the number of slugs also increases the rate of production of $\bar{A}$, so that the cycle now has a shorter duration than the previous cycle, resulting in a smaller length



(a)



(b)

FIG. 17. Sierpiński triangles: (a) Shell pigmentation depicting a fractallike pigmentation pattern in *Cymbiola innexa*. Image © Guido & Philippe Poppe [36]. (b) Space-time plot of the system depicting fractallike patterns similar to Sierpiński triangles. Also depicted in the lower plot is the behavior of λ exhibiting different timescales of oscillations.

scale of the triangular slugs. This occurs repeatedly and the scale of the triangles continues to decrease until the transition becomes so fast that some of the slugs fail to generate. At this point, the total number of slugs in the system abruptly reduces, and the scale of the new slugs is much larger than the ones in the previous cycle. The process of scale reduction then repeats again, and one gets triangular structures of various scales with the overall fractal pattern resembling Sierpiński triangles.

F. Spatial variations

In the previous subsections, we have treated λ as a global variable, which has no spatial variation, so that the changes in

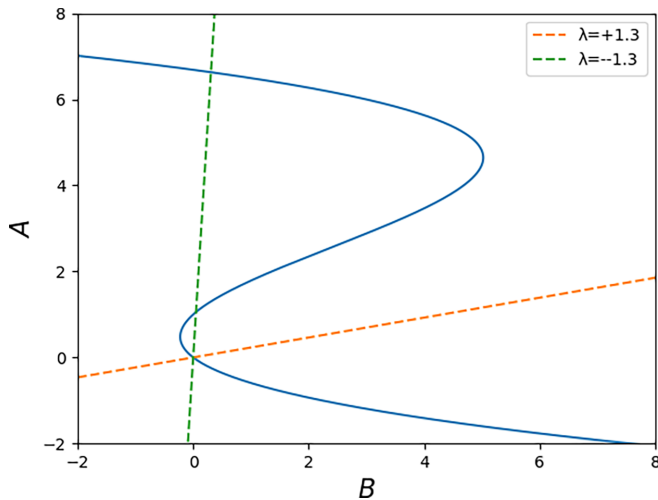


FIG. 18. Nullclines of the system that lead to the generation of patterns resembling Sierpiński triangles.

the excitable structure occur simultaneously across the whole domain. Global changes in the system were also recognized by Meinhardt [10], which were reflected by the occurrence of simultaneous branching from several traveling waves. Nonetheless, on several occasions the patterns in shells clearly reflect the fact that the underlying system exhibits spatial variations, such as can be deduced by the coexistence of both pulselike and sluglike structures at the same time instance. It is likely that in real biological systems the mechanism reflected by the λ variable is not entirely global but may have spatial variations. Such variations may be static, such that λ may vary over space but does not have dynamic evolution in time. Or, that λ is indeed dynamic and varies in space but is strongly correlated over a certain length scale. Such a correlation may easily be incorporated in to the model by considering a spatially varying λ and the integral in the definition of $\bar{A}$ to be defined over a characteristic length scale instead of the whole domain. Such spatial variability would arise from the biology that underlies the pattern-forming system and as such it is difficult to define an *a priori* model for such variations, which may very well be specific to each individual mollusc. Indeed, the need for such spatial variability is recognized in Ref. [10], wherein, despite the plethora of models introduced, the author still finds it necessary to include *ad hoc* variations of coefficients to generate some of the patterns in shells.

Such spatial variations are not considered here in any depth since the goal of the study is not to explain every possible pattern in shell pigmentation but rather to try and identify the essential mechanisms that may lead to the large variability of patterns. However, we point out two canonical cases of static spatial variations—step changes in λ and sinusoidal changes in λ —which lead to identifiable pigmentation patterns.

Consider the system characterized by the nullclines as depicted in Fig. 19 along with a spatially sinusoidal variation of λ . The region $\lambda = -1.3$ corresponding to a slug state and the region with $\lambda = +1.3$ corresponding to a pulse state. The system varies in space sinusoidally between these two states. The system is solved using an initial condition of $A = 2$ and $B = 0$ uniformly in space within the domain $x \in [0, 30]$. λ is held constant in time with the prescribed spatial variation.

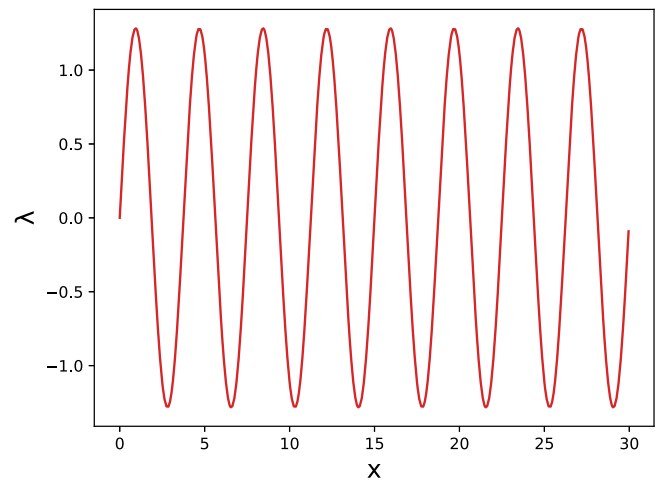
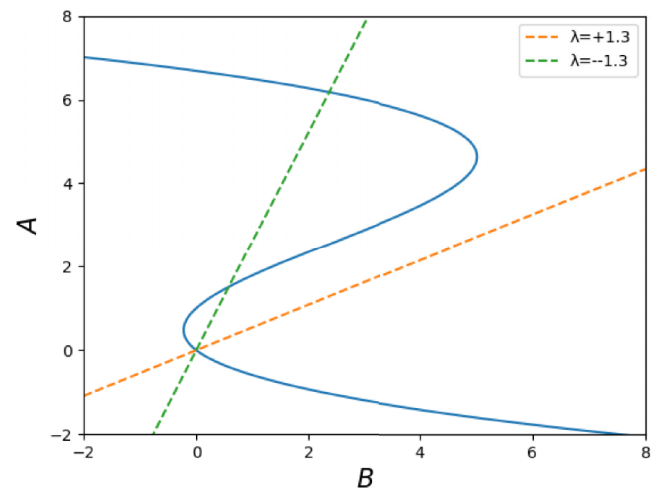


FIG. 19. (Top) Nullclines of the system in conjugation with (bottom) the spatial variation of λ that leads to the generation of nonpigmented spots in a pigmented background.

The resulting space-time plot is shown in Fig. 20(b), which resembles the pigmentation pattern in Fig. 20(a), with dense pigmentation pattern throughout the domain interspersed with nonpigmented spots. The variations of spot size itself can be obtained by considering a more refined model of spatial variation; however, this is not undertaken.

Alternately, consider a system with nullclines as depicted in Fig. 21, along with the spatial variation of λ . For $\lambda = 1.3$, the system is effectively stable and all excited states return to the stable fixed point in this region. On the other hand, in the region with $\lambda = -1.3$, the system is unstable and is in an oscillatory state. The λ variable is no longer considered as a dynamic variable, and its value is held constant. The system is numerically evaluated for $x \in [0, 30]$ and initialized with a random initial condition, centered around $(A, B) = (2.0, 1.5)$, a point lying close to the repelling branch. The space-time plot of the solution is depicted in Fig. 22(b), which resembles the spotted patterns observed in Fig. 22(a). The initial condition does not significantly vary the resulting pattern with a constant initial condition leading to perfectly aligned spots being generated, while an initial condition with significant noise leads to misalignments of the spots.

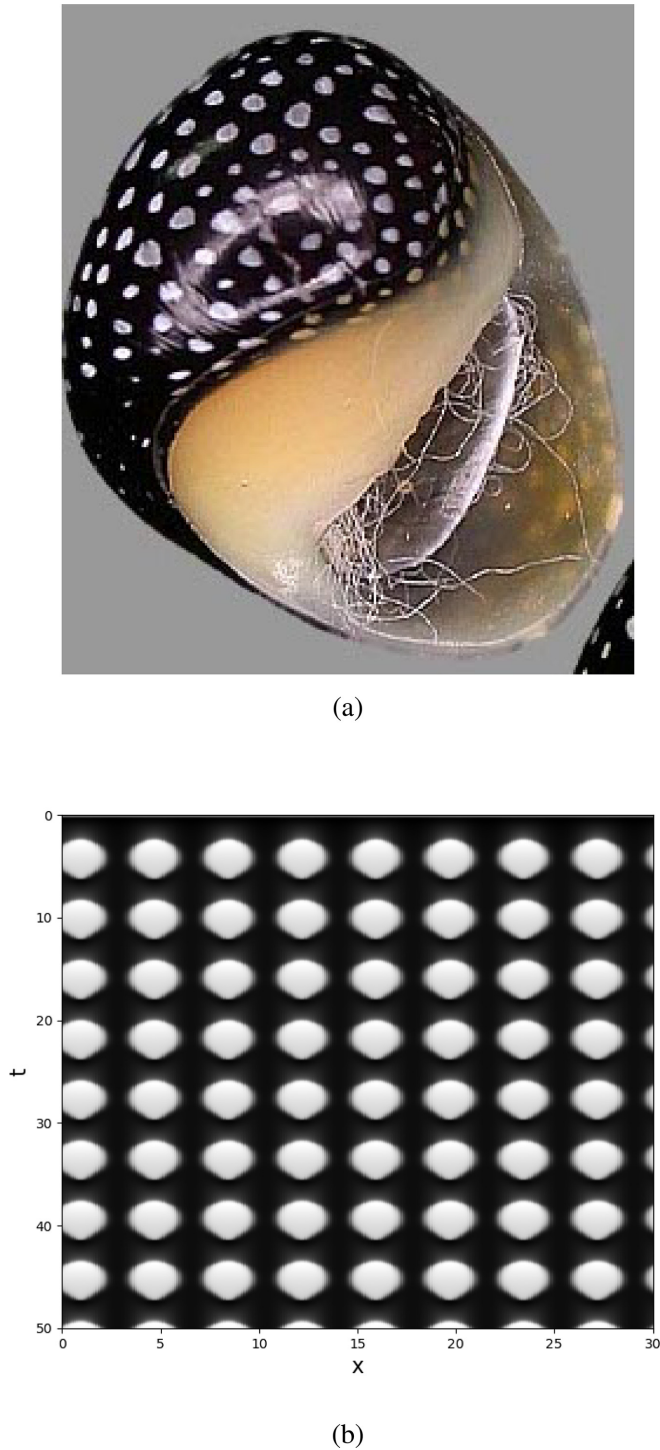


FIG. 20. Spotted patterns: (a) Shell pigmentation depicting non-pigmented spots within a dense pigmented background in *Vitta clenchi*. Image © Conquiliologistas do Brasil (used with permission) [37]. (b) Space-time plot of the system depicting the generation of spotted patterns due to spatial variations of λ .

IV. DISCUSSION

The modeling results of Secs. II and III clearly show that excitability plays a significantly more important role in the generation of pigmentation patterns than has been appreciated so far. What were previously considered disparate classes of

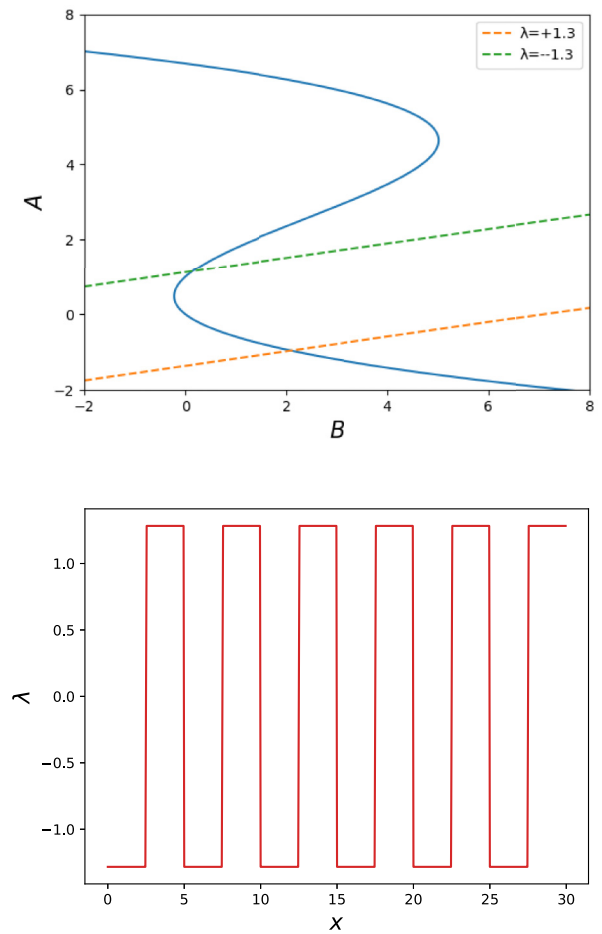
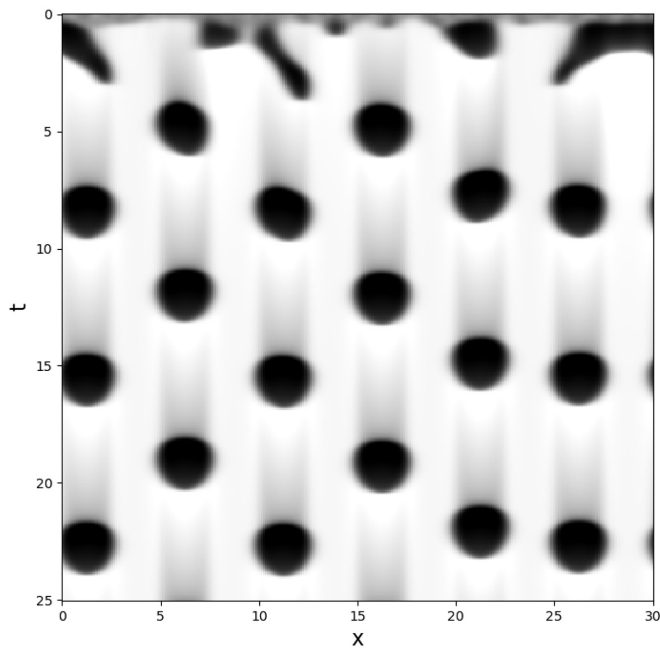


FIG. 21. (Top) Nullclines of the system in conjugation with (bottom) the spatial variation of λ that leads to the generation of spotted patterns.

patterns, each requiring their own evolution model, may be interpreted through the unified framework of dynamic excitability to be simply emerging from a single model under a limited variation of parameters. The model lends itself to a simple interpretation of the variables as well as the dynamics. Fundamentally, the pigmentation is a result of interaction of two variables—the activator A and the inhibitor B —which are governed by excitable dynamics. Such a system leads to four characteristic patterns—stationary striped patterns, oscillatory patterns, propagating pulses, and pigmentation slugs. Of these, propagating pulse and slug states appear to be of particular importance. The excitable system itself depends implicitly on the average activator in the system, and large deviations from some equilibrium value A_{eq} cause the system to switch between different characteristic states. This fast switching of states is responsible for many of the complex patterns that are observed on mollusk shells. The switching from pulse to slug and back to pulse state is of particular import since it explains the emergence of branching waves, crossing waves, and branching triangles as essentially the same dynamical phenomenon under different timescale and sensitivity conditions. The occurrence of triangular structures is the inverse evolution where the system switches from a slug state to pulse state and back to slug state, which in certain



(a)



(b)

FIG. 22. Spotted patterns: (a) Shell pigmentation depicting spots in *Conus pulicarius* Hwass [38]. (b) Space-time plot of the system depicting the generation of spotted patterns due to spatial variations of λ .

parameter regimes may lead to fractal patterns resembling Sierpiński triangles. The ubiquity of traveling pulse and slug states in shell patterns, and the fact that many more complex patterns are a result of transitions between these states, seems to suggest that these two states may in fact be fundamental

characteristics of the underlying biological mechanism that produces pigmentation in molluscs. This interpretation would suggest that the biological mechanism is a self-regulating system that tries to maintain an equilibrium pigmentation production by the mollusc. The global variable λ provides the primary signaling for the maintenance of this equilibrium. The hypothesis of pigmentation patterns being associated with developmental stability put forward by Bauchau *et al.* [39] is pertinent in this regard since the current modeling strongly points to a self-regulatory mechanism behind the production of observed patterns. When the pigmentation production drops too low, the system switches to a slug state that rapidly increases pigmentation production. On the other hand, when the production is too high, the system switches to a pulse state (or to a “no-pigmentation” state) that may rapidly lower pigmentation production. The equilibrium pigmentation and sensitivity of the system to variations in total pigmentation may possibly be determined by other biological or environmental factors. The key signal for the self-regulation has been modeled in most cases as a global variable λ , which has no spatial dependence. There are several indications in the observed patterns that point to such global signaling, such as the occurrence of simultaneous branching in several different propagating pulses. Similarly, several pigmentation slugs abruptly end at the same time in Fig. 4(a). Such effects clearly point to the global nature of the change in the system. This global variation is also recognized in Ref. [10], where branch initiation is also modeled via global control. The modeling work of Ermentrout and co-workers [3] also places emphasis on the “nonlocal” property of their model as being responsible for a much larger space of patterns.

It is likely, however, that λ (or other parameters characterizing the dynamic variation of the phase space) being uniform across the entire domain is too strong an assumption to be universally valid. It is more probable that some of the parameters vary over space, but with strong correlations over long length scales. In such a case, different fundamental patterns may coexist in various parts of the domain, as can be seen in one of the images in Fig. 4(a) (right), where both slugs and pulses have simultaneous occurrence. Such coexisting patterns may also be recognized in many of the images reported in Ref. [10]. Such cases are not modeled in the current study since our focus is on elucidating the essential patterns. However, new fundamental patterns can emerge if the length scale of such variations becomes comparable to the length scale of the pigmentation patterns described so far. Spotted patterns clearly seem to fall within this category where the spatial variation of λ occurs over a relatively short length scale. It is unclear to the authors whether there are any universal aspects to such spatial variations, and hence the modeling of such spatial variations is not pursued further beyond the two canonical cases mentioned.

The occurrence of striped patterns and oscillatory bands is not the typical features of excitable systems; however, the nullclines of the proposed systems generating such patterns clearly show that despite the differences in dynamics, the local phase spaces are closely related to those of excitable systems. Such a phase-space analysis also sheds light on the cause of variations in pigmentation band widths for oscillatory patterns (at least from a dynamical point of view).

While the current model describes the generation of several classes of pigmentation patterns, as pointed out in the reporting of Ref. [10], the diversity of molluscan pigmentation patterns is quite large and many of the patterns defy classification. A large number of them may indeed require finely tuned spatial variations of system parameters, specific to individual cases, rather than being more universal features of the pattern-forming system. There also exist shells with multicolored patterns. Such patterns are not considered in the current modeling effort.

It is important to emphasize here that *dynamic excitability* is distinctly different from what is sometimes referred to as “regime shifts” in the excitable systems modeling [40]. In typical excitable systems literature such as in turbulence [15] or ecology [40,41], the system may exhibit multiple equilibrium points with their corresponding domains of attractions. While these equilibria and their basins of attraction remain unchanged throughout the dynamics, it is the system state that switches between these different attraction basins, usually through the action of stochastic events, and the system is then considered to have undergone a “regime shift.” In *dynamic excitability*, the emphasis is on the changes in the underlying phase-space structure, such that individual equilibrium states (and their basins of attraction) may themselves vanish or reappear as the system evolves. For example, when a system shifts from a traveling pulse to a slug state, it is not due to noise or external impulses, rather it is because the equilibrium point (corresponding to an isolated pulse) itself ceases to exist and the only nontrivial equilibrium point that the system can support is the slug state. The converse being true in the slug to pulse transition. Many of the patterns are thus the result of the system state adjusting to the appearance and disappearance of the equilibrium points (on a fast timescale), as opposed to the usual scenario where the fixed points remain unchanged and the system state being pushed to a different basin of attraction.

An important question, of course, is the connection of the mathematical model with the underlying biological structures (and their signaling dynamics). However, at the current stage, the question remains a difficult one to answer, in large part because the biological literature has largely focused on the possible genetic correlations of pigmentation color rather than on the selection of pigment patterns (or their transitions). Connections between biological structures and the modeling therefore remain in the realm of speculation. An important study on making biomolecular connections to pigmentation has been the work of Budd and co-workers [2], where pigment containing tubules were found in the mantle of the tropical abalone, *Haliotis asinina*. These tubules are the primary delivery mechanism for the pigmentation material onto the shell. However, the tubules do not act in isolation, with pigmentation first accumulating in the many smaller vesicles that surround the tubules before being poured into the tubule lumen. This may suggest that the λ variable in the current mathematical model may represent the coarse graining or collective action of the vesicles in the production of pigmentation. Some of the tubules themselves were found to be connected to each other, suggesting that there might be multiple layers of synchronization before the pigmentation is finally deposited on to the shell. Furthermore, tubules were found with varying states of

activity from empty, accumulating, to active secretion, pointing to spatially inhomogeneous pigmentation deposition. It is likely that the level of secretions in a particular tubule provides a feedback to the neighboring vesicles, which regulates the rate of pigment production. This would be in line with the self-regulatory nature of the current model as well as the hypothesis of Ref. [39] on pigmentation being part of a regulatory function. Further connections to the dynamics of vesicle secretions would require deeper understanding of the regulatory dynamics of such vesicles. It is known that diet affects the produced pigmentation [1] so that these dynamics are likely to be affected by both intrinsic as well as extrinsic factors. However, as the authors of Ref. [2] note, existence of these tubules can not be assumed to be universal, and they were unable to find such tubular structures in *Stomatella impertusa*. Although there might be other structures that play a similar role to the tubule. Despite the numerous mathematical models, studies linking biological structures and their activity to the pattern of the pigmentation still seem to be at a very nascent stage and these remarks should be treated as a speculative direction for making such connections. Nonetheless, connections of the model with the underlying biological structures are important and can pave the way for further meaningful quantitative comparisons between model output and the observed patterns, such as the thickness or speed of traveling pulses, or possible timescales of branching waves and triangles. It may then be possible to theoretically isolate intrinsic and extrinsic effects in the formation of such patterns and thereby infer the biological system state generating them. This would likely also require a more systematic accumulation of pigmentation data beyond the visual images available for the current work.

Finally, it is pointed out that the current work obviously is not an exhaustive search in the parameter space of the model proposed in Eqs. (3) and (4). It is likely that a larger parameter space exploration will find more patterns that can be identified with observed molluscan pigmentation patterns.

V. CONCLUSION

A new class of pattern-forming system with excitable dynamics is introduced, referred to as *dynamic excitability*, which is an extension of the standard FitzHugh-Nagumo model of excitable systems. The fundamental idea behind the extension is that the phase-space structure of the underlying FitzHugh-Nagumo model varies dynamically, leading to a wider range of spatiotemporal patterns. The emerging patterns can be fruitfully understood as the transitions between the various coherent states of the underlying excitable system. Dynamic excitability is shown to underlie several classes of complex patterns that are observed in molluscan shells. This particular framework allows one to interpret many of the observed pigmentation patterns in a unified manner. In particular, branching waves, crossing waves, branching triangles, and even Sierpiński triangle-like patterns—all arise from state transitions between pulse and slug states of the excitable system. The model in fact points to a certain interpretation, which is that pigment patterns may arise due to a self-regulating excitable mechanism, and the various timescales within the self-regulation process lead to the enormous diversity of the pigmentation patterns.

TABLE I. System parameters for the excitable model without dynamic variations.

Parameter Name	Figure 1 Phase flow	Figure 3 Traveling waves	Figure 5 Dense triangles	Figure 7 Striped	Figure 9 Symmetric oscillations	Figure 9 Asymmetric oscillations
α_1	-0.0659	-0.0659	-0.0659	-0.0659	-0.0659	-0.0659
α_2	6.6877	6.6877	6.6877	6.6877	6.6877	6.6877
α_3	-0.4540	-0.4540	-0.4540	-0.4540	-0.4540	-0.4540
ϵ	0.1	0.1	0.1	0.1	0.1	0.1
D_A	0.0	2.0	2.0	2.0, 40.0	2.0	2.0
β_0	0.0	0.0	0.0	1.3666	-1.1103	-0.5468
β_1	0.7809	0.7809	0.5300	-0.1918	0.6362	0.8812
β_2	-0.6247	-0.6247	-0.8480	-0.3645	-0.2172	-0.3008

Tantalizingly, the model indicates that there could be a universal mechanism active behind the diversity of molluscan shell pigmentation.

ACKNOWLEDGMENTS

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DATA AVAILABILITY

The data that support the findings of this article are openly available [42].

APPENDIX: SYSTEM PARAMETERS

The system parameters for the different excitable models without λ variation are provided in Table I, while those with the self-regulating variable λ are provided in Table II.

TABLE II. System parameters for models with dynamic excitability.

Parameter Name	Figure 11 Branching waves	Figure 14 Wave crossings	Figure 16 Branching triangles	Figure 18 Sierpiński triangles	Figure 19 Nonpigmented spots	Figure 21 Pigmented spots
α_1	-0.0659	-0.0659	-0.0659	-0.0659	-0.0659	-0.0659
α_2	6.6877	6.6877	6.6877	6.6877	6.6877	6.6877
α_3	-0.4540	-0.4540	-0.4540	-0.4540	-0.4540	-0.4540
ϵ	0.1	0.1	0.1	0.1	0.1	0.1
D_A	2.0	2.0	2.0	2.0	2.0	5.0
β_0	0.0	0.0	0.0	0.0	0.0	0.0783
β_1	0.5070	0.5735	0.6508	0.6402	0.6585	0.6525
β_2	-0.8619	-0.8192	-0.7593	-0.7682	-0.7526	-0.1262
β_3	0.0	0.0	0.0	0.0	0.0	0.6234
$\Delta\phi$	-0.3023	-0.3023	-0.4535	-0.4988	-0.2721	0.0
γ_1	3.8490	3.8490	3.8490	3.8490	—	—
A_{eq}	0.30	0.30	0.47	0.30	—	—
δ_1	1.50	1.20	0.60	5.7	—	—
ν	0.030	0.009	0.030	0.061	—	—

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