A simple model for pattern formation in clonal-growth plants

Daniel Ruiz-Reyñés\textsuperscript{1}, Francesca Schönberg\textsuperscript{1,2}, Emilio Hernández-García\textsuperscript{1} and Damià Gomila\textsuperscript{1}

\textsuperscript{1}IFIC (CSIC-UIB). Instituto de Física Interdisciplinar y Sistemas Complejos, E-07122 Palma de Mallorca, Spain
\textsuperscript{2}SISSA. Scuola Internazionale Superiore di Studi Avanzati, 34136 Trieste, Italy

(Dated: August 14, 2019)

Clonal plants reproduce by generating new plants from a piece of an existing one without the need of producing seeds or spores. They form a whole family of plants, including terrestrial and marine species. However, the specific features of clonal growth are not taken into account in prototypical models to study vegetation patterns. On the other hand, including all details leads to a rather complicated model. Here we propose a generic model that includes all main clonal-growth features and reproduces the phase diagram of a fully detailed model. The relation of each term of the model with the mechanisms of clonal growth is discussed.

The spatial distribution of vegetation is a key factor in ecosystems functionality as it may reorganize completely the pathways of energy and resources through the system \cite{1}. Besides the simple homogeneous coverage, and disordered configurations, several types of inhomogeneous vegetation distributions have been reported, ranging from isolated gaps, scattered gaps arranged in a more or less regular lattice, stripes or labyrinthine patterns, patches arranged in a regular lattice or isolated patches \cite{1,2}. Although there is a variety of mechanisms responsible for creating and maintaining the spatial inhomogeneities, they are always associated to feedbacks across space \cite{3,4} from which similar patterns arise in completely different environments. Even the sequence in which the different patterns appear when changing a control parameter is often the same \cite{2}, which gives a universal character to the phenomenon of vegetation pattern formation.

Most studies of vegetation patterns consider arid environments, so that plant competition for water is the basic factor introducing destabilizing feedbacks. On the other hand vegetation propagation is usually assumed to occur by seed dispersal. However, a recent study of pattern formation in underwater meadows of seagrasses \cite{1} was clearly outside the domain of applicability of these two standard hypothesis. First, although the mechanism for plant interactions was not uniquely identified, competition for water can not be the relevant mechanisms for pattern formation in these marine plants. Second, the main mode of reproduction of these plants was not seed production, but clonal growth. Clonal plants (examples include most grasses and seagrasses) reproduce by originating new plants from a rhizome which grows horizontally. The rhizome, in turn, can branch creating a new rhizome propagating in a different direction. Altogether clonal plants can expand without the need of producing seeds or spores, although most species alternate the clonal and the flower/seed modes of reproduction under some circumstances.

A numerical model to describe meadows of clonal plants, the ABD model, was proposed in \cite{1} and successfully reproduced the observed patterns in seagrass meadows. However, the model was highly complex due to the need to account for the direction of growth of the different rhizomes. In this work we propose a single partial differential equation for the vegetation density which reproduces qualitatively patterns and dynamics of clonal plant growth. We first derive the model heuristically from the main mechanisms of growth and symmetry properties. In this way the model is a generic one, which could be in principle applied to any instance of clonal growth. The specific mechanisms of feedback and competition would only enter through the particular values of the model parameters. Then, we also derive the equation from the fully detailed ABD model of \cite{1} under certain approximations. This allows us to relate the underlying growth mechanisms with the different terms in the simplified description.

In the following we propose an heuristic large-scale model (meadow or landscape scales) for a clonal-growth vegetation density $n(\vec{r},t)$. This quantity gives the biomass or the number of shoots per unit area at location $\vec{r}$ in a two-dimensional location in the meadow. The model takes the form of a single partial differential equation for $n(\vec{r},t)$ and is derived under four general considerations: First, the homogeneous unpopulated solution (i.e. $n(\vec{r},t) = 0$, representing bare soil) should be one of the possible solutions of the equation for any values of the parameters (we do not consider the possibility of plant immigration from outside the meadow). Second, as usual when deriving large-scale equations which are supposed to represent generic pattern formation processes \cite{6}, we include in the equation only low-order polynomial dependencies in the density and in its lowest order gradients. Third, despite individual rhizomes grow in different directions, at large scales and not close to vegetation borders, we should have all growth directions locally represented and then the equation for the total density of plants growing in all directions, $n(\vec{r},t)$, should be rotationally invariant in the plane. And fourth, $n(\vec{r},t)$ can never be negative.

Taking into account these requirements, a general partial differential equation that contains in its right-hand side polynomial terms up to 3rd order in $n$ and up to 4th...
order in gradients is
\[ \partial_t n = -\omega n + an^2 - bn^3 + \epsilon \nabla^2 n + \alpha (\nabla^2 n)n + \delta \parallel \nabla n \parallel^2 + \beta (\nabla^2 n)n . \] (1)

The absence of terms independent of \( n \) implements our first requirement. Also, only the rotationally invariant terms containing gradients are present in Eq. (1). A term containing \( \nabla^4 n \) could in principle be added to Eq. (1), but it easily induces negative values of \( n \), and when it does not, it does not add any qualitatively new behavior with respect to the terms already present. We neither include terms such as \( \parallel \nabla^2 n \parallel^2 \), nor others of higher order, since Eq. (1) already explains the relevant phenomenology, and it will be later derived in this form from the ABD model.

In Eq. (1), \( \omega \) is readily interpreted as the local net death rate in a linear regime, i.e. in the absence of plant interactions. Negative values of \( \omega \) would indicate local linear net growth. Negative values of \( \omega \) would indicate local linear net growth. Negative values of \( \omega \) would indicate local linear net growth. Negative values of \( \omega \) would indicate local linear net growth. The signs are chosen so that \( \omega > 0 \) corresponds to a facilitative interaction (decrease of death rate with density). In order to have a finite maximum homogeneous density we need \( b > 0 \), which models plant competition (increase of death rate with density).

Equations similar to (1) have been derived from models of dryland vegetation dynamics under competition for water [7–9] or in more general contexts involving species competition [10]. In these contexts, the terms proportional to \( \alpha \) and \( \beta \) are recognized as interaction terms that respect the requirements of existence of a bare-soil solution \( n = 0 \) and maintain positivity of the density. They are an effective way to include, to lowest order in gradients, interactions between distant plants mediated by water or any other long-range competitive process [7–10]. In these models, the diffusive term \( \epsilon \nabla^2 n \) accounts for plant propagation by seed dispersion. The new term here, absent in previous works, is \( \delta \parallel \nabla n \parallel^2 \). When \( \delta > 0 \), it always produces an increase in density at any place where there is a non-zero gradient. This is the effect that clonal growth by rhizome elongation would produce, so that we interpret this term as the distinct signature of clonal reproduction. Derivation of Eq. (1) from the ABD model will confirm this.

We next attempt a systematic derivation of Eq. (1) from the ABD full model [1], under certain approximations. This will allow us to express the parameters in (1) in terms of biologically relevant ones.

Previous works have approximated the space occupancy of clonal plants from a simple random-walk process [11] or through the definition of discrete growth rules [12]. The latter work identified three key modeling ingredients which can be up-scaled to models of large landscapes, as needed to deal with pattern formation phenomena. First, the rhizome of a plant, whose tip is called apex, grows horizontally at constant velocity \( \nu \), leaving behind new shoots separated by a characteristic distance \( \rho \). Second, the shoots and apices have a lifetime depending on the environmental conditions which translates into a mortality rate \( \omega_d \). Finally, the rhizomes can generate new branches growing in other directions separated by a characteristic angle \( \phi \) from the initial one. Branching happens with a rate \( \omega_b \). The ABD model, introduced in [1], is an implementation at the landscape level and in terms of population densities of the above mechanisms: the time evolution of the spatial and angular density of apices \( n_a(\vec r, \phi, t) \), where \( \phi \) is the angle of the growth direction, and of shoots \( n_s(\vec r, t) \), is ruled by
\[
\partial_t n_a(\vec r, \phi, t) = -\omega_d[n_a(\vec r, \phi, t) - \vec v(\phi) \cdot \nabla n_a(\vec r, \phi, t)] + \frac{\omega_b}{2} (n_a(\vec r, \phi + \phi_0, t) + n_a(\vec r, \phi - \phi_0, t)) \tag{2}
\]
\[
\partial_t n_s(\vec r, t) = -\omega_d[n_s(\vec r, t)] + \frac{\nu}{\rho} \int_0^{2\pi} n_a(\vec r, \phi, t) d\phi, \tag{3}
\]
where the growth-velocity vector is \( \vec v = \nu (\cos \phi, \sin \phi) \) and \( \nabla = (\partial_x, \partial_y) \). The first term in the r.h.s. of Eq. (2) accounts for the mortality of apices, the second is an advection term that displaces apices in the direction of growth \( \phi \) due to the elongation of the rhizome. The third corresponds to the branching process where the density of apices in adjacent directions \( \phi \pm \phi_0 \) contribute to increase the density of apices growing with the direction \( \phi \). The first term in Eq. (3) corresponds to shoots death (same mortality rate is assumed for shoots and apices) and the second contribution accounts for shoots left behind the apices while the rhizomes grow in all directions.

The death rate of the plant \( \omega_d \) depends on the total density \( n_t(\vec r, t) = n_a(\vec r, t) + n_s(\vec r, t) \), where
\[
\omega_d(\vec r, t) = \int_0^{2\pi} n_a(\vec r, \phi, t) d\phi
\]

The first contribution accounts for the death rate of a single isolated shoot or apex. The second is a saturating term accounting for the environmental carrying capacity. Finally, the third one is an integral term which describes in a very general way the interactions across space. The kernel \( \mathcal{K} \) includes both facilitative and competitive interactions. It does not assume any specific interaction mechanism, but encodes its strength and spatial scales.

For appropriate choices of the parameters and of the kernel \( \mathcal{K} \) this model can describe accurately growth and pattern formation in seagrass meadows [11]. One of the
particularities of the model is that it includes explicitly the directions of growth. Although this provides a complete description, it is highly demanding from a computational point of view, as one has to deal with a three-dimensional field for the apices ($n_a$ depends on $r'$ and $\phi$) plus a two-dimensional field for the shoots. One can eliminate the dependence on the angle and find a single equation for the total density by introducing a number of approximations detailed in the Supplemental Material [13]. The result is that an approximate equation for the total density reads

$$\partial_t n_t = (\omega_b - \omega_d n_t) n_t - \nu \nabla \cdot \vec{a'},$$  

and

$$\vec{a'} = -(c_0 + c_1 n_t) \nabla n_t,$$

$c_0$ and $c_1$ are approximately given by

$$c_0 = \frac{\nu}{2(\omega_{a,0,M} - \omega_b \cos \phi_b)}$$

and

$$c_1 = \frac{\nu}{2n_{a,0,M}^*} \left( \frac{1}{\omega_b \cos \phi_b - \omega_{a,0,M}} - \frac{1}{\omega_b \cos \phi_b - \omega_b} \right)$$

being $n_{a,0,M}^*$ the homogeneous stationary value of density at the Maxwell point ($\omega_{a,0} = \omega_{a,0,M}$), where a front between the populated homogeneous solution and bare soil does not move.

The term $\omega_b - \omega_d n_t$ in Eq. (5) can be interpreted as a net growth rate at location $\vec{r}$ depending on the density there and in a neighborhood (because of the integral term in $\omega_d n_t$). The form of Eq. (5) also indicates that $\vec{a'}$ is a flux of biomass arising from propagation mechanisms. These were just clonal growth in the original equations of the ABD model. Thus, the propagation contribution to Eq. (5):

$$- \nu \nabla \cdot \vec{a'} = \nu \left( c_0 \nabla^2 n_t + c_1 n_t \nabla^2 n_t + c_1 \| \nabla n_t \|^2 \right)$$

encodes the contribution from clonal growth. The first and the second term in Eq. (9) have a functional form already encountered in other models of vegetation dynamics, where they accounted respectively for seed dispersion and interactions. But here they arise from multidimensional rhizome growth and branching and, as anticipated, the presence of the new term $\| \nabla n_t \|^2$ is a distinct signature of this clonal mode of propagation.

To follow further towards the derivation of Eq. (11), we approximate the exponential term $1 - e^{-a_r n_t}$ in (10) to first order in $a_r n_t$, and expand the resulting integral using a moment expansion [14]. Then we obtain the following expression for the nonlocal interacting terms in $\omega_d$:

$$\int \int K(\vec{r} - \vec{r'}) (1 - e^{-a_r n_t(r', t)}) d\vec{r'} \simeq a_r \sum_{j=0}^{\infty} d_j \nabla^{2j} n_t(\vec{r}, t),$$

where

$$d_j = \frac{(-1)^j d^{(2j)} K(q)}{(2j)!} \left. \frac{d^j q}{dq^{2j}} \right|_{q=0} = \frac{(-1)^j}{(2j)!} 2\pi J_0^{(2j)}(0) \int_0^{\infty} r^{2j+1} K(r)dr$$

are the corresponding moments of the kernel and $J_0^{(2j)}(0)$ is the $2j$th derivative of the Bessel function $J_0$ of the first kind evaluated at the origin. Considering terms only until fourth order and replacing them, together with Eq. (9), in Eq. (22) we get exactly Eq. (1) with the identification of $n(\vec{r}, t)$ with the total density $n_t(\vec{r}, t)$, and $\omega = \omega_{a,0} - \omega_b$, $a = -a_r a_0$, $b = B$, $\epsilon = \nu c_0$, $\delta = \nu c_1$, $\alpha = \nu c_1 - a_r d_1$, and $\beta = -a_r d_2$.

We can now identify the contribution of the different mechanisms to each term of Eq. (1). As anticipated, the difference between the mortality and branching rates $\omega_{a,0}$ and $\omega_b$ determines the net growth $\omega$, but the rate $\omega_b$ appears also explicitly in other coefficients. The parameters determining rhizome propagation, $\nu$ and $\phi_b$, also enter in the expressions for some of the spatial coupling terms.

We next analyze some predictions of model (1). In the following, by rescaling $n$ we set $b = 1$ without loss of generality. Eq. (1) has three homogeneous steady states (HSS): $n_0^* = 0$ and $n_\pm^* = (a \pm \sqrt{a^2 - 4\omega})/2$. The first one corresponds to bare soil (unpopulated solution), while the other two emerge from a saddle node bifurcation located at $a^2 - 4\omega = 0$, so that $n_\pm^*$, representing homogeneous populated solutions, exist only for sufficiently low mortalities, $\omega < a^2/4$. Since $n$ is a density, only positive values are considered in the following. Depending on the sign of $a$, either $n_+^*$ or $n_-^*$ connect with $n_0^*$ in a transcritical bifurcation at $\omega = 0$. With facilitative interactions, $a > 0$, $n_+^*$ is stable against homogeneous perturbations while $n_-^*$ is unstable and connects with $n_0$ subcritically. As a result there is a region of coexistence between the populated and the unpopulated states. On the other hand, if $a < 0$ only $n_-^*$ takes positive values and the transition is supercritical. Here we focus in the case $a > 0$ as in [1]. Figure 1 shows an example of the bifurcation diagram of the homogeneous solutions as a function of the mortality $\omega$ in this subcritical case. In this and in the next figures, parameters used in our simplified model are roughly of the order of those determined from the ones appropriate for the seagrass Posidonia oceanica in the ABD model [14].

Fig. 2 shows the location of different bifurcation and stability domains in the two-parameter space $(\omega, a)$, as identified from a linear stability analysis of the HSS against perturbations of the form $e^{\lambda t + iq \cdot \vec{r}}$. It reveals that the unpopulated solution $n_0^*$ is unstable for $\omega < 0$ leading to an homogeneous growth of the density until the solution $n_+^*$ is reached. This branch $n_+^*$ is stable against homogeneous perturbations $q = 0$, where $q = ||q||$. How-
ever, for \( \omega \) above a certain threshold \( \omega_c \), it becomes unstable against modulations with a given critical wavenumber \( q_c \), what is known as a modulation (or Turing) instability (MI). For values of \( \omega > \omega_c \), the HSS \( n^*_s \) remains unstable until the saddle node bifurcation (see Figs. 1 and 2). In the supercritical case, \( a < 0 \), the homogeneous state becomes unstable at the MI and the region of instability persists until a second MI close to the transcritical bifurcation at \( \omega = 0 \). The phase diagram in Fig. 2 reproduces all the qualitative features present in the ABD model (compare with Fig. S3 in [1]). Beyond the qualitative agreement the shape and velocity of a front between the populated and unpopulated solutions, as well as the position in parameter space of the MI in the ABD model, can be quantitatively predicted by the reduced model if the full nonlocal term is kept, but this quantitative accuracy is partially lost when the expansion of the integral term is truncated linearly in \( n_t \) and to fourth order in the gradients, which is the roughest approximation in our derivation.

The nonlinear regimes of the dynamics cannot be inferred just by the linear stability analysis. We perform numerical simulations to determine the presence of different patterns and their different regions of stability. Fig. 1 shows the different patterns observed for different values of the growth rate \( \omega \). Although the value of the parameters for which the different patterns appear does not precisely correspond with the ones in the ABD model [1], the type and sequence of patterns when the mortality is increased are the same, as expected from the general theory [2].

The new term \( \delta \| \nabla n_t \|^2 \), distinctive of clonal growth, affects mainly the dynamics of fronts. This term contributes always to the velocity of a front in the direction from higher to lower densities. This favors the expansion of the populated solution over the zero state, which we interpret as the result of the elongation of the rhizomes outwards the meadows. As a consequence the position of the Maxwell point moves to higher mortalities as compared to the same equation with \( \delta = 0 \) [15], i.e., clonal-growth plants can colonize new empty space under unfavorable conditions more efficiently than if the propagation is driven by seed dispersal (diffusion) only.

Summarizing, we have proposed a simple model to describe the growth and dynamics of clonal-plant meadows. We have also derived the equation from a realistic model, providing analytical expressions for the effective parameters as a function of the biologically relevant parameters of the full model. The reduced model provides a qualitative description of clonal-growth plants, reproducing all the possible stationary spatial distributions and dynamical regimes. Moreover, beyond a qualitative description, accurate quantitative results can be obtained depending on the level of approximation of the non-local interacting terms. We expect this simple model, applicable to a wide variety of clonal plants, to allow deeper theoretical studies on the dynamics of clonal growth not tractable using a fully detailed model.

We acknowledge financial support from MINECO/AEI/FEDER through project SuMaEco (RTI2018-095441-B-C22) and the María de Maeztu
Program for Units of Excellence in R&D (MDM-2017-0711). D.R.-R. also acknowledges the fellowship BES-2016-076264 under FPI program of MINECO, Spain.

[1] E. Meron, *Nonlinear Physics of Ecosystems* (CRC Press, Boca Raton, 2015).
[2] K. Gowda, H. Riecke, and M. Silber, Physical Review E **89**, 022701 (2014).
[3] M. Rietkerk and J. van de Koppel, Trends in Ecology & Evolution **23**, 169 (2008).
[4] S. Getzin, H. Yizhak, B. Bell, T. E. Erickson, A. C. Postle, I. Katra, O. Tzuk, Y. R. Zelnik, K. Wiegand, T. Wiegand, and E. Meron, Proceedings of the National Academy of Sciences **113**, 3551 (2016).
[5] D. Ruiz-Reynés, D. Gomila, T. Sintes, E. Hernández-García, N. Marbà, and C. M. Duarte, Science Advances **3**, e1603262 (2017).
[6] M. C. Cross and P. C. Hohenberg, Rev. Mod. Phys. **65**, 851 (1993).
[7] O. Lejeune and M. Tlidi, Journal of Vegetation Science **10**, 201 (1999).
[8] O. Lejeune, M. Tlidi, and P. Couteron, Phys. Rev. E **66**, 010901(R) (2002).
[9] C. Fernandez-Oto, O. Tzuk, and E. Meron, Phys. Rev. Lett. **122**, 048101 (2019).
[10] P. V. Paulau, D. Gomila, C. Lópe, and E. Hernández-García, Phys. Rev. E **89**, 032724 (2014).
[11] R. D. Routledge, Journal of Applied Probability **27**, 1 (1990).
[12] T. Sintes, N. Marbà, C. M. Duarte, and G. A. Kendrick, Oikos **108**, 165 (2005).
[13] See Supplemental Material at http://…
[14] J. D. Murray, *Mathematical Biology I: an Introduction, Vol. 17 of Interdisciplinary Applied Mathematics* (Springer, 2002).
[15] A. J. Alvarez-Socorro, M. G. Clerc, G. González-Cortés, and M. Wilson, Phys. Rev. E **95**, 010202(R) (2017).
In this Supplemental Material we give details on the derivation, as an approximation to the ABD model, of our simplified model for the spatial distribution of the density $n(\vec{r}, t)$ of clonal plant vegetation:

$$\partial_t n = -\omega n + an^2 - bn^3 + \epsilon \nabla^2 n + \alpha (\nabla^2 n) n + \delta \| \nabla n \|^2 + \beta (\nabla^4 n) n .$$  \hfill (S1)

This will allow us to give a one to one correspondence of the parameters in \(\text{(S1)}\) with biologically relevant parameters.

The ABD model, introduced in \(\text{[S1]}\), models the time evolution of the spatial and angular density of apices $n_a(\vec{r}, \phi, t)$, where $\phi$ is the angle of the growth direction, and of shoots $n_s(\vec{r}, t)$, in a meadow:

$$\partial_t n_a(\vec{r}, \phi, t) = -\omega_d[n_a] n_a(\vec{r}, \phi, t) - \vec{v}(\phi) \cdot \nabla n_a(\vec{r}, \phi, t) + \frac{\omega_b}{2} (n_a(\vec{r}, \phi + \phi_b, t) + n_a(\vec{r}, \phi - \phi_b, t)) \hfill (S2)$$

$$\partial_t n_s(\vec{r}, t) = -\omega_d[n_a] n_s(\vec{r}, t) + \nu \int_0^{2\pi} n_a(\vec{r}, \phi, t) d\phi , \hfill (S3)$$

where the growth-velocity vector is $\vec{v} = \nu (\cos \phi, \sin \phi)$ and $\nabla = (\partial_z, \partial_\theta)$.

The death rate of the plant $\omega_d[n_t(\vec{r}, t)]$ depends on the total density $n_t(\vec{r}, t) = n_a(\vec{r}, t) + N_a(\vec{r}, t)$, where $N_a(\vec{r}, t) = \int_0^{2\pi} n_a(\vec{r}, \phi, t) d\phi$ is the total density of apices growing in all directions, as

$$\omega_d[n_t(\vec{r}, t)] = \omega_d n_s + Bn_t^2 + \int \int K(\vec{r} - \vec{r}')(1 - e^{-\alpha n_a(\vec{r}')}) d\vec{r}' .$$ \hfill (S4)

where the kernel $K$ is the difference of two normalized Gaussians $G$ of different strengths $\kappa$ and $\mu$, and widths $\sigma_\kappa$ and $\sigma_\mu$:

$$K(\vec{r}) = \kappa G(\sigma_\kappa, \vec{r}) - \mu G(\sigma_\mu, \vec{r}) .$$ \hfill (S5)

We first obtain a relationship for the steady homogeneous solutions, $n_s(\vec{r}, t) = n_s^*$ and $n_a(\vec{r}, \phi, t) = n_a^*$, from which $N_a^* = 2\pi n_s^*$. From Eq. \(\text{(S2)}\) we obtain that $(-\omega_d[n_a] + \omega_b) n_a^* = 0$, which, for a non-empty population, implies equality between branching and death rates, $\omega_b = \omega_d[n_a]$. Using this into the steady state of Eq. \(\text{(S3)}\) we get $\nu n_s^* = \omega_d n_s^* = 0$, or $n_a^* = (\nu/\omega_d) N_a^*$. Inserting in $n_t^* = n_a^* + N_a^*$ we find the following relationship between the total-apex density and the total plant density:

$$N_a^* = \frac{\rho \omega_b}{\nu + \rho \omega_b} n_s^* \equiv \eta n_s^* \hfill (S6)$$

Returning to the complete equations \(\text{(S2)-S3})\), and in order to eliminate the dependence on the angle and find a single equation for the total density, one must first write the density of apices as a Fourier series in the angle $\phi \in [0, 2\pi]$:

$$n_a(\vec{r}, \phi, t) = \frac{a_\phi(\vec{r}, t)}{2} + \sum_{m=1}^{\infty} (a_m(\vec{r}, t) \cos (m \phi) + b_m(\vec{r}, t) \sin (m \phi)) . \hfill (S7)$$

Note that $\pi a_0(\vec{r}, t) = N_a(\vec{r}, t)$. Using Eq. \(\text{(S2)}\) one can find the evolution equations for all the amplitudes $a_m$, $b_m$. This gives an infinite hierarchy of coupled equations such that modes $m$ are coupled to modes $m + 1$. From numerical simulations and the linear stability analysis one can check, however, that modes with $m > 1$ are not contributing substantially to the dynamics. Therefore these terms can be neglected. As a second approximation we assume that the relation \(\text{(S6)}\) obtained between the density of apices and the total density in the populated homogeneous steady state is also valid for all $\vec{r}$ and $t$ in any heterogeneous spatial distribution. We have checked the accuracy of this approximation using numerical simulation. The maximum error in a stationary pattern is less than ten per cent of the total density of apices.
With these approximations Eqs. \([S2]\) and \([S3]\) can be simplified to three equations (for \(n_t, a_1, \) and \(b_1\)). Defining \(\vec{a} \equiv (a_1, b_1)\), \(A = \|\vec{a}\|\) and \(\theta = \arctan(b_1/a_1)\), they can be written as

\[
\begin{align*}
\partial_t n_t &= (\omega_b - \omega_d[n_t]) n_t - \frac{\nu \pi}{\eta} \nabla \cdot \vec{a} \\
\partial_t A &= (\omega_b \cos \phi_b - \omega_d[n_t]) A - \frac{\nu \eta}{2 \pi} \nabla n_t \| \cos(\theta - \gamma) \\
\partial_t \theta &= \frac{\nu \eta}{2 \pi} \nabla n_t \| \sin(\theta - \gamma)
\end{align*}
\]

(S8)

(S9)

(S10)

where \(\gamma(\vec{r}, t) = \arctan(\partial_n n_t/\partial_\theta n_t)\) is the angle that the gradient of the total density forms with the \(x\)-axis. From equation \([S10]\), the evolution of the system will drive the angle \(\theta\) to the stable fixed point \(\theta = \gamma + \pi\). This means that, in the long run, the density gradient and the vector \(\vec{a}\) have opposite directions: \(\vec{a} = -C \nabla n_t\), or \(A = C \| \nabla n_t\|\), with \(C\) a positive constant. Introducing this result in the Fourier series \([S7]\), truncated to \(m = 1\), the density of apices takes the following form:

\[
n_a(\vec{r}, \phi, t) = \frac{N_a(\vec{r}, t)}{2\pi} + C \| \nabla n_t(\vec{r}, t)\| \cos(\phi - \gamma(\vec{r}, t) - \pi).
\]

(S11)

In regions where the total density is homogeneous \(\nabla n_t\) is zero and the densities of apices growing in all directions are equal and proportional to the total density of apices \(N_a\). On the other hand, in regions where \(\nabla n_t \neq 0\) there is an angular modulation of the density. For example, considering a circular patch, those apices growing outwards (normal to the vegetation border) have enhanced density while those growing inwards are depleted as it can be seen in Fig. \([S1]\) from numerical simulations. The value of \(C\) is related to the amplitude of the modulation at the borders of the patch, and in general it will be a complicated function of \(n_t\) and its derivatives. Considering only the leading terms of a power expansion of \(C(n_t, \nabla n_t, ...)\) we take:

\[
\vec{a} = \frac{\eta}{\pi} \vec{a}^* = -\frac{\eta}{\pi} (c_0 + c_1 n_t) \nabla n_t,
\]

(S12)

where \(c_0\) and \(c_1\) are constants to be determined. Introducing \([S12]\) in \([S8]\), one obtains a closed equation for the total density \(n_t\):

\[
\partial_t n_t = (\omega_b - \omega_d[n_t]) n_t + \nu (c_0 \nabla^2 n_t + c_1 \| \nabla n_t\|)^2 + c_1 n_t \nabla^2 n_t.
\]

(S13)

This equation is used in the main text, together with an expansion of the integral in \(\omega_d[n_t]\) and identifying \(n\) with the total plant density \(n_t\), to establish the simplified model \([S1]\).

Parameters \(c_0\) and \(c_1\) have not been determined so far. It is possible to determine their value close to the Maxwell point where a front between the populated homogeneous steady state and bare soil is at rest. Assuming such stationary front and introducing Eq. \([S12]\) in \([S9]\), recalling that \(\theta = \gamma + \pi\), one obtains the following expression:

\[
\left\{ (\omega_b \cos \phi_b - \omega_d[n_t])(c_0 + c_1 n_t) + \frac{\nu}{2} \frac{\eta}{\pi} \| \nabla n_t\| \right\} = 0.
\]

(S14)

A priori the front profile is not known, however we know it connects with the populated solution on one side and with the unpopulated solution on the other, so we can write \(n_t = n^{*}_t + \varepsilon e^{\lambda x}\) where \(n^{*}_t\) is zero for the unpopulated solution in one side and takes the value of the stationary homogeneous density \(n^{*}_{t,M}\) for the populated solution at the Maxwell point \((\omega_{d0} = \omega_{d0,M})\). Here \(\lambda\) is the spatial eigenvalue of each solution. Introducing these expressions in Eq. \([S14]\), at the lowest order in \(\varepsilon\) we obtain

\[
c_0 = \frac{\nu}{2(\omega_{d0,M} - \omega_b \cos \phi_b)}
\]

(S15)

\[
c_1 = \frac{\nu}{2 n^{*}_{t,M}} \left( \frac{1}{\omega_b \cos \phi_b - \omega_{d0,M}} - \frac{1}{\omega_b \cos \phi_b - \omega_b} \right)
\]

(S16)

for the unpopulated \((n^{*}_t = 0)\) and populated \((n^{*}_t = n^{*}_{t,M})\) solutions respectively.

---

[S1] D. Ruiz-Reynés, D. Gomila, T. Sintes, E. Hernández-García, N. Marbà, and C. M. Duarte, Science Advances 3, e1603262 (2017).
FIG. S1. Densities (in shoots per square meter, $sh/m^2$) of apices of a circular domain invading the unpopulated solution for the ABD model with parameters appropriate for the seagrass Posidonia oceanica but without nonlocal interactions $[S1]$: $\omega_b = 0.06$ year$^{-1}$, $\omega_{d0} = 0.038$ year$^{-1}$, $\nu = 6.11$ cm/year, $\rho = 2.87$ cm, $\phi_b = 45^\circ$, $b = 1.25$ cm$^3$ year$^{-1}$, $\kappa = 0.048$ year$^{-1}$, $\sigma_\kappa = 0$ cm, $a = 27.38$ cm$^2$, $\sigma_\mu = 0$ cm, $\mu = \omega_{d0}$. The inset in green represents the density of apices growing to the right ($\phi = 0$), and the dashed line indicates the cut shown in the main plot. The blue line represents the mean angular density of apices ($\bar{N}_a = N_a/2\pi$). The dashed (dot-dashed) line shows the density of apices growing to the right (left). The red line shows the amplitude $A$ of the first mode ($m = 1$) in Eq. $[S7]$. 

$N_a(\vec{r}, t) (sh/m^2)$

$n_a(\vec{r}, 0) (sh/m^2)$

$n_a(\vec{r}, \pi) (sh/m^2)$

$A(\vec{r}) (sh/m^2)$