



Non-linear and non-local plant–plant interactions in arid climate: Allometry, criticality and desertification

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ABSTRACT

We present a model that considers the non-linear and non-local facilitative and competitive interactions in arid and semiarid climates. These two botanical processes are interconnected and operate at different spatial scales. Seed dispersal is modeled as a diffusion process. We consider landscapes populated by a dominant species to be isotropic and homogeneous environmental conditions. We included the allometric factor in the modeling, considering the age classes. We show that allometry tends to move the critical and tipping points towards a low level of aridity. This alteration of aridity conditions can prevent desertification and thus avoid vegetation collapse. Unlike other interaction redistribution models, we show that even in the absence of allometry, critical and tipping points have a finite biomass. Consequently, a branch of low-biomass density is stabilized. Finally, we show that the allometric factor reduces the range of symmetry-breaking instability and favors the formation of homogeneous cover rather than vegetation patterns.

1. Introduction

Desertification and the loss of fertile soils are central phenomena affecting ecology and the economy. By understanding how plants develop, adapt, and survive in arid and semi-arid ecosystems, Scientists can better contribute to developing future strategies to preserve or utilize limited soil resources. These ecosystems' landscapes are characterized by densely populated regions that alternate with sparsely populated ones. This spatial distribution of vegetation, generally referred to as a “vegetation pattern”, is an endogenous phenomenon that prevails in many arid landscapes and is not exclusive to certain plants or soils. It is now widely recognized in the field of plant ecology that instability through symmetry-breaking can give rise to large-scale self-organized periodic vegetation patterns [1–5]. The self-organization phenomenon is universal and appears in many far-from-equilibrium systems, such as chemistry, fluids, nonlinear optics, and laser physics [6–8]. Vegetation patterns could be aperiodic, such as localized patches that can be isolated and randomly distributed in space, creating a well-defined spatial pattern [9–12] or labyrinth [13]. Spatial periodic and localized patterns are a well-documented issue in various areas of the natural sciences, ranging from population dynamics to chemistry and optics [14–16].

Unlike physicochemical systems, for which mathematical models are derived from conservation laws. Biological and ecological systems

suffer from the absence of physical first principles, which makes mathematical modeling complex. Two main theoretical approaches have been proposed in the literature. The first approach is based on non-local interactions associated with facilitation and competition exerted by the plants themselves, via their above-ground and below-ground parts, and by seed dispersion [1,2] (see an overview, [17]). The second approach is based on reaction–diffusion models that explicitly incorporate water transport [18–23]. The range of these nonlocal interactions between plants is generally a few tens of centimeters for grasses and a few meters for shrubs and trees, whereas the vegetation pattern wavelength measured can reach several tens of meters. When the degree of aridity increases, i.e., when conditions for plant development become more unfavorable, the average density of vegetation decreases, while the wavelength of the pattern increases. Arid ecosystems show a direct correlation between pattern wavelength and degree of adversity [1].

Populations of plants are made up of individuals of various sizes that correspond to various age groups. It is essential to consider allometry in the mathematical modeling of population vegetation. The relationship between the elements of a plant, such as leaves, stems and roots, and the way they develop proportionally to each other as the plant matures, is called the allometric factor. A simple approach to this problem is to link the different plant sizes to their individual biomass [24–29].

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The combined influence of facilitative and competitive interactions on the self-organization of ecological communities is an active area of research [30–33]. The first modeling approach based on the interaction redistribution model considers facilitation to be nonlinear and non-local, while competition affecting carrying capacity is considered to be non-local but linear [1]. Later, a new strategy was proposed, considering that facilitation is non-local but linear and that competition affects the mortality parameter of neighboring plants [26]. Another difference is that in the [1] model, seed dispersal affects the growth of the logistic term, whereas in the [26] model, seed dispersal is modeled as an additive contribution to biomass growth. Both types of interaction appear to act simultaneously, and the balance between them depends mainly on the level of adversity of environmental conditions [33–36]. They are, therefore, interconnected; if facilitation is non-linear, competition should be too.

The aim of this article is to propose a model based on facilitation and competition, assuming that these two non-local processes are nonlinear. With these modifications, we show that even in the absence of the allometric factor, the critical point associated with the second-order critical transition that marks the onset of a hysteresis loop occurs for finite biomass and not for zero biomass. Consequently, a low-density vegetation branch is stabilized even without allometry. More importantly, we show that allometry can stabilize the arid ecosystem by shifting the critical point associated with bistability to a low level of adversity. Finally, we show that allometry can stabilize the symmetry-breaking instability responsible for the emergence of vegetation patterns.

2. Interaction redistribution model and crown-root allometry

2.1. Interaction redistribution model

The absence of physical first principles for biological systems in general and ecological systems in particular makes mathematical modeling difficult. Several continuous models in time and space have been proposed in the literature. They can be classified into two types: interaction redistribution nonlocal models [1,26] and reaction–diffusion models [18–23]. In what follows, we adopt the approach based on interaction redistribution nonlocal models [1,26]. These models consider a landscape populated by a dominant species, neglecting genetic variation between the plant species present in a landscape and ignoring phenotypic differences. We modify the non-local model [26], by considering that the two facilitative and competitive interactions are both non-linear and non-local functions of the biomass. The kinetic equation describing the evolution of the biomass density $u(\mathbf{r}, t)$ at time t and point $\mathbf{r} = (x, y)$ is

$$\partial_t u = u(1 - u)m_f - \mu u m_c + d\nabla^2 u \quad (1)$$

The functions m_f and m_c represent the facilitation and competition feedback mechanisms, respectively. The parameter μ models the adversity and we call it the aridity parameter, which is mainly attributed to unfavorable environmental conditions; note that the linear growth rate of the biomass density in a given plot of land is $m_f - \mu m_c$. The seed dispersion is considered as a diffusive process describing the large-scale behavior of a general non-local dispersion [26], d is a diffusion coefficient, and $\nabla^2 = \partial_{xx} + \partial_{yy}$ is the Laplace operator acting in the plane (x, y) . In the absence of non-local interactions between plants, i.e., $m_f = m_c = 1$, we recover the well-known paradigmatic model for the study of population dynamics, namely the Fisher–Kolmogorov–Petrovsky–Piskunov (FKPP) equation [28] as long as $\mu < 1$.

The explicit forms of the non-local functions $m_{f,c}$ are

$$m_{f,c} = \exp \left[\int \phi_{f,c}(|\mathbf{r}'|) u(\mathbf{r}' + \mathbf{r}, t) [1 + \omega_{f,c} u(\mathbf{r}' + \mathbf{r}, t)] d\mathbf{r}' \right], \quad (2)$$

where $u = u(\mathbf{r}, t)$ represents the biomass density (units: kg m⁻²) at time t . $d\mathbf{r}' = dx'dy'$ is the infinitesimal surface element. The $m_{f,c}$ are state functions that describe how the biomass distribution around the plot at position \mathbf{r} affects the growth and death rates of that plot. The facilitative part m_f involves mainly the effects generated by the aerial part of the plant (crown); several aspects come into play: the accumulation of nutrients in the vicinity of the plants, the provision of shade, and the water balance in the soil [35–37]. Competitive interactions m_c operate mainly at the level of the root system (rhizosphere) for the absorption of water and nutrients [34], and more generally, they encompass all interactions affecting negatively the biomass growth [1]. $\omega_{f,c}$ measure the first nonlinear correction to non-local facilitation and competition effects. For the sake of simplicity, we assume that the kernels or influence functions $\phi_{f,c}$ are Gaussian functions of $\mathbf{r} = (x, y)$

$$\phi_{f,c}(\mathbf{r}) = n_{f,c} \exp \left(-\frac{|\mathbf{r}|^2}{l_{f,c}^2} \right), \quad (3)$$

where $n_{f,c}$ are the normalization constants associated with facilitative and competitive interactions, respectively.

The modeling approach used here is based on two opposite feedbacks: positive feedback associated with the facilitating interaction, which operates at the level of plant size l_f , tends to increase the total biomass (activator) of the surrounding plants. On the other hand, the negative feedback associated with the competitive interaction between plants operates at the level of the size of the plant's roots and tends to inhibit the growth of the biomass (inhibitor) of surrounding plants up to a distance l_c . Field measurements of different plants have validated this modeling approach: *Combretum micranthum* [27], *Festuca orthophylla* [38] and alfa or *Stipa tenacissima* L. [39,40].

Let us now complete the Eq. (1) model taking into account allometry, which considers age-class effects in monospecific subpopulations. The allometric factor helps us to understand how the size of one part of the plant changes in relation to another as the plant grows. In general, this factor expresses the relationship between the different parts of a plant, such as leaves, stems, and roots, and how they develop in proportion to each other as the plant grows; for example, it could describe how the plant crown depends on the mass of the plant. An individual plant exerts facilitating and competitive influences on neighboring plants. As they grow, the radius of the plant root and crown increases. Compared with the size of their crown, plants spread their roots over a considerable surface area to absorb water and nutrients and survive harsh climatic conditions. A young plant covers a relatively small territory compared to a mature plant. To account for the distance dependence of interaction lengths between different growth stages, the effective interaction ranges associated with facilitation and competition will depend on biomass density. The most common allometric relationships for plant growth [24–29] are as follows.

$$L_{f,c}(\mathbf{r}, t) = c_{f,c} \left(\frac{u(\mathbf{r}, t)}{u_s} \right)^p, \quad (4)$$

where p is the allometric factor and c_{0f} and c_{0c} , respectively, are the lengths of the competitive and facilitative interactions brought on by the crown and root sizes of mature plants with a biomass density u_s .

2.2. Criticality and tipping points

To determine the critical point above which the system exhibits a bistable behavior between homogeneous covers, we first determine the homogeneous steady states, u_s , solutions of Eq. (1). By taking into account nonlocal interactions Eqs. (2), the Kernels Eqs. (3), and the allometric relationships for plant growth Eq. (4), we obtain the homogeneous steady states: the trivial solution $u_0 = 0$ presents a bare state, a state entirely devoid of vegetation, and obviously exists for all parameter values. The other uniform branches of the solutions representing uniform plant cover obey the equation

$$\mu = (1 - u_s) \exp \left[(\omega_f - \omega_c) u_s^{2(p+1)} \right] \quad (5)$$

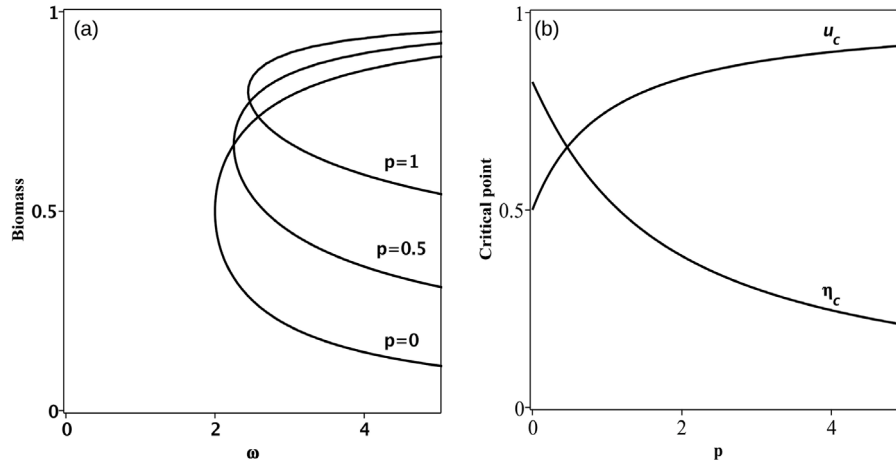


Fig. 1. Criticality and tipping points. (a) Coordinate the tipping points according to the effective cooperativity $\omega = \omega_f - \omega_c$. (b) Coordinates of the critical point as a function of the allometric factor corresponding to the plot of u_c and η_c expressions given by Eqs. (7).

For $\omega_f = \omega_c$, the homogeneous steady states are determined by the straight line $u_s = 1 - \mu$. When $0 < \mu < 1$, the plant population becomes monotonous and decreases until $u = 0$ at the point $\mu = 1$. The logistic term $(1 - u_s)$ in Eq. (5) guarantees that the physically accepted biomass lies within the interval $[0, 1]$.

At the onset of bistability, there is a critical point where biomass as a function of aridity has an infinite slope. The vicinity of the critical point is characterized by a critical slowing down. The coordinates of the critical point must satisfy two conditions: $\partial\mu/\partial u_s = 0$ and $\partial^2\mu/\partial u_s^2 = 0$. The first condition leads to

$$2(p+1)(\omega_f - \omega_c)(1 - u_{s\pm})u_{s\pm}^{2p+1} = 1 \quad (6)$$

This condition determines the coordinates of the switching or tipping points. There are no simple analytical solutions of Eq. (6) for $p > 0$. The equilibrium biomass plot as a function of the allometric factor is shown in Fig. 1. This figure indicates that for any $p > 0$, there exist always two tipping points above the critical point. This is in agreement with previously published interaction-redistribution models [26–28]. However, for $p = 0$, the coordinate of the tipping point solutions of Eq. (6) are $2u_{s\pm} = 1 \pm \sqrt{\omega - 2}$, where $\omega = \omega_f - \omega_c$ is referred to as the effective cooperativity. There exists a wide region of parameters where two tipping points exist, namely when $\omega > 2$, as shown in Fig. 1. When $\omega < 2$, then $x_{s\pm} < 0$ becomes unphysical since the density is a positively defined quantity. In this case, there is no tipping point, and the ecosystem operates in a monostable regime.

The second condition $\partial^2\mu/\partial u_s^2 = 0$ together with Eq. (6) allows us to determine the coordinates of the critical point associated with bistability for any p :

$$u_c = \frac{2p+1}{2(p+1)}, \quad \omega_c = \frac{1}{u_c^{2p+1}}, \quad \mu_c = \frac{\exp(u_c)}{2(p+1)}. \quad (7)$$

The allometric factor controls the coordinates of the critical point associated with the second-order critical transition, which marks the onset of a hysteresis loop. Plots of the critical expressions associated with the biomass u_c and the corresponding aridity parameter μ_c as a function of the allometric factor p are shown in Fig. 1. This figure indicates that as the allometric factor increases, the critical aridity decreases while the critical value of biomass increases.

This result is essential for the vegetation model approach Eq. (1). An important aspect is that the critical point is no longer on the aridity axis, as the critical point $u_c = 1/2$ for $p = 0$ is finite $u_c \neq 0$. This contrasts strongly with previous work based on interaction-redistribution models [26–28]. In other words, even in the ideal case of identical plants with no age variation ($p = 0$), the model Eq. (1) predicts the appearance of a critical point at finite biomass density, as shown in Fig. 1(a). If the critical point lies on the x -axis at zero biomass,

then, facilitation and competition interactions become negligible at that point, and edaphic factors should not influence the space-time dynamics of ecosystems operating near a critical condition. Fig. 1(b) shows the critical aridity parameter as a function of the allometric factor. As the allometric factor p increases, the critical biomass point increases, and the corresponding critical aridity parameter decreases.

After characterizing the criticality, we examine how the allometry affects homogeneous covers. The homogeneous steady state solutions Eq. (5) are plotted in Fig. 2 for different values of the allometric factor. The aridity parameter μ controls the stability between the uniform trivial solution u_s and the spatially homogeneous (non-trivial) states, or between two uniform homogeneous states, u_0 is unstable for $0 \leq \mu < 1$, and stable for $\mu \geq 1$. It can be seen that all the curves cross the bifurcation point ($u_0 = 0, \mu = 1$), which is the point where the solution u_0 changes the stability.

Note that even in the absence of the allometry $p = 0$, a branch of vegetation at low density is stabilized, as shown by the red curve in Fig. 2(a). When the allometric factor is increased, the critical point and the tipping points are shifted towards a regime of low aridity conditions as shown in Fig. 2(b,c). In this case, the transition from high density to low becomes less abrupt as the allometric factor increases, as shown in Fig. 2(c). Taking age classes into account may, therefore, show that vegetation is more robust than previously thought against collapse [41–43].

2.3. Symmetry-breaking instability and vegetation patterns

We are now investigating the conditions under which spatially uniform vegetation distributions become unstable under inhomogeneous perturbations. For this purpose, we linearized Eq. (1) around the high and small density homogeneous steady states u_{s3} and we consider small deviations from these states in the form of $\exp(\lambda_q t + i\mathbf{q} \cdot \mathbf{r})$ with $\mathbf{r} = (x, y)$ and the wavevector $\mathbf{q} = (q_x, q_y)$. The dispersion relation reads

$$\lambda_q = e^{(1+\omega_f u_s) u_s^{2p+1}} \left[(1 - 2u_s) + u_s^{p+1} (1 - u_s) (1 + 2\omega_f u_s) e^{-\frac{q^2 u_s^{2p}}{4}} \right] - \mu e^{(1+\omega_c u_s) u_s^{2p+1}} \left[1 + u_s^{p+1} (1 + 2\omega_c u_s) e^{-\frac{q^2 u_s^{2p}}{4}} \right] - dq^2. \quad (8)$$

This dispersion relation determines the critical point associated with symmetry-breaking instability provided that $\lambda_q(q_T) = 0$ and $\partial_q \lambda_q(q_T) = 0$. In the Fourier space, unstable modes are characterized by a finite range of wave numbers excluding the origin. This range must exclude all long wavelengths (short wavenumbers) corresponding to quasi-uniform distributions, and very short wavelengths (long wavenumbers)

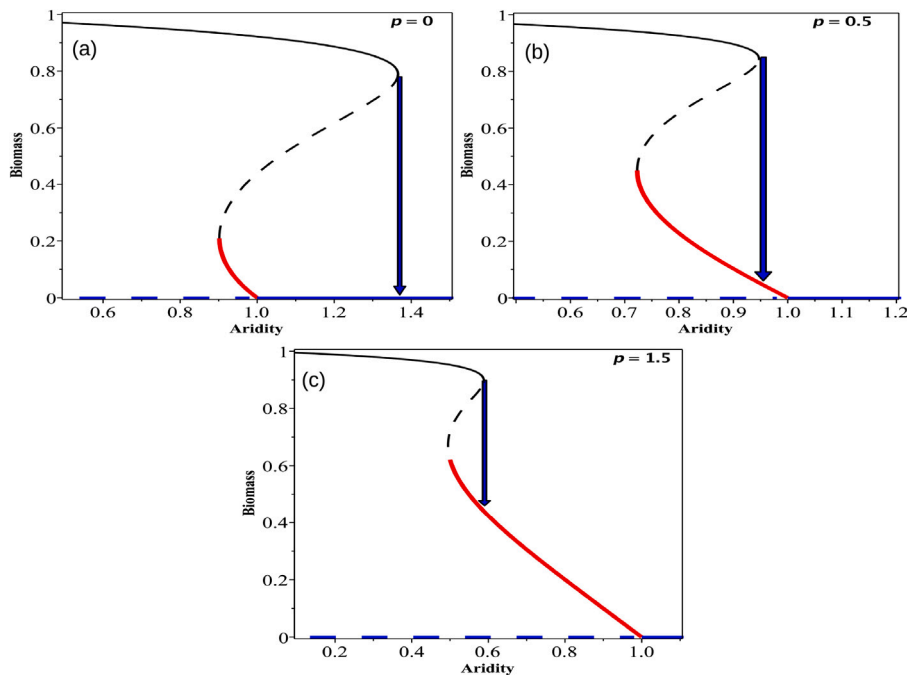


Fig. 2. Homogeneous steady states as a function of the aridity parameter for different values of the allometric factor p . The red curve corresponds to the branch of low-biomass density that exists even in the absence of an allometric factor ($p = 0$). The bare state u_0 corresponding to zero biomass density is indicated in blue. Solid lines indicate stable branches and dotted lines indicate unstable branches. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

corresponding to inhomogeneities smaller than the interaction ranges. They ensure that fluctuations of arbitrarily small and large wavelengths are damped. At the threshold of the symmetry breaking instability, the eigenvalue $\lambda_q(q_T) = 0$ and its first derivative must vanish for a finite intrinsic wavelength $\Lambda_T = 2\pi/q_T$. When neglecting the seed dispersion ($d = 0$), and by replacing μ by $(1 - u_s) \exp[\omega u_s^{2(p+1)}]$, the most unstable wavenumber q_T is

$$q_T^2 = \frac{4 \log \left[\left(\frac{l_f}{l_c} \right)^2 (1 + 2\omega u_T) \right]}{(l_f^2 - l_c^2) u_T^{2p}} \quad (9)$$

The corresponding wavelength is

$$\Lambda_T = \frac{2\pi}{q_T} = \pi u_T^p \sqrt{\frac{l_f^2 - l_c^2}{\log \left[\left(\frac{l_f}{l_c} \right)^2 (1 + 2\omega u_T) \right]}} \quad (10)$$

This Turing-type symmetry-breaking instability generates vegetation patterns characterized by the critical intrinsic wavelength Λ_T , which is determined by the lengths of the facilitative and competitive interactions, the effective cooperativity, and the allometric factor. It is an intrinsic property of the system that is determined solely by the dynamical parameters rather than by geometrical factors and/or boundary conditions. The threshold associated with spatial instability is a solution of

$$u_T^p (1 - u_T) \left[(1 + 2\omega u_T) \exp \left[-\frac{q_T^2 l_f^2 u_T^{2p}}{4} \right] - \exp \left[-\frac{q_T^2 l_c^2 u_T^{2p}}{4} \right] \right] = 1. \quad (11)$$

Let us first consider the symmetrical case where the cooperativities associated with facilitation and competition are equal, i.e., $\omega_f = \omega_c$. In this case, the effective cooperativity is $\omega = 0$, and the homogeneous equilibrium states are u_0 and $\mu = (1 - u_s)$. Allometry does not affect homogeneous cover, and biomass decreases monotonically until $\mu = 1$, where the state of uniform cover coincides with the state of zero biomass u_0 . For $\mu > 1$, only the bare state u_0 becomes linearly stable. Taking spatial fluctuations into account, the linear stability analysis shows that the homogeneous cover becomes unstable in a finite range of aridity level ($\mu_{T1} < \mu < \mu_{T2}$), as shown in Fig. 3.

At both thresholds associated with the symmetry-breaking instability, the most unstable wavelength is the same. In the asymmetrical case where the nonlinearity associated with facilitation is different from that of competition, i.e., $\omega_f \neq \omega_c$, the wavelength at the two symmetry-breaking instabilities is not the same $\Lambda_{T1} \neq \Lambda_{T2}$ as shown in Fig. 4. The range of symmetry-breaking instability indicated by the red dashed lines decreases with the allometric factor p , as shown in Fig. 4(b). The balloons of unstable spatial modes shown in Fig. 4(a) shrink as the allometric factor increases. We, therefore deduce, that taking into account the effects of age classes predicts a more robust homogeneous cover.

3. Conclusions

We have proposed a mathematical model in which facilitation and competition are non-local and non-linear functions since the two processes are interconnected. Seed dispersal is considered like an additive contribution to biomass growth in the form of a diffusive process describing the large-scale behavior of non-local dispersion [26]. Unlike the previous model where competition affects carrying capacity [1], we have considered that competition affects the aridity parameter as in [26], but as a non-linear function of the biomass density. We neglected genetic variation between plant species and considered landscapes populated by a dominant species. Isotropic and homogeneous environmental conditions are assumed. We have included the allometric factor, which takes age classes into account. With these modifications, we have shown that the spatiotemporal behavior of vegetation patterns in arid and semi-arid landscapes is strongly affected by nonlinear plant-plant interactions. The model Eq. (1) tends to show that:

- A non vanishing allometric factor tends to shift the critical point associated with the second-order critical transition to a low aridity parameter and can prevent vegetation collapse in arid ecosystems.
- The critical point associated with bistability possesses a finite biomass, even when neglecting the allometry effects. As a result, the low-density homogeneous cover branch exists. This contrasts

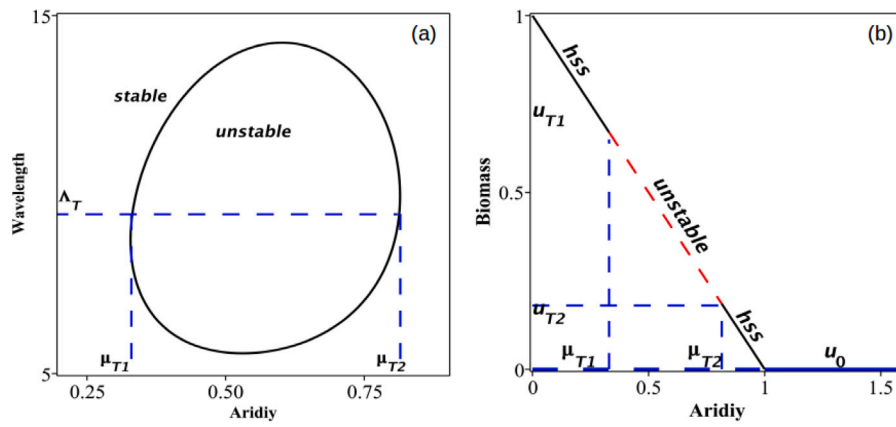


Fig. 3. Linear stability of the homogeneous steady states (hss) in the symmetric case where $\omega_f = \omega_c$. (a) The marginal stability curve showing the stable and unstable homogeneous cover in the plane wavelength as a function of biomass density. (b) homogeneous biomass coverage as a function of the aridity parameter showing a finite unstable portion indicated by a dotted red line. The bare state u_0 corresponding to zero biomass density is indicated in blue. Parameters are $l_f = 1, l_c = 5, d = 0.1, \omega_f = \omega_c = 1.5$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

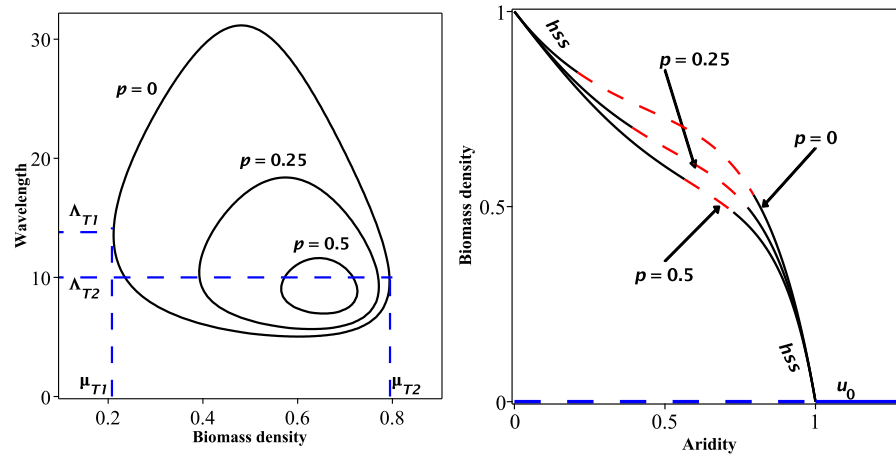


Fig. 4. Linear stability of homogeneous steady states (hss) in the asymmetric case where $\omega_f \neq \omega_c$. (a) The marginal stability curves show the stable and unstable homogeneous cover in the plane wavelength as a function of biomass density for different values of the allometric factor p . (b) homogeneous covers as a function of aridity parameter showing a finite unstable portion indicated by dotted red lines. The bare state u_0 corresponding to zero biomass density is indicated in blue. Parameters are $l_f = 1, l_c = 5, d = 0.5, \omega_f = 3, \omega_c = 1.5$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

with previous non-local models of interaction redistribution [26, 27].

- The allometric factor stabilizes the symmetry-breaking instability and reduces the instability range.

We have limited our study to a linear regime; in the near future, we plan to present (i) Non-linear analysis by drawing all branches of the periodic or localized vegetation patterns solutions of Eq. (1). (ii) Numerical simulations will be carried out using continuation algorithms to characterize vegetation patterns and compare them with theoretical results. (iii) Realistic model parameterization based on available experimental data.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Compliance with ethics requirements

This article does not contain any studies with human or animal subjects.

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