Vegetation pattern formation in semiarid systems without facilitative mechanisms

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[1]   Regular vegetation patterns in semiarid ecosystems are believed to arise from the interplay between long-range competition and facilitation processes acting at smaller distances. We show that, under rather general conditions, long-range competition alone may be enough to shape these patterns. To this end we propose a simple, general model for the dynamics of vegetation, which includes only long-range competition between plants. Competition is introduced through a nonlocal term, where the kernel function quantifies the intensity of the interaction. We recover the full spectrum of spatial structures typical of vegetation models that also account for facilitation in addition to competition. **Citation:** Martínez-García, R., J. M. Calabrese, E. Hernández-García, and C. López (2013), Vegetation pattern formation in semiarid systems without facilitative mechanisms, *Geophys. Res. Lett.*, *40*, 6143–6147, doi:10.1002/2013GL058797.

1.   Introduction

[2]   Regular patterns and spatial organization of vegetation have been observed in many arid and semiarid ecosystems worldwide, covering a diverse range of plant taxa and soil types [*Klausmeier*, 1999; *Rietkerk and van de Koppel*, 2008; *Thompson et al.*, 2009]. A key common ingredient in these systems is that plant growth is severely limited by water availability, and thus plants likely compete strongly for water [*Rietkerk et al.*, 2002]. The study of such patterns is especially interesting because their features may reveal much about the underlying physical and biological processes that generated them in addition to giving information on the characteristics of the ecosystem. It is possible, for instance, to infer their resilience against anthropogenic disturbances or climatic changes that could cause abrupt shifts in the system and lead it to a desert state [*van de Koppel et al.*, 2002; *D'Odorico et al.*, 2006a, 2006b].

[3]   Much research has therefore focused on identifying the mechanisms that can produce spatial patterning in water-limited systems [*Lefever and Lejeune*, 1997; *Klausmeier*, 1999; *Pueyo et al.*, 2008]. An important class of deterministic vegetation models (i.e., those not considering noise associated with random disturbances) that can produce regular patterns are the kernel-based models [*D'Odorico et al.*, 2006a]. These models produce patterns via a symmetry-breaking instability (i.e., a mechanism by which the symmetric-homogeneous state loses stability and a periodic pattern is created) that has its origins in the interplay between short-range facilitation and long-range competition [*D'Odorico et al.*, 2006b; *Rietkerk and van de Koppel*, 2008; *Borgogno et al.*, 2009], with field observations confirming this hypothesis in some landscapes [*Dunkerley*, 2002]. Therefore, it has been long assumed that both of these mechanisms must be present in semiarid systems to account for observed vegetation patterns, although quantifying the importance of each one has proven to be a difficult and contentious task [*Barbier et al.*, 2008; *Veblen*, 2008]. A key role theory that can play here is to identify the minimal requirements for pattern formation to occur. *Rietkerk and van de Koppel* [2008] have speculated that pattern formation, under certain conditions, could occur without short-range facilitation. More recently, a model proposed for mesic savannas included fire and plant-plant competition as key ingredients [*Martínez-García et al.*, 2013]. Fire introduces a positive feedback so that this model considers both competition and facilitation mechanisms. However, the model still produced regular patterns even when the facilitative interaction, fire, was considered at its very short-range (in fact, local) limit. These considerations suggest that local facilitation may be superfluous for pattern formation, and that a deeper exploration of the range of conditions under which pattern formation can occur in the absence of facilitation is therefore warranted.

[4]   Here we study a simple but quite general single-variable model that considers the time evolution of vegetation density in water-limited regions, with only competitive interactions among plants. We show that when only a single broadly applicable condition is met, which competitive interactions have a finite range, the full set of regular patterns formerly attributed to the interaction between short-range facilitation and long-distance competition can be produced in the absence of facilitation.

2.   The Model

[5]   Arid and semiarid ecosystems are typified by patches of vegetation interspersed with bare ground. Water is a very limited resource for which juvenile plants must compete with those that have already established. Logistic-type population models have been used in a wide variety of applications including semiarid systems and savannas [*Calabrese et al.*, 2010], and thus form a reasonable and very general starting point. Specifically, we consider the large-scale

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long-time description of the model in terms of a continuous-time evolution equation for the density of trees, $\rho(\mathbf{x}, t)$. Death occurs at a constant rate α, whereas population growth occurs via a sequence of seed production, dispersal, and seed establishment processes. Seed production occurs at a rate β_0 per plant. For simplicity we consider dispersal to be purely local and then if all seeds would give rise to new plants, the growth rate would be $\beta_0 \rho(\mathbf{x}, t)$. But once a seed lands, it will have to overcome competition in order to establish as a new plant. We consider two different competition mechanisms. First, space availability alone limits density to a maximum value given by ρ_{max}. Thus, $0 \leq \rho(\mathbf{x}, t) \leq \rho_{max}$. The proportion of available space at site $\mathbf{x}$ is $1 - \rho(\mathbf{x}, t)/\rho_{max}$ so that the growth rate given by seed production should be reduced by this factor. Second, once the seed germinates, it has to overcome competition for resources with other plants. This is included in the model by an additional factor $r = r(\tilde{\rho}, \delta)$, $0 \leq r \leq 1$, which is the probability of overcoming competition. This probability decreases with increasing average vegetation density within a neighborhood $\tilde{\rho}$, and the strength of this decrease depends on the competition intensity parameter, δ. Higher values of δ represent more arid lands, and thus stronger competition for water. In the following, we measure density in units so that $\rho_{max} = 1$. Combining all processes, the evolution equation for the density then takes the form

$$\frac{\partial \rho(\mathbf{x}, t)}{\partial t} = \beta_0 r(\tilde{\rho}, \delta) \rho(\mathbf{x}, t)(1 - \rho(\mathbf{x}, t)) - \alpha \rho(\mathbf{x}, t). \quad (1)$$

$\tilde{\rho} = \tilde{\rho}(\mathbf{x}, t)$ is the nonlocal density of vegetation that is obtained by averaging (with a proper weighting function) the density of plants in a neighborhood:

$$\tilde{\rho}(\mathbf{x}, t) = \int G(|\mathbf{x} - \mathbf{x}'|) \rho(\mathbf{x}', t) \mathrm{d}\mathbf{x}', \quad (2)$$

where $G(\mathbf{x})$ is a normalized kernel function, which accounts for the weighted mean vegetation density, and defines the neighborhood of the plant. A Laplacian term could be included in the right-hand side of equation (1) as a way to model long-range seed dispersal, but doing so would not qualitatively change our results, so we have left it out.

[6] In previous kernel-based vegetation models [*Lefever and Lejeune*, 1997; *D'Odorico et al.*, 2006a], the kernel function contained information on the class of interactions present in the system, which were both competitive (inhibitory) and facilitative. On the contrary, we introduce purely competitive interactions through the nonlocal function $r(\tilde{\rho}, \delta)$, where the kernel defines the area of influence of a focal plant and how its influence decays with distance. Competition is included by assuming that the probability of establishment r decreases with increasing vegetation density in the surroundings:

$$\frac{\partial r(\tilde{\rho}, \delta)}{\partial \tilde{\rho}} \leq 0. \quad (3)$$

As δ modulates the strength of the competition, it must be that $r(\tilde{\rho}, \delta = 0) = 1$ and $r(\tilde{\rho}, \delta \to \infty) = 0$. This means that when water is abundant ($\delta = 0$) competition for water is not important ($r = 1$), whereas new plants cannot establish in the limit of extremely arid systems, $\delta \to \infty$.

[7] Note the generality of the vegetation competition model: a spatially nonlocal population growth term of logistic type with rate fulfilling equation (3) and a linear death

term. We note that previous work has shown that competitive interactions entering multiplicatively in the death term [*Birch and Young*, 2006] or additively in the model equation [*Borgogno et al.*, 2009] may also lead to pattern formation. A complete description of our model should specify both the kernel function G and r, but we can go further with the analysis in general terms.

3. Results

[8] The possible homogenous stationary values of the density for equation (1) are (a) no vegetation $\rho = 0$ and (b) the vegetated state $\rho = \rho_0$. The system will show either one or the other depending on the relationship between the birth and death rates, β_0 and α [*Calabrese et al.*, 2010]. The non-trivial homogeneous stationary solution, ρ_0, can be obtained by solving

$$\beta_0 r(\rho_0, \delta)(1 - \rho_0) - \alpha = 0, \quad (4)$$

that has only one solution in the interval $\rho_0 \in [0, 1]$ because of the conditions imposed on the function r in equation (3). We now ask if this stationary solution gives rise to periodic structures via a symmetry-breaking instability as happens in other models that include not only competition but also facilitation mechanisms in the vegetation interactions [*Borgogno et al.*, 2009]. To explore this possibility in our model, we perform a linear stability analysis [*Cross and Hohenberg*, 1993] by adding a small perturbation to the stationary solution, so $\rho(\mathbf{x}, t) = \rho_0 + \epsilon \psi(\mathbf{x}, t)$, with $\epsilon \ll 1$. Technical details of this derivation may be found in Appendix A. We obtain a perturbation growth rate

$$\lambda(\mathbf{k}) = -\alpha \rho_0 \left[\frac{1}{1 - \rho_0} - \frac{r'(\rho_0, \delta)}{r(\rho_0, \delta)} \hat{G}(\mathbf{k}) \right], \quad (5)$$

where $\hat{G}(\mathbf{k})$ is the Fourier transform of the kernel, $\hat{G}(\mathbf{k}) = \int G(\mathbf{x}) \exp(i\mathbf{k} \cdot \mathbf{x}) \mathrm{d}\mathbf{x}$ and $r'(\rho_0, \delta) \equiv \left(\frac{\partial r}{\partial \tilde{\rho}} \right)_{\tilde{\rho} = \rho_0}$.

[9] Patterns appear if the maximum of the growth rate (i.e., of the most unstable mode), $\lambda(k_c)$, is positive, which means that the perturbation grows with time. From equation (5), this is only possible if the Fourier transform of the kernel function, $\hat{G}(\mathbf{k})$, takes negative values, since $r'(\rho_0, \delta) < 0$. This happens, for example, for all stretched exponentials $G(|\mathbf{x}|) \propto \exp(-|\mathbf{x}/R|^p)$ with $p > 2$, where R is a typical interaction length [*Pigolotti et al.*, 2007, 2010]. Kernels satisfying this criterion have broader shoulders and shorter tails (i.e., are more platykurtic) than the Gaussian function, which is obtained for $p = 2$. In reality, any competitive interaction among plants will have finite range because their roots, which mediate the interaction, have finite length. The interaction range R between two plants will be twice the typical root length. Kernels with finite range can, in general, be modeled by considering a truncated function such that $G(|x|) = CF(|x|)\Pi(|x|)$, where C is a normalization constant, $\Pi(x)$ is a unit step function defined as $\Pi(x) = 1$ if $|x| \leq R$ and $\Pi(x) = 0$ if $|x| > R$, and $F(|x|)$ is a function of the distance that models the interactions among the plants. Because of the finite range in the kernel function, the Fourier transform will show oscillations and thus will always take negative values. The functional form of the probability of surviving the competition, $r(\tilde{\rho}, \delta)$, changes only the parameter regime where patterns first develop, but they will appear in the system, regardless of its form, for $r'(\rho_0, \delta)/r(\rho_0, \delta)$ large enough.
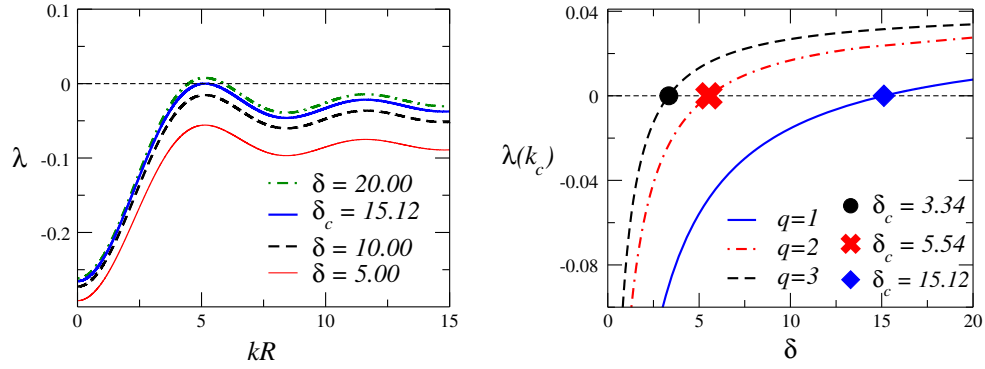
Figure 1. (left) Perturbation growth rate given by equation (9) using a unit-step kernel for different values of δ. From bottom to top $\delta = 5.00$, $\delta = 10.00$, $\delta_c = 15.12$, and $\delta = 20.00$. (right) $\lambda(k_c)$, as a function of δ, using $r(\tilde{\rho}, \delta)$ given by equation (7). From right to left $q = 1$, $q = 2$, and $q = 3$. In both panels, other parameters: $\beta_0 = 1.0$ and $\alpha = 0.5$.

[10] For the rest of our analysis, we will use $F(x) = 1$, so the kernel is given by $G(x) = 1/\pi R^2$ if $|x| \leq R$ and $G(x) = 0$ if $|x| > R$, which defines an interaction area of radius R (that is, roots of typical length $R/2$). Its Fourier transform (in two dimensions) is

$$\hat{G}(\mathbf{k}) = \frac{2J_1(|\mathbf{k}|R)}{|\mathbf{k}|R}, \tag{6}$$

where $J_1(|\mathbf{k}|R)$ is the first-order Bessel function. We will further specify the model by assuming particular forms for the growth rates. Let us consider a probability of surviving competition given by

$$r(\tilde{\rho}, \delta) = \frac{1}{(1 + \delta\tilde{\rho})^q}, \tag{7}$$

with $q > 0$. In the particular case of $q = 1$, the homogeneous density, ρ_0, and the perturbation growth rate, λ, can be obtained analytically. Numerical evaluations must be done if $q \neq 1$. In the following, for simplicity, we consider the case $q = 1$ and only briefly discuss other values. The nontrivial stationary solution, $\rho_0 \neq 0$, can be obtained analytically

$$\rho_0 = \frac{\beta_0 - \alpha}{\beta_0 + \alpha\delta}, \tag{8}$$

where $\beta_0 \geq \alpha$. Equation (8) shows that the homogeneous density of trees in the stationary state decays as $\sim \delta^{-1}$ with increasing competition strength (i.e., large δ). It can be analytically shown that the same dependence of ρ_0 on large δ occurs for any value of q.

[11] From equation (5), the growth rate of perturbations can also be calculated

$$\lambda(\mathbf{k}) = \frac{(\alpha - \beta_0)(\beta_0 + \alpha\delta\hat{G}(\mathbf{k}))}{\beta_0(1 + \delta)} \tag{9}$$

and is shown in Figure 1 (left) for different values of the competition strength. When the growth rate of the most unstable mode (i.e., the maximum of $\lambda(k)$), k_c, becomes positive, patterns emerge in the system [*Borgogno et al.*, 2009]. To obtain the critical value of the competition parameter at the transition to patterns, δ_c, we have to calculate the most unstable mode as the first extreme of $\lambda(\mathbf{k})$ at $k \neq 0$, i.e., the first zero of the derivative of $\hat{G}(\mathbf{k})$. This value only depends on R (the range defining $G(\mathbf{r})$) and it is $k_c = 5.136/R$. Because a periodic pattern of n cells of vegetation is characterized by a wave number $k_c = 2\pi n/L$, where L is the system size, the

typical distance between two maxima of vegetation, $d = L/n$, is given by $d \approx 1.22R$. This value changes depending on the kernel, but in the case of kernels with a finite range (i.e., truncated by a unit step function of radius R) it is always on this order. The critical wave number is determined mainly by the contribution of the unit step function to the Fourier transform, which is always the same. This result is also independent of the other parameters of the system and shows that the nonlocal competition mechanism is responsible for the formation of patterns in the system.

[12] To identify the parameter values for the transition to patterns, we solve $\lambda(\mathbf{k}_c) = 0$ in equation (9), which shows that patterns emerge when competition strength exceeds $\delta_c = -\beta_0/\alpha\hat{G}(\mathbf{k}_c)$, which is positive because $\hat{G}(\mathbf{k}_c) < 0$. Figure 1 (right) shows the growth rate of the most unstable mode as a function of competition strength for different values of the exponent q for fixed values $\beta_0 = 1$ and $\alpha = 0.5$. Note that the critical value of the competition parameter depends on the functional form of r. This dependence could be used to tune the value of q to have a realistic competition strength for the transition to patterns, provided that one has sufficient data.

[13] We can also explain the separation length between clusters of plants using ecological arguments. Consider a
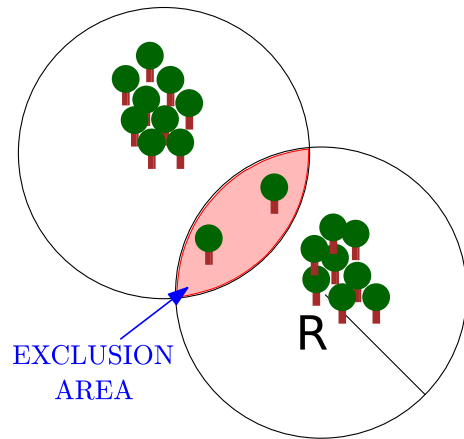

Figure 2. Schematic representation of the formation of exclusion areas, where plants have to compete with two different vegetation patches, whereas plants in each patch compete only with individuals in its own patch.
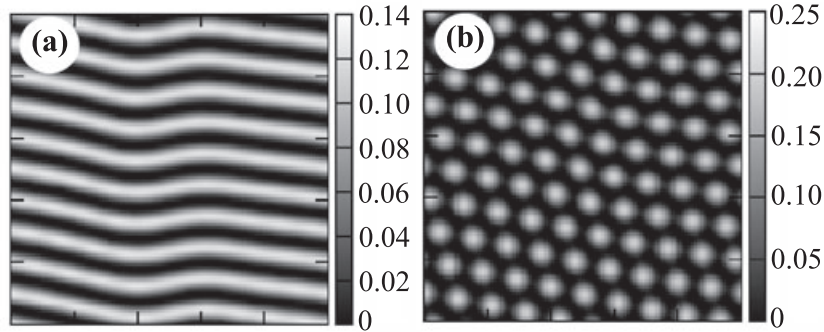
Figure 3. Steady spatial structures shown by the model using the $r(\tilde{\rho}, \delta)$ given by equation (7) with $q = 1$. Darker grey levels represent smaller densities. (a) Vegetation stripes, $\delta = 16.0$. (b) Vegetation spots, $\delta = 17.0$. Other parameters: $\beta_0 = 1.0$ and $\alpha = 0.5$

random and inhomogeneous distribution of plants. Maxima of this distribution identify places with the highest plant density. Imagine that two such maxima occur at a distance larger than R but smaller than $2R$ from each other. There will be no direct interaction between the roots of plants in these different patches, because they are separated by a distance larger than the interaction range R (twice the root extension). But there is an area in between which is simultaneously within the range of both patches. Compared with plants occurring inside a cluster, which only have to compete with plants in their own cluster, those that occur in between clusters will experience stronger competition and will therefore tend to disappear (Figure 2). We call these regions featuring very strong competition *exclusion areas*, consistent with previous studies of competition-driven spatial pattern formation [*Hernández-García and López*, 2004; *Pigolotti et al.*, 2007, 2010]. The disappearance of plants in these exclusion areas in turn reduces competition on the two well-populated patches, so that a positive feedback appears reinforcing the establishment of plants in patches periodically separated with a distance between R and $2R$. We stress again that competition alone is responsible for the symmetry-breaking instability, and no facilitative interactions are needed for pattern formation.

[14] Finally, we have numerically integrated equation (1) in a patch of 10^4 m^2 with periodic boundary conditions and a competition range of $R = 8$ m. Time stepping is done with a Euler algorithm. The results (see Figure 3) exhibit steady striped and spotted vegetation patterns. This spectrum of patterns, typical in pattern formation arising from symmetry breaking, is also observed in models that include a short-range facilitation mechanism in addition to long-range competition [*Lejeune and Tlidi*, 1999; *Rietkerk et al.*, 2002].

[15] We have checked that similar results can be obtained for different growth rates, for example, stretched exponentials

$$r(\tilde{\rho}, \delta) = e^{-\delta \tilde{\rho}^p}. \tag{10}$$

This further confirms our result that competition is the only necessary ingredient for the formation of vegetation patterns in the present framework, and that this does not depend on the functional form of the probability of surviving competition (growth rate) provided it verifies the requirements given by equation (3).

4. Summary and Conclusions

[16] We have studied the formation of spatial structures of vegetation in arid and semiarid landscapes, where water is a limiting resource for which plants must compete. We have considered a simple model with a linear death and a logistic-type growth term in which the growth/birth rate depends on the average vegetation density in the surroundings. Competition enters the model by inhibiting plant growth when local density increases. Arid and semiarid ecosystems correspond to intermediate and high values of the model parameter δ, which modulates competition intensity. Our main result is that patterns appear in the system despite the absence of short-range facilitation mechanisms, and that these patterns exist regardless of the functional form of the nonlocal growth rate, provided that competition is strong enough. Previous studies have included an interaction term that accounts for a short-range positive effects of high local vegetation density, as well as for long-range competition. This combination of mechanisms is justified by arguing that water percolates more readily through the soil in vegetated areas [*D'Odorico et al.*, 2005] (short range), and that plants compete for water resources over greater distances via long lateral roots (long range). In addition, recent studies on mesic savannas [*Martínez-García et al.*, 2013] have shown that in the infinitesimally short limit (i.e., local) of facilitative interactions, tree patterns still appear in the system. In contrast with these studies, in the simple situation that we present competition is the only mechanism responsible for pattern formation, provided that the Fourier transform of the kernel function takes negative values. It is important to note that the simple requirement of just competitive interactions among plants is rather general and does not depend on the way these interactions are introduced in the model. For example, considering a death term that increases with nonlocal density through a competition kernel also gives rise to pattern formation (see *Birch and Young* [2006] for a related study in a different context). In addition, if nonlocal competition enters in the model additively, one may also obtain spatial structures that are determined by the properties of the Fourier transform of the kernel.

[17] The finite interaction range typical of any real competitive interaction implies a truncation of the kernel function, and as we have shown, this greatly expands the range of kernels that can lead to pattern formation. The development

of exclusion zones between maxima of the plant density, where competition is stronger, is the mechanism by which patterns emerge, because competition tends to prevent the growth of vegetation in those regions.

[18] We have demonstrated that our vegetation model recovers the gapped and striped patterns observed in arid and semiarid landscapes when the finite range of the competitive interaction is considered, and thus there is a kernel function whose Fourier transform may have negative values. This is a rather general condition if we consider the finite length of the roots. Therefore, our findings support the notion that, under fairly broad conditions, only long-range competition is required for patterns to occur and suggest that the role of short-range facilitation mechanisms may not be as fundamental to pattern formation as has previously been thought.

Appendix A: Calculation of the Perturbation Growth Rate

[19] We start from equation (1) and perform a complete linear stability analysis to obtain the perturbation growth rate of equation (5). The objective of this technique, broadly used in the study of nonlinear phenomena, is to obtain the temporal evolution of small perturbations to the stationary homogeneous state of the system. Considering small perturbations, the density is $\rho(\mathbf{x}, t) = \rho_0 + \epsilon \psi(\mathbf{x}, t)$, with $\epsilon \ll 1$. Substituting it into the model equation (1), neglecting nonlinear terms in the perturbation, and performing a first-order Taylor expansion of the probability of overcoming competition, r, we obtain an equation for the evolution of the perturbation

$$\frac{\partial \psi(\mathbf{x}, t)}{\partial t} = \beta_0 r(\rho_0, \delta)(1 - 2\rho_0)\psi(\mathbf{x}, t) - \alpha \rho_0 \psi(\mathbf{x}, t) + \beta_0 r'(\rho_0, \delta)\rho_0(1 - \rho_0) \int G(|\mathbf{x} - \mathbf{x}'|)\psi(\mathbf{x}', t)\mathrm{d}\mathbf{x}',$$

(A1)

which is a linear integro-differential equation with constant coefficients that can be solved using the Fourier transform. The transformed equation is

$$\frac{\partial \hat{\psi}(\mathbf{k}, t)}{\partial t} = \beta_0 r(\rho_0, \delta)(1 - 2\rho_0)\hat{\psi}(\mathbf{k}, t) - \alpha \rho_0 \hat{\psi}(\mathbf{k}, t) + \beta_0 r'(\rho_0, \delta)\rho_0(1 - \rho_0)\hat{G}(\mathbf{k})\hat{\psi}(\mathbf{k}, t),$$

(A2)

where $\hat{\psi}(\mathbf{k}, t) = \int e^{i\mathbf{k}\cdot\mathbf{x}}\psi(\mathbf{x}, t)\mathrm{d}\mathbf{x}$ is the Fourier transform of the perturbation, and equivalently, $\hat{G}(k)$ is the Fourier transform of the kernel.

[20] Finally, equation (A2) is solved by $\hat{\psi}(\mathbf{k}, t) \propto \exp(\lambda(\mathbf{k})t)$, with the following expression for the linear growth rate of the perturbation

$$\lambda(\mathbf{k}) = \beta_0 \left[r(\rho_0, \delta)(1 - 2\rho_0) + (1 - \rho_0)\rho_0 r'(\rho_0, \delta)\hat{G}(\mathbf{k}) \right] - \alpha. \quad \text{(A3)}$$

[21] Using the equation for the stationary solution, equation (4), and equation (3) for the probability of overcoming competition, we arrive at the expression of equation (5).

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