I. INTRODUCTION

Vegetation distribution in space is often found to be spatially inhomogeneous even in quite homogeneous terrains, a factor that has been recognized as very relevant to understanding ecosystem resilience, functioning and health [1–3]. Spatial self-organization of different types of plants has been reported and modeled in a wide range of habitats, from arid or semiarid environments to wetlands [2–5] and, more recently, in submerged seagrass meadows [6]. Detailed models of the competition of plants for scarce water have been set up to understand pattern formation in dry ecosystems [6–10]. In other approaches, water is not explicitly modeled but a generic approach using an integral kernel, which takes into account nonlocal competition processes with typical interaction ranges, is used [11–14]. This last approach is more easily generalizable to situations in which water is not the limiting resource driving competitive interactions, as in the case of marine plants [6].

In most of the previous models, propagation of vegetation over a landscape is assumed to occur by seed dispersal, modeled as an isotropic diffusion. Clonal growth by rhizome elongation, however, has directional characteristics, a fact that has been modeled at various levels of detail [6, 15, 16]. In [6], the so-called advection-branching-death (ABD) model, describing the growth of clonal plants at a landscape level, was introduced. This model consists of two partial integro-differential equations for the evolution of the density of shoots and apices of the plant. This model was derived directly from the microscopic mechanisms involved in clonal plant growth, namely apex elongation (which appears in the model as an advection term), branching, and death, and its parameters can be directly linked to rates and quantities directly measured in underwater seagrass meadows [6]. Plant interactions were modeled in terms of a nonlocal competition kernel. Although the model describes vegetation distribution in two-dimensional space, the need to include the direction of growth of the apices introduces a new (angular) variable that makes this model effectively three-dimensional and so carries a high computational cost. Fortunately, this angular coordinate does not appear to play a crucial role in most of the observed phenomenology [13]. For this reason, in [16] a single equation for the total density of shoots that captures all the dynamical regimes of the ABD model was proposed, the clonal-growth model. Under certain approximations this equation can be derived from the full model, establishing a connection between the effective parameters of the simple description and the biologically relevant parameters of the full model.

In this work we study in detail the spatially extended and spatially localized solutions of the clonal-growth model in one dimension and explore two levels of approximation for the interaction terms. These are described in Sec. II, and involve keeping the nonlocal character of the interactions or replacing them by an effective local description. The stationary solutions of the resulting equations are presented and compared in Sec. III. The dynamics of fronts between different states, both stable and unstable, are analyzed in Sec. IV and in some cases the predicted front speeds are compared with those determined via direct numerical simulation.

II. MODEL

In Ref. [16], we proposed a sequence of approximations that lead from the full ABD model to a single differential equation describing the evolution of the shoot density of a plant undergoing vegetative or clonal growth, the clonal-growth model. In one spatial dimension, the model reads:

$$\partial_t n = (\omega_b - \omega_d[n]) n + d_0 \partial_x^2 n + d_1 n \partial_x^2 n + d_1 |\partial_x n|^2, \quad (1)$$
where \( n(x, t) \) is the plant shoot density, \( \omega_b > 0 \) is the branching rate of the plant, i.e., the birth term, and \( \omega_d[n] > 0 \) is the mortality rate, which depends on the density. The terms involving derivatives with coefficients \( d_0 \) and \( d_1 \) stem from advection and branching in the original model. These coefficients may depend on environmental conditions and hence on space, but we take both to be constant. Note that the same coefficient \( d_1 \) appears in the last two terms.

### A. Version I: full nonlocal interaction

As a first level of description, hereafter version I, we take Eq. (1) and retain the original nonlocal terms accounting for the interaction between plants [6]:

\[
\omega_d[n] = \omega_{d0} + \int \int \mathcal{K}(r-r')(1-e^{-an(r')})dx^2 + bn^2. \tag{2}
\]

The first term \( \omega_{d0} \) in (2) is the intrinsic mortality. The second term accounts for interactions across space in such a way that the density of shoots at a given position can affect the growth in a neighborhood weighted by the kernel \( \mathcal{K}(r-r') \). The last term is a local nonlinear term which prevents unlimited growth, with the parameter \( b \) determining the maximum value of the density. The kernel \( \mathcal{K} \) is taken to be the difference of two normalized Gaussian functions \( \mathcal{G} \), both with zero mean but with different amplitudes (\( \kappa, \omega_{d0} > 0 \)) and widths (\( \sigma_k, \sigma_0 \)):

\[
\mathcal{K}(r) = \kappa \mathcal{G}(\sigma_k, r) - \omega_{d0} \mathcal{G}(\sigma_0, r). \tag{3}
\]

The first term on the rhs of (3) accounts for all the competitive effects, since it increases the mortality rate, while the second accounts for facilitative effects. The range of the competitive and facilitative interaction is given by \( \sigma_k \) and \( \sigma_0 \), respectively. We assume that \( \sigma_k > \sigma_0 \) as appropriate for the observations in marine plants [6].

In addition to a qualitative agreement with the dynamical regimes of the full ABD model [6], version I of the reduced model reproduces a high degree of accuracy the position in parameter space of the modulational instability (MI) of the homogeneously populated solution (Fig. 1). This description thus provides quantitatively accurate results, while providing a simplified model of clonal plant growth.

### B. Version II: effective local description

A second level of approximation, version II, results from performing a moment expansion of the integral term \( \omega_d[n] \) and truncating at the lowest possible order. Specifically, we first expand the exponential inside the integral and then truncate the moment expansion of the kernel at fourth order. Although this approximation provides good qualitative agreement with the behavior of version I in terms of the observed dynamical regimes (compare Fig. 2 with Fig. 1), it lacks quantitative agreement. The inclusion of higher order terms in the expansion may improve accuracy but implies loss of simplicity. We therefore choose the parameters in version II to preserve as much of possible the behavior of version I while keeping its simple form. The mortality now reads

\[
\omega_d(n) = \omega_{d0} + a'(\kappa - \omega_b)n + b'n^2 - \omega_{d0} - \beta \partial_x^4 n. \tag{4}
\]

with the intrinsic mortality \( \omega_{d0} \) the same as before. The coefficient \( a'(\kappa - \omega_b) \) controls the degree of bistability. We write this coefficient in this way to facilitate a comparison with version I. The coefficient \( b' \) determines the saturation level, while \( \alpha \) and \( \beta \) come from the expansion of the nonlocal term and are responsible for the presence or absence of spatial patterns. The parameters \( a' \) and \( b' \) are chosen to generate a bifurcation diagram similar to that of version I. The conditions imposed are:

(i) having the same density of shoots at \( \omega_{d0} = \omega_b \) and

(ii) having the saddle-node bifurcation of the homogeneously populated state at the same value of the mortality rate \( \omega_{d0} \). These conditions are imposed at the value \( \kappa = 0.048 \text{year}^{-1} \) which will be used throughout the paper. The parameters \( \alpha \) and \( \beta \) are chosen to generate the modulational or Turing instability at a similar mortality rate as in version I for the same chosen value of \( \kappa \), and with a similar critical wavelength.
III. STATIONARY PATTERNS AND LOCALIZED STRUCTURES

In this section we discuss the different stationary solutions supported by versions I and II of the model in one dimension. We first show the results for version I with the full nonlocal interaction term, and then for version II based on the truncated moment expansion, highlighting the main differences between them. Throughout we use the mortality rate $\omega_{d0}$ as the main control parameter. In order to follow stationary solutions we use a pseudo-arclength continuation method \cite{17,18} where the Jacobian is calculated in Fourier space. Starting with an initial condition obtained using numerical simulations we continue the stable and unstable branches changing $\omega_{d0}$ as a control parameter.

A. Version I: patterns and localized structures

Different solutions are observed when the mortality $\omega_{d0}$ changes as summarized in the bifurcation diagram shown in Fig. 3. When mortality is large the branching rate $\omega_b$ is insufficient to sustain growth and the only stable solution is bare soil or unpopulated state (U). In contrast, when the death rate is small compared to the branching rate the homogeneous populated state (P) prevails. In between one finds a region of coexistence between P and U; this region terminates in a saddle node bifurcation labeled $SN$. Both the populated and unpopulated states are shown in red in the figure. When the branching and mortality rates are comparable the upper P state may become unstable to spatial modulations that develop into a periodic pattern that we call a stripe pattern (S), shown in green in Fig. 3. The emerging stripe pattern bifurcates subcritically but undergoes a fold, thereby generating a region of coexistence between stable stripes and the stable upper P state for mortalities below MI. The stripe pattern turns out to be rather robust and stable stripes are found far beyond the region of existence of the homogeneous state, coexisting with the bare soil state U over a broad range of values of $\omega_{d0}$ above the transcritical bifurcation $T$ of U. With increasing mortality rate the stable stripes eventually terminate in a fold bifurcation.

The unstable S states that result in turn terminate at a second MI or Turing bifurcation located on the unstable (middle) branch of P, very close to zero density (Fig. 3). We mention that between these two Turing bifurcations there are other pairs of Turing bifurcations that also give rise to spatially periodic stripes but with wavelengths different (smaller and larger) from the critical wavelength corresponding to the MI of the P state, which is the one displayed here. Thus, the S state is by no means unique.

Figure 3 shows that in addition to the S branch, the MI or Turing bifurcation on the upper P branch generates a pair of branches of spatially localized structures (LS) that also emerge subcritically, creating a window in the mortality rate, called a snaking region \cite{19,20}, within which one finds stable stationary states consisting of segments of the periodic S state of arbitrary length, embedded in the background P state. The purple lines in Figs. 3 and 4 show the resulting snaking bifurcation diagram revealing the presence of two intertwined LS branches consisting of states with odd and even numbers of close-packed troughs. A single-trough state corresponds to a single region of nearly bare soil embedded in P, i.e., a hole in an otherwise homogeneous state, analogous to fairy circles in two spatial dimensions. Based on the general theory developed for the prototypical Swift-Hohenberg equation we expect that opposing folds on the odd and even branches are connected by (unstable) branches of asymmetric states. Owing to the nonvariational structure of the present problem we expect that these states drift, cf. \cite{22}. In this work we do not follow unstable states of this type. We also note that the region of existence of LS extends beyond the left fold of the S branch shown in the figure. This is possible when the wavenumber selected by the LS in the snaking region differs sufficiently from the critical wavenumber at MI to force the LS branches to terminate on a different S branch (see Fig. 4). In the present case the resulting snaking region extends almost to the fold of this second S branch indicating that the chosen parameter values are very close to a transition that breaks up the snaking scenario. This transition occurs when the left LS folds touch the left fold of the corresponding pattern state \cite{23}.

For mortalities larger than the branching rate, $\omega_{d0} > \omega_b$, a different type of stable spatially localized structure is found, consisting of isolated vegetation patches on bare soil (see orange lines in Figs. 3 and 4). The bifurcation structure of these LS differs from the previous case, and they do not lie on a standard snaking branch. Instead these states bifurcate from the unstable P branch close to zero density and below the MI bifurcation at which the S state terminates (see inset in Fig. 5). This bifurcation
cution corresponds to a long wavelength instability, and generates a state with wavelength equal to the system size. The low-amplitude one-patch solution that arises is unstable and grows in amplitude with increasing mortality until it reaches a fold where it acquires stability and becomes a high amplitude stable single patch solution. Beyond the fold the patch state continues to grow in amplitude but now for decreasing mortality until it reaches a second fold. Near this second fold the solution starts to change shape, the central part of the patch developing a relative minimum that continues to decrease along the subsequent branch. Thus, the patch starts to divide into two patches until, after a third fold, two low-amplitude LS are present and these gradually decrease in amplitude with decreasing mortality until the branch terminates back on the unstable P branch. Very close to this bifurcation both peaks become very shallow and their maxima move rapidly apart until they are separated by \( L/2 \), i.e., half the system size. Thus, the termination point corresponds to a pattern-forming bifurcation of the unstable P state to a two-peak state much like the long-wave bifurcation to the single peak state that occurs at a lower value of the density. The bifurcation to the two-peak state is in fact a pitchfork bifurcation, one fork of which corresponds to the termination of the two-peak state generated from the single peak state via peak-splitting as just described, while the other takes part in a similar scenario but based on a a two-peak state. This scenario results, again via peak-splitting, in a four-peak state that terminates on P at yet higher (but still small) density (Fig. 5). Once again, close to this termination point the four peaks become equidistant, i.e., separated by \( L/4 \), allowing this branch to terminate in a pattern-forming bifurcation to a periodic state. In fact this behavior is observed for any number of equispaced identical peaks, even or odd, generated in corresponding bifurcations along the unstable P branch. Similar bifurcation structures have been found in other systems [24, 25]. We conjecture that in the limit of an infinite domain the wavelength along the unstable S branch increases by wavelength doubling that occurs via the same process as that occurring for the one-peak and two-peak states, i.e., via repeated peak-splitting [24, 25], ultimately reaching the transcritical bifurcation T and zero wavenumber, much as occurs in the Gray-Scott model [26, 27]. This scenario is supported by the fact that in all cases the folds on the right align at \( \omega_{d0}/\omega_b \approx 3.538 \), a value that is close to that of the fold on the S branch, while the folds on the left align at \( \omega_{d0}/\omega_b \approx 2.207 \); the intermediate folds are also aligned (at \( \omega_{d0}/\omega_b \approx 3.044 \)). Ref. [25] describes a scenario whereby the single peak state may reconnect with or turn into a pattern state.

**B. Version II: patterns and localized structures**

Figure 4 shows the corresponding bifurcation diagram for the P, U, S and LS states in version II of the model.

The bifurcation scenario is qualitatively similar to that observed in version I (compare Fig. 6 with Fig. 3), confirming the fact that this simpler version of the model captures all the basic mechanisms. However, substantial quantitative differences are observed. For instance, the mortality ranges in which each solution exists are reduced, while the solution profile becomes more triangular. As a result the bare soil minima in the S state are much narrower.

\[ \frac{\omega_{d0}}{\omega_b} \approx 0.48 \text{ year}^{-1} \text{ and the remaining parameters are as in Fig. 4.} \]
FIG. 4. Close-up of the snaking region of version I of the model, emerging from the modulational instability of the P state in Fig. 3 using the norm of the difference between this state and P to reveal details of the snaking bifurcation diagram. The dark purple curve represents LS with an even number, while the bright purple curve represents LS with an even number. The green curves correspond to stripe patterns S with two different wavenumbers, one with the critical wavenumber and the other with the wavenumber selected by a stationary front between the homogeneous and pattern states, which determines the wavelength within the LS. The upper panels show the solution profiles corresponding to the labeled locations in the bifurcation diagram (lower panel). The parameters are as in Fig. 3.

IV. FRONTS

Figure 4 for version I and Fig. 6 for version II reveal the existence of several different regions of coexistence between the U, P and S states owing to the presence of multiple stable solutions, raising the possibility of a number of different fronts connecting these states. As many as three stable spatially extended states can coexist simultaneously, a situation that also arises in other vegetation pattern-forming models [28]. Here we study the fronts connecting the populated state with the unpopulated state (P-U fronts), the populated state with the stripe pattern (S-P fronts) and the stripe pattern with the unpopulated state (S-U fronts). Front dynamics depend strongly on the stability of the states that are involved. The velocity of moving fronts connecting two linearly stable states necessarily depends on nonlinear processes, i.e. processes occurring beyond the immediate vicinity of the front. Such fronts are called pushed [29]. In contrast, fronts of constant form describing the invasion of a linearly unstable state by a stable one may travel at a speed determined via a linear mechanism that requires that perturbations ahead of the front grow at just such a rate that a front of constant form is maintained [29]. These fronts are thus pulled by the linear instability ahead of them. It should be mentioned, however, that the existence of pulled fronts does not imply that such fronts are selected. Pushed fronts can exist in the same parameter regime and these would travel with a different speed. In the case of coexistence between pulled and pushed fronts, the front with the larger velocity is usually the one that is observed [30, 31].

The speed $v$ of a pulled front can be obtained by considering infinitesimal perturbations, of the form $e^{ikx+\lambda(k)t}$ or equivalently $e^{ikx'+\Lambda(k)t}$ with $\Lambda(k) = ikv + \lambda(k)$, to the unstable state in the comoving reference frame $x' = x - vt$ [28, 32]. Applying the condition of marginal stability, i.e., that in the frame moving at $v$ perturbations neither grow nor decay, leads to the requirement that the (complex) group speed and the growth rate of the perturbation both vanish, yielding three con-
A. Fronts in version I of the model

In this section we show the results obtained with version I, using the bare mortality $\omega_{d0}$ as the main control parameter and keeping the other parameters as in Fig. 3. Our numerical simulations use a pseudospectral method with periodic boundary conditions and $\Delta t = 1.667 \cdot 10^{-3}$ years, $\Delta x = 0.255$ m and $N = 4096, 8192$ and 16384 grid points starting with a homogeneous initial condition, the U or P state, with a very narrow step function at $x = 0$ to excite a competing solution. In the cases in which two distinct fronts are possible (tristability) we use the profile of the desired front obtained for other values of the mortality as initial condition.

We study first the P-U fronts between the two homogeneous solutions. We can distinguish two cases. When $\omega_{d0}/\omega_b > 1$ (but below a value at which the state P behind the front destabilizes, see below) the front is a pushed front as both P and U are stable. The front velocity as well as the direction of advance is thus determined by nonlinearities. We observe numerically that P always invades U. Figure 7 shows an example of this type of front. On general grounds, one would expect to find a sufficiently large value of the mortality, a Maxwell point, beyond which the direction of the front reverses and the bare soil will invade the populated solution. However, it turns out that this occurs beyond the mortality rate for the instability of the P solution to pattern formation (MI), and we never observe this type of desertification front.

For $\omega_{d0}/\omega_b < 1$ the U state is unstable and a pulled front whereby P advances into U exists. Its speed can be computed from the marginal stability approach. In Fig. 8 we show, as a function of $\omega_{d0}/\omega_b$, the velocity $v$ of the pulled front computed analytically (red line, see Appendix) and from numerical simulations (red dots). It is clear that the marginal stability prediction for the front velocity fails. The front speed for $\omega_{d0}/\omega_b < 1$ appears to be a continuation of the pushed front speed for $\omega_{d0}/\omega_b > 1$. We have investigated the discrepancy between the linear marginal stability prediction and numerics by performing numerical simulations in which the nonlinear terms that do not appear in the linear calculation are removed. First we removed the term $d_t |\partial_x n|^2$ but the resulting change in the speed of the front is small (blue dot in Fig. 8 for $\omega_{d0}/\omega_b = 0.4$). We then removed the nonlocal competition term as well by setting $\sigma_\kappa = 0$ (black dot in Fig. 8). In this second case the velocity changes dramatically and coincides with the linear marginal stability prediction. This result points to the nonlocal interaction term as the source of discrepancy between the linear marginal stability prediction and the speed of the front in the full system. We ascribe this effect to an inhibiting effect of existing plants at the edge of the front on the growth of plants a certain distance ahead of the front, thereby decreasing the speed of propagation. This interpretation is supported by the presence of a density maximum in the front profile lo-
cated at the front edge and generated by long range interactions (Fig. 7). We note that in systems of reaction-diffusion equations the speed selection problem is more complex (the fastest front is not always the one selected) than in single-equation ones and nonlocal systems such as that studied here are, somewhat loosely, equivalent to a higher-dimensional system [33]. Other effects of nonlocal terms on the speed of fronts have been studied in [14, 34, 35].

The P-U front is observed for $\omega_{00}/\omega_b$ below a critical value $1.325 \pm 0.008$ (which is close to but below the MI occurring at $\omega_{00}/\omega_b \approx 1.345$). In this region P always invades U and no Maxwell point (i.e., a value of $\omega_{00}$ at which propagation direction reverses) is found. When $\omega_{00}/\omega_b \geq 1.325 \pm 0.008$, the P state behind the front destabilizes so that the front generates a stripe pattern in its wake, i.e., it becomes a S-U front. We note, however, that there is a small region $(1.277 \pm 0.014 \leq \omega_{00}/\omega_b \leq 1.325 \pm 0.008)$ of coexistence between the two fronts (yellow dots in Fig. 8).

Figure 7 shows a space-time representation of an S-U front at $\omega_{00}/\omega_b = 1.395$. This front, whereby S invades U, is pushed since both S and U are stable at this mortality rate. The front’s leading edge is very steep, and is followed by a sloping plateau that leads to the formation of a deep hole that is characteristic of the S state at this mortality rate. Once the hole forms the plateau relaxes, reproducing the S profile near its maxima. Note that in the reference frame moving with the front the deposition of successive holes is an oscillatory process with a well-defined temporal period and we conjecture that, in that reference frame, the S-U front forms via a (subcritical) Hopf bifurcation of the P-U front. For this reason the leading edge of the S-U front at, say, $\omega_{00}/\omega_b \sim 1.395$ closely resembles that of the corresponding P-U front (Fig. 10), a fact that is likely responsible for the similar speeds of these two fronts (Figs. 8 and 11). Indeed, Figs. 11(a,c) show the profiles of the S-U and P-U fronts at equispaced times, with (a) showing the initiation of the deep hole associated with the S state. No such hole is generated behind a P-U front. Panels (b,d) show that these fronts can be viewed, respectively, as heteroclinic connections between a limit cycle (the S state) and the trivial or zero state (the U state), and between two equilibria, one corresponding to the P state and the other to the U state, indicated by the black spots in the figure. Note the similarity of the trajectory leaving the zero state. In both cases the density profile has a pronounced maximum just behind the leading edge of the front, which we ascribe to the absence of competition ahead of the front. Such overshoots are characteristic of fairy circles in arid ecosystems as well.

The S-U front is observed for $\omega_{00}/\omega_b \geq 1.277 \pm 0.014$ and travels with a speed that decreases monotonically with $\omega_{00}$ until $\omega_{00}/\omega_b \approx 2.205 \pm 0.005$ where its speed vanishes (Fig. 11). In this interval of mortalities the S-U front selects a well-defined and nonzero wavenumber $q = k_r$ in its wake, with values shown in Fig. 11. Beyond $\omega_{00}/\omega_b \approx 2.205$ no new holes are generated and a stationary state consisting of equispaced, widely separated stripes is observed. The stopping of the front is not the result of conventional front pinning [20], since the spatial eigenvalues of U cannot be complex owing to the requirement that the density $n(x)$ is everywhere non-negative. We have been unable to determine whether the selected wavenumber $q$ remains non-zero at $\omega_{00}/\omega_b \approx 2.205$ but we mention that the region $\omega_{00}/\omega_b \geq 2.205$ is in any case populated by a number of stable stationary equispaced-patch states resembling the 1-peak, 2-peak localized structures described in Sec. III.1; only one of these
would be selected by the moving front as \( \omega_{d0}/\omega_h \to 2.205 \), most likely corresponding to \( q = 2\pi/L \) or the 1-peak state. Thus, the transition at \( \omega_{d0}/\omega_h \approx 2.205 \) would correspond to a transition from a state with an intrinsic wavelength \( 2\pi/q \) to one where the wavelength is determined by the domain size \( L \).

The last front we consider is an S-P front between the stripe pattern S and the populated state P. The stability of the P state changes at the MI instability (occurring at mortality \( \omega_{d0,c} \), with \( \omega_{d0,c}/\omega_h = 1.345 \)), whereas S is always stable in the region of coexistence with P. For \( \omega_{d0} < \omega_{d0,c} \) the only possible front is pushed since both S and P are stable. As \( \omega_{d0,c}/\omega_h \) decreases from 1.345 the speed of the pushed front also decreases and falls to zero at the right boundary of a pinning region which extends from \( \omega_{d0}/\omega_h = 1.294 \) to the saddle-node bifurcation at which the S state selected by the front is created (see Fig. 3). For mortalities above MI (\( \omega_{d0}/\omega_h > 1.345 \)) the pushed front continues to be selected over the pulled front that now exists, until the speed of the latter exceeds that of the pushed front; thereafter the pulled front prevails (Fig. 3(a)). An example of this pulled front advancing into the P state is shown in Fig. 12. The transition from pushed to pulled takes place around \( \omega_{d0,c}/\omega_h \approx 1.375 \) where an abrupt change in the dependence of the front speed with mortality is clearly visible. This change in the behavior of the front speed is associated with a similar change in the wavenumber of the S state deposited by
the front (Fig. 12b). The pulled S-P front that prevails at sufficiently high mortalities remains stable until the saddle-node bifurcation SN of the P state; its speed is well predicted by the linear marginal stability calculation throughout this range. Similar results have been found in other systems [30, 31].

B. Fronts in version II of the model

In this section we study briefly the same fronts as in Section IV A but for version II of the model. Simulations are again done with a pseudospectral method using periodic boundary conditions with \( \Delta t = 0.167 \text{ years} \), \( \Delta x = 0.025 \text{ m} \) and \( N = 1024 \). Initial fronts are formed by connecting smoothly the two desired spatially extended states. The following figures summarize the results. As before, we take \( \omega_{db} \) as the control parameter, with the other parameters as in Fig. 3.

Figure 14 shows an example of a P-U front at \( \omega_{db}/\omega_b = 1.15 \), i.e., a pushed front connecting the two homogeneous states P and U, which are both stable at this mortality value. The figure shows that P invades U. For the parameter values used the front has a constant but nonmonotonic profile and travels at constant speed \( v \approx 1.091 \cdot 10^{-3} \text{ m/years} \).

Figure 15 shows a space-time representation of a S-U front at \( \omega_{db}/\omega_b = 1.25 \), i.e., a front connecting the stable stripe state S to the stable bare ground state U. This is a pushed front whereby the stripe state colonizes bare ground via a time-dependent precursor that evolves into a stationary stripe pattern. For our parameter values the invasion speed \( v \approx 4.330 \cdot 10^{-4} \text{ m/year} \).

Finally, Fig. 16 shows a classic example of a pinning-depinning transition associated with S-P fronts [21]. The speed \( v \) of the front decreases as one approaches the edge of the pinning region containing stationary spatially localized structures; sufficiently close to the edge the speed is expected to vary as the square root of the distance from the edge. Within the pinning region the front is self-pinned, i.e., it is pinned to the pattern state behind it, and in the depinned regime \(|v| > 0\) the front is pushed.
We have explored two versions of a simplified model for clonal plant growth [16], motivated by undersea patterns observed in *Posidonia oceanica* meadows [6]. The first version takes into account nonlocal competition and facilitation through appropriately formulated, albeit phenomenological kernels. The second simplifies these kernels via a gradient expansion and, after truncation, leads to a nonlinear but local evolution equation. In both cases we have taken the mortality parameter $\omega_{d0}$ as the bifurcation parameter and explored the behavior of each version as the mortality varies. In both cases we have made every effort to employ realistic values of the remaining parameters.

The key findings of our work are:

(i) There is a qualitative agreement between the nonlocal and local models in that both exhibit the same sequence of transitions between the three spatially extended states, the populated state P, the unpopulated state U, and the transition between them.

(ii) The speed of the P-U front $v_{P-U}$ is approximately $1.091 \cdot 10^{-3}$ m/year, and the speed of the S-U front $v_{S-U}$ is approximately $3.330 \cdot 10^{-4}$ m/year.

(iii) The speed of the S-P front $v_{S-P}$ is approximately $4.419 \cdot 10^{-3}$ m/year.

(iv) The pinning region, in which the front is stationary, is observed for $\omega_{d0}/\omega_b < 0.75$.

V. CONCLUSIONS
state U and the pattern state S, as $\omega_{d0}$ varies. Nevertheless, substantial quantitative differences are seen. The nonlocal version is believed to provide more accurate predictions for the real vegetation dynamics, whereas the local approximation, because of its simpler structure, can be used as a qualitative tool to understand the transitions between different regimes.

(ii) In addition to spatially extended states both systems also exhibit two types of spatially localized structures, one resembling holes in the homogeneously populated state and the other resembling vegetation patches on bare ground, i.e., embedded in the U state. These states are organized within distinct bifurcation structures.

(iii) Both systems exhibit a variety of fronts connecting the extended states, and these may be either pushed or pulled. In the former case the speed of the front is determined by nonlinear processes while in the latter the front speed can be computed from a marginal stability criterion as described in [28]. In many systems, pulled fronts with marginal stability velocities are good descriptions of fronts describing stable states invading unstable states. Here we have found situations in which this is the case, but also cases in which pushed fronts prevail. The characteristic front speeds are in all cases very slow, of the order of centimeters per year, a result that is consistent with the observed slow evolution of Posidonia oceanica meadows, the case to which model parameters were fitted.

The spatial period-doubling we observe at small amplitude near the transcritical bifurcation of the U state appears to be characteristic of many vegetation models. In the present case it takes place via peak-splitting as the mortality parameter $\omega_{d0}$ increases, a process that occurs in related systems as well [24, 28]. This process requires that near their termination the peaks that result adjust their mutual position to generate a periodic state, since only periodic states can terminate in a Turing bifurcation. Other systems exhibit spatial period division organized within a foliated snaking structure which does not require the localized structures to adjust their location [36, 40]. Related period division is found in other systems [25]. The fact that the region of stability of periodically spaced vegetation patches appears to extend all the way down to zero wavenumber (in an infinite domain) allows sensitive wavelength adaptation when parameters are varied [41].

**ACKNOWLEDGMENTS**

DRR, LM, EHG and DG acknowledge financial support from MINECO/AEI/FEDER through project SuMaEco (RTI2018-095441-B-C22) and through the María de Maeztu Program for Units of Excellence in R&D (MDM-2017-0711). DRR also acknowledges the fellowship BES-2016-076264 under FPI program of MINECO, Spain. The work of EK was supported in part by National Science Foundation under grant DMS-1908891, and by a visiting position at IFISC funded by the University of the Balearic Islands.

**Appendix: Marginal stability predictions for pulled P-U and S-P fronts**

In this Appendix we use the notation $A^* = an^*e^{-an^*}$, $e_\nu = e^{-(k^2 - k^2)\nu^2/2}$ and $e_0 = e^{-(k^2 - k^2)\nu^2/2}$. The dispersion relation obtained from the linearization of version I of the model around the state $\nu = n^*$, which is the value of the density at the uniform populated state given by the solution of the equation $\omega_\nu - \omega_d(n^*) = 0$, can be used to write the condition $v k_i = \Re [\lambda(k)]$ in the form

$$v k_i = -2b n^* - (d_0 + d_1 n^*)(k_r^2 - k_i^2) - A^* (\kappa e_\nu \cos(k_r k_i \sigma_0^2) - \omega_d e_0 \cos(k_r k_i \sigma_0^2)).$$

(A.1)

Similarly the condition $\Re \left[ \frac{d\lambda(k)}{dk} \right] = 0$ becomes

$$0 = \left( - (d_0 + d_1 n^*) + A^* (\kappa e_\nu \cos(k_r k_i \sigma_0^2) - \omega_d e_0 \cos(k_r k_i \sigma_0^2) \frac{\sigma_0^2}{2}) \right) 2 k_r + A^* (\kappa e_\nu \sin(k_r k_i \sigma_0^2) - \omega_d e_0 \sin(k_r k_i \sigma_0^2) \frac{\sigma_0^2}{2}) 2 k_i,$$

(A.2)

while condition $v = -\Im \left[ \frac{d\lambda(k)}{dk} \right]$ takes the form

$$v = \left( + (d_0 + d_1 n^*) - A^* (\kappa e_\nu \cos(k_r k_i \sigma_0^2) - \omega_d e_0 \cos(k_r k_i \sigma_0^2) \frac{\sigma_0^2}{2}) \right) 2 k_i + A^* (\kappa e_\nu \sin(k_r k_i \sigma_0^2) - \omega_d e_0 \sin(k_r k_i \sigma_0^2) \frac{\sigma_0^2}{2}) 2 k_r.$$

(A.3)

These three equations are solved numerically for the unknowns $v$, $k_r$ and $k_i$ characterizing the speed and leading edge profile of a pulled front, specifically a pulled S-P front as illustrated in Fig. (solid line). The same procedure around $n = 0$ leads to the analytical solution $v = 2\sqrt{d_0(\omega_\nu - \omega_{d0})}$, $k_r = 0$ and $k_i = \sqrt{(\omega_\nu - \omega_{d0})/d_0}$ for a pulled P-U front, as illustrated in Fig. (solid line).
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