Species coexistence in vegetation patterns facilitated by the interplay of spatial self-organisation and intraspecific competition

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Abstract

The exploration of mechanisms that enable species coexistence under competition for a sole limiting resource is widespread across ecology. Two examples of such facilitative processes are intraspecific competition and spatial self-organisation. A classical example of an ecosystem governed by the latter is dryland vegetation patterns. Previous theoretical investigations have explained coexistence in patterned vegetation by making strong assumptions on the differences between species (e.g. contrasting dispersal behaviours or different functional responses to soil moisture). In this paper, I show that the interplay between the competitive effects of intraspecific competition and the facilitative nature of self-organisation forms a coexistence mechanism that does not rely on species-specific assumptions. I use an eco-hydrological reaction-advection-diffusion system that captures the interactions of two plant species with an explicitly modelled resource to show that coexistence relies on a balance between species' colonisation abilities and their local competitiveness, provided intraspecific competition is sufficiently strong. Crucially, the requirements on species' self-limitation for coexistence to occur differ on opposite ends of the precipitation (resource input) spectrum. For low resource levels, coexistence is facilitated by strong intraspecific dynamics of the species superior in its colonisation abilities, but for larger volumes of resource input, strong intraspecific competition of the locally superior species enables coexistence. Results presented in this paper also capture the empirically observed spatial species distribution within bands of vegetation and propose differences in plants' dispersal behaviour as its cause.

Keywords: banded vegetation; semi-arid ecosystems; reaction-advection-diffusion model; mathematical modelling; competition and coexistence; pattern formation.

1 Introduction

A classical result of coexistence theory states that species coexistence in ecological and biological systems cannot occur if species compete for a single limiting resource; this is often referred to as Tilman's R^* rule [41]. For any given species, R^* denotes the smallest resource level at which that species is able to persist. The species that can depress the resource to its lowest level (i.e. has the smallest R^* value) is able to monopolise the limiting resource and outcompete all other species, according to Tilman's R^* rule. Nevertheless, it is evident that this principle is an oversimplification and is insufficient to fully describe the outcome of competition as species coexistence occurs in many ecosystems despite competition for a single resource. Hence, this suggests that other processes prevent resource monopolisation by one species and thus enable coexistence [31].

One such mechanism that has been singled out as a common facilitator of species coexistence is intraspecific competition (e.g. [7, 31]). The inclusion of self-limitation due to negative density-dependent effects is an integral part of investigating coexistence through Lotka-Volterra competition models (e.g. [7]). More recently, such dynamics have also been added to Rosenzweig-MacArthur-type models in which interactions of consumer species with a sole limiting resource are explicitly modelled [31]. The impact of self-limitation on consumer competition dynamics is that, if sufficiently strong, it limits the abundance of each species so that no single species is able to monopolise the resource in the sense of Tilman's R^* rule. This allows the limiting resource to be shared among two or more species and thus enables coexistence.

A different mechanism that has been found to promote species coexistence is spatial self-organisation. As opposed to local intraspecific competition, self-organisation principles are characterised by positive density-dependent effects on short spatial scales in combination with long-range competition for resources [37]. The formation of spatial patterns of consumer species due to such scale-dependent feedbacks can create spatial heterogeneities in environmental conditions (e.g. resource availability) in otherwise homogeneous environments [10, 21]. Such heterogeneous landscapes lead to spatial separation of competitive and facilitative interactions between different consumer species, which creates a balance that enables species coexistence [10]. This mechanism is not unique to self-organised consumer communities, but has also been attributed to enrich species richness in other ecological systems where the underlying spatial heterogeneities are not induced by the species themselves [46].

A classical example of a self-organised ecosystem in which species coexistence occurs is dryland vegetation patterns [38, 45]. This state is characterised by alternating patches of high biomass and areas of bare soil and forms an interface along the precipitation gradient between full deserts and arid savannas, where plants form a continuous biomass cover. The self-organisation of plants into mosaics of vegetated patches and regions of bare soil is induced by a positive feedback between local vegetation growth and water redistribution towards areas of high biomass [22, 37]. This is caused, for example, by the formation of biogenic soil crusts on bare soil which inhibit water infiltration and induce overland water flow, or by the combination of laterally extended root systems with a soil type that facilitates fast water diffusion and hence causes resource redistribution below-ground [32]. As a consequence, plants facilitate their growth on short spatial scales, but compete for water across long spatial scales. This results in a scale-dependent feedback due to which self-organisation occurs.

Vegetation patterns occur in a range of different shapes, including regular stripes parallel to contours of gentle slopes [45]. Long-term field studies indicate that such vegetation stripes gradually move upslope over a generational timescale [13]. This uphill migration occurs because the water run-off from low-permeability interband regions aggregates near the top edges of existing stripes, creating a heterogeneous resource landscape within vegetation bands that causes upslope expansion and downslope contraction [11]. Transects through vegetation bands typically feature a group of species dominating the upslope edges of each band (typically annual grasses), and a group of plant types mostly confined to the centre and downslope regions of the stripes (typically perennial grasses, shrubs and trees) [38]. The former are often regarded as the driving force of the bands' uphill migration and are therefore commonly referred to as *coloniser species*.

In this paper, I use banded vegetation as a case study to unite the two strands of coexistence theory discussed above (intraspecific competition and spatial self-organisation) in a theoretical framework. Dryland vegetation represents an ideal candidate for such an approach, since its ecosystem dynamics have been the subject of countless mathematical modelling studies over the last three decades [5, 29, 48]. The existing modelling frameworks provide a good foundation for further theoretical investigations of the ecosystem dynamics and in particular species coexistence.

This paper is not the first mathematical model to investigate species coexistence in dryland vegetation patterns. Baudena and Rietkerk [3] have shown that coexistence can be induced by

facilitation of a species unable to form spatial patterns by a self-organising species. Similarly, Ursino and Callegaro [6, 44] have included the adaptation of plant species to different soil moisture niches in a theoretical framework to successfully capture coexistence. However, a shortfall of both these approaches is that they rely on the assumption that the plant species fundamentally differ in their interaction with the environment and are thus not applicable to a general setting.

In a previous paper, I have shown that self-organisation is a sufficient mechanism to enable coexistence in arid savannas, where no segregation between vegetated and bare patches occurs [21]. Crucially however, I have also argued that other processes must be involved in the facilitation of coexistence in vegetation patterns if species do not differ in their functional responses to the environment. This hypothesis is based on a description of the resource-consumer dynamics of two species (or two groups of species) whose difference from each other only manifests itself quantitatively through different parameter estimates of basic properties (e.g. growth and death rates) but not qualitatively through different functional responses to the environment. In this setting, coexistence occurs if one (group of) species is superior in its colonisation abilities but is outcompeted locally by a second (group of) species. Consequently, the former are referred to as *colonisers* and the later as the *locally superior species*, a terminology that will be carried over to this paper. This mechanism only gives insights into the coexistence of both species groups. Coexistence within those groups may occur due to other facilitative processes that are independent of spatial self-organisation principles. For brevity, I will refer to such species groups as single species in the remainder of the paper.

This previous study functions as the baseline case of the unification of spatial self-organisation and intraspecific competition dynamics in coexistence theory of vegetation patterns presented in this paper. I argue that the inclusion of self-limitation is crucial to capture coexistence of a coloniser species with a locally superior species in vegetation patterns that occur under severe water scarcity. Moreover, the importance of spatial self-organisation in the coexistence of dryland vegetation is reinforced by the result that strong intraspecific competition of different species facilitates coexistence at different ends of the precipitation (resource input) spectrum. Finally, this unified approach is the first to capture the spatial species distribution within vegetation bands, confirming verbal arguments that the patterns' uphill migration is indeed driven by the coloniser species [38].

This paper focusses on the ecological implications obtained through a comprehensive model analysis of the system presented in Sec. 2 below. As such, only stable model outcomes are considered. Nevertheless, the mathematical model also admits unstable solutions, an analysis of which aids greatly to the understanding of the bifurcations in the system. A comprehensive bifurcation analysis aimed at a more mathematics-oriented readership and an analysis of the impact of intraspecific competition dynamics in single-species ecosystems are presented in a separate publication [17].

2 Model & Methods

A well-established mathematical model describing the ecohydrological dynamics of vegetation stripes on sloped terrain is the single-species reaction-advection-diffusion system by Klausmeier [24]. This phenomenological model stands out due to its deliberate simplicity and thus provides a rich framework for model extensions (e.g. [4, 9, 16, 18, 19, 28, 40]). One recent extension has introduced a second plant species to the system, based on the assumption that plant species only differ from each other quantitatively in their basic parameters but not qualitatively in any of their functional responses [20, 21]. This model forms the basis of the theoretical framework presented below.

2.1 Model details

The per capita growth rates of both plant species in the multispecies model presented in [20, 21] are

$$\begin{aligned} G_{\infty}^{u_1} &= w\left(u_1 + Hu_2\right), \\ G_{\infty}^{u_2} &= Fw\left(u_1 + Hu_2\right), \end{aligned} \tag{2.1}$$

where $u_1 = u_1(x,t)$ and $u_2 = u_2(x,t)$ denote the nondimensional (see the supplementary material for a nondimensonalisation) plant densities at time $t \geq 0$ at the space point $x \in \mathbb{R}$. The rate of plant growth not only increases with the resource density $w = w(x,t)$, describing water availability, but also with both plant densities u_1 and u_2. This positive density-dependence represents the short-range facilitative effects of plants on each other which is caused, for example, by increases of soil permeability in vegetated areas. The strength of facilitation differs between the two species and is accounted for by the nondimensional constant H. The nondimensional constant F describes the ratio of the two species' water-to-biomass conversion capabilities.

To account for intraspecific competition dynamics among plant species in the theoretical framework, I convert the growth rates (2.1) into logistic-growth-type terms by setting

$$\begin{aligned} G_{k_1}^{u_1} &= w\left(u_1 + Hu_2\right)\left(1 - \frac{u_1}{k_1}\right), \\ G_{k_2}^{u_2} &= Fw\left(u_1 + Hu_2\right)\left(1 - \frac{u_2}{k_2}\right). \end{aligned} \tag{2.2}$$

The parameters k_1 and k_2 denote the maximum standing biomasses of both species. In this context, self-limitation does not refer to intraspecific competition for water, as the ecohydrological dynamics are explicitly modelled. Instead, the strength of intraspecific competition depends on other factors, such as the maximum biomass of a single individual, which limit the total biomass a species can reach in a fixed area [33]. The per capita growth rates (2.2) capture both the intraspecific facilitation and intraspecific competition that occur in dryland ecosystems (Fig. 2.1). For low biomass densities, the per capita growth rate of a species increases with that species' density (facilitation), but decreases for higher biomass densities (competition).

Replacing the plant growth rates (2.1) in the multispecies model presented in [20, 21] by (2.2) yields

$$\frac{\partial u_1}{\partial t} = \overbrace{wu_1\left(u_1 + Hu_2\right)\left(1 - \frac{u_1}{k_1}\right)}^{\text{plant growth}} - \overbrace{B_1 u_1}^{\text{plant mortality}} + \overbrace{\frac{\partial^2 u_1}{\partial x^2}}^{\text{plant dispersal}}, \tag{2.3a}$$

$$\frac{\partial u_2}{\partial t} = \overbrace{Fwu_2\left(u_1 + Hu_2\right)\left(1 - \frac{u_2}{k_2}\right)}^{\text{plant growth}} - \overbrace{B_2 u_2}^{\text{plant mortality}} + \overbrace{D\frac{\partial^2 u_2}{\partial x^2}}^{\text{plant dispersal}}, \tag{2.3b}$$

$$\frac{\partial w}{\partial t} = \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\text{evaporation and transpiration}} - \underbrace{w\left(u_1 + u_2\right)\left(u_1 + Hu_2\right)}_{\text{water uptake by plants}} + \underbrace{\nu\frac{\partial w}{\partial x}}_{\text{water flow downhill}} + \underbrace{d\frac{\partial^2 w}{\partial x^2}}_{\text{water diffusion}}, \tag{2.3c}$$

where time $t \geq 0$ and the space variable $x \in \mathbb{R}$ increases in the uphill direction of the one-dimensional domain, representing sloped terrain. The consideration of a one-dimensional space domain instead of an ecologically more intuitive two-dimensional domain is justified by the appearance of vegetation patterns as regular stripes parallel to the contours of the slope. Solution profiles of (2.3) thus represent a transversal cut along the gradient of the terrain.

Water is added to the system at a constant rate A and is removed through evaporation and transpiration processes that are assumed to be proportional to the water density. Water is

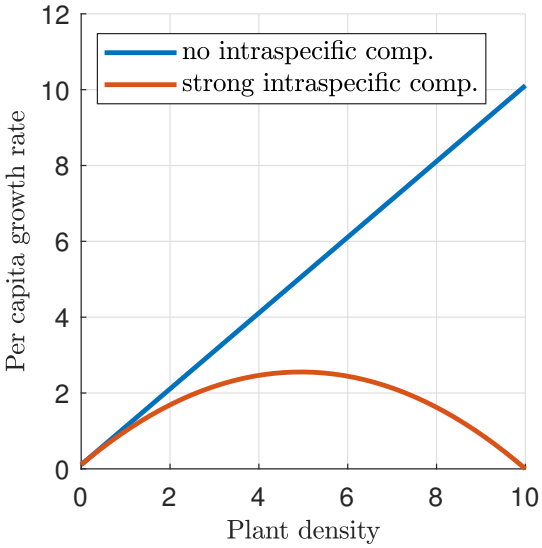


Figure 2.1: Per capita plant growth rates. Sketches of a plant species' growth rate in the absence of intraspecific competition (G_∞, blue curve) and with the inclusion of self-limitation (G_{10}, red curve) are shown. Even if intraspecific competition is considered, the growth rate captures facilitative intraspecific effects of plants on each other for low biomass densities. For larger plant densities, the negative density-dependent effects dominate and the species' growth rate decreases. Densities of u_2 and w are kept constant in this visualisation.

consumed by plants, represented by the third term on the right hand side of (2.3c). The rate of water uptake by plants does not only depend on the total consumer density $(u_1 + u_2)$, but also on the enhancement of the plants' water consumption capabilities in areas of high biomass $(u_1 + Hu_2)$, as discussed above. Plant mortality is assumed to be proportional to plant density and occurs at rates B_1 and B_2, respectively. Finally, all three densities undergo diffusion, and water is assumed to flow downhill on the sloped terrain. The description of the latter by advection is based on the assumption that the slope does not exceed gradients of a few percent, consistent with field observations of striped vegetation patterns [45]. The diffusion parameters D for species u_2 and d for water, as well as the advection speed ν compare the respective dimensional parameters to the diffusion coefficient of species u_1.

In the following, I assume that u_1 and u_2 represent a *coloniser species* and a *locally superior species*, respectively. A number of theoretical models on dryland vegetation have been proposed over the last three decades and therefore all parameter values in (2.3) are obtained from previous models. Details on how parameter estimation for those models is performed are presented in [1, 24, 30]. The distinction between a coloniser and a locally superior species yields qualitative assumptions on the model parameters [21]. The coloniser both grows and dies at a faster rate ($F < 1, B_1 > B_2$, but see comment below), has a stronger impact on the soil's permeability per unit biomass ($H < 1$) and disperses faster ($D < 1$) [21]. The locally superior species is assumed to outcompete the coloniser species in a spatially uniform setting in the absence of any self-limitation. This requires $B_2 < FB_1$ [20] and I assume that this relation holds throughout the paper.

2.2 Model analysis

Typically, both single-species solutions and coexistence solutions of (2.3) are either spatially constant or spatially patterned. In the latter case, these are periodic travelling waves, i.e. spatially periodic functions that move in the uphill direction of the domain at a constant speed. The uphill migration speed is an emergent property of model solutions, but can be made explicit through a change of coordinates that transforms (2.3) into a travelling wave framework. In travelling wave coordinates, spatio-temporal patterned solutions can be represented by a single variable only (see supplementary material). This facilitates a bifurcation analysis (the study of qualitative changes to the solution structure under variations of system parameters), which is performed by a combination of analytical tools and numerical continuation (see supplementary material). In particular, the stability calculations of the periodic travelling wave solutions of

the system are performed using a numerical continuation method for the calculation of essential spectra by Rademacher et al. [35].

Numerical simulations of the PDE system (2.3) are obtained using the method of lines, with the resulting system being solved by a standard numerical solver for ordinary differential equations (ODEs) (e.g. ode15s in MATLAB).

The spatial distribution of species in a single vegetation band is quantified by the linear correlation between both plant species' solution components. The linear correlation is given by

$$\rho(U_1, U_2) = \frac{\mathrm{cov}(U_1, U_2)}{\sigma(U_1)\sigma(U_2)},$$

where U_1 and U_2 are two vectors obtained by discretising the spatial domain in space and evaluating the plant densities u_1 and u_2 on this mesh. Here, $\mathrm{cov}(\cdot, \cdot)$ denotes the covariance of two vectors, and $\sigma(\cdot)$ the standard deviation. The linear correlation satisfies $-1 \leq \rho(U_1, U_2) \leq 1$, and a larger correlation corresponds to a more in-phase-like appearance of both plant patterns. Numerical continuation of model solutions using AUTO-07p [15] allows for an exhaustive calculation of the linear correlation in the parameter space.

3 Results

3.1 Spatially uniform coexistence

Depending on the precipitation volume, the multispecies model (2.3) has up to four biologically relevant spatially uniform equilibria: a desert steady state that is stable in the whole parameter space; a single-species equilibrium for each plant species; and a coexistence state. Under sufficiently high rainfall levels, the single-species equilibria are stable in the absence of a second species, but may become unstable if a competitor is introduced. Stability to the introduction of a second species requires both sufficiently weak intraspecific competition and a higher local average fitness than the competitor. Moreover, the stability regions of both single-species equilibria do not overlap and it is straightforward to determine the species of higher local average fitness based on their parameter values. In particular, only changes to growth and mortality rates, but not variations in the strength of the intraspecific competition can change which species is of higher local average fitness (see supplementary material for more details).

As intraspecific competition of the locally superior species increases, its single-species equilibrium loses stability to the coexistence equilibrium. In other words, spatially uniform coexistence occurs if intraspecific competition among the locally superior species is sufficiently strong compared to the interspecific competition for water, which is quantified by the rainfall parameter (Fig. 3.1 and 3.2). The characterisation of the strength of interspecific competition through such a proxy is necessitated by the explicit modelling of the resource dynamics. This makes it impossible to directly quantify the competitive impact of one species on the other. In particular, this does not allow for a quantitative comparison with the strength of intraspecific competition dynamics, quantified by the carrying capacities k_1 and k_2. Strong intraspecific competition reduces equilibrium densities and hence renders the locally superior species unable to utilise all of the available resource. This allows for the invasion of a second species and thus facilitates coexistence. The strength of intraspecific competition among the locally inferior species has no significant impact on the occurrence of spatially uniform coexistence.

For each of the non-desert equilibria of (2.3), there exists a complementary unstable steady state with the same species composition. Their instability for all biologically realistic parameter values causes them to bear no influence on the model outcomes discussed in this paper. Nevertheless, details on unstable equilibria of (2.3) can be found in the supplementary material.

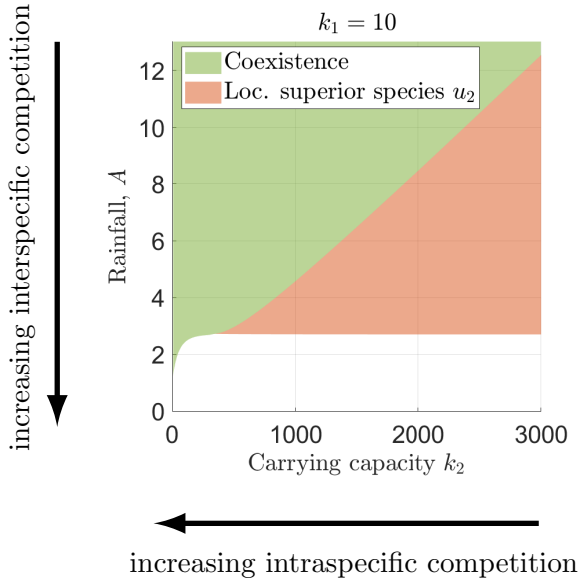


Figure 3.1: Stability of spatially uniform equilibria in the nonspatial model. Stability regions of the coexistence equilibrium and the equilibrium of the locally superior species are shown under changes to interspecific (rainfall parameter A) and intraspecific (carrying capacity k_2) competition. The equilibrium of the coloniser species is always unstable and the trivial desert steady state is stable in the whole parameter region (not shown). Parameter values are $B_1 = 0.45$, $B_2 = 0.05$, $F = 0.11$, $H = 0.11$.

3.2 Patterned species coexistence

Decreases in precipitation cause the spatially uniform states of (2.3) to lose stability to spatio-temporal patterns. Patterns either feature both plant species or consist of the coloniser species only. Single-species patterns of the locally superior species are always unstable to the introduction of the coloniser species, despite being stable in the absence of any competitor. In particular, a solution's species composition is not necessarily conserved across a transition from a spatially uniform to a spatially patterned state. For example, if intraspecific competition of the locally superior species is insufficient to stabilise spatially uniform coexistence, the spatially uniform single-species state nevertheless loses stability to a coexistence pattern (Fig. 3.2 (b)).

Moreover, the precipitation volume also determines if a solution represents a vegetation pattern or a spatially non-uniform savanna. The former state is attained for low rainfall levels at which plant densities oscillate between a level of high biomass and zero, corresponding to alternating bands of vegetation and bare soil. By contrast, spatially patterned savanna solutions occur for larger precipitation volumes and are characterised by oscillations between two non-zero biomass levels. Crucially, coexistence in a vegetation pattern state is only possible if intraspecific competition among the coloniser species is sufficiently strong (Fig. 3.2 (a) and (b)). If self-limitation of the coloniser species is weak, then the beneficial effects of its colonisation abilities outweigh the local superiority of its competitor for a wider range of precipitation volumes. The destabilisation of coexistence thus occurs at higher rainfall levels, where solutions represent a savanna state (Fig. 3.2 (c) and (d)).

Under high-volume rainfall regimes, a unique spatially uniform stable state exists for each value of the precipitation parameter, but multistability of stable equilibria occurs for lower rainfall amounts. Firstly, if a spatial pattern is a stable model outcome for a given precipitation volume, then a range of other patterned solutions are also stable. Such patterns differ in their wavelengths (distance between two consecutive biomass peaks) and their uphill migration speeds

(Fig. 3.2 and Fig. 3.3 (a)). Secondly, multistability of single-species and coexistence patterns, as well as coexistence patterns and spatially uniform states also occurs, especially if intraspecific competition among the coloniser species is strong (Fig. 3.2 (a) and (b)).

This singles out patterns' wavelengths and uphill migration speeds as crucial pieces of information in the understanding of transitions between species coexistence and single-species states. Typically, if a patterned state of a given wavelength loses its stability due to changes in precipitation, a transition, such as that depicted in Fig. 3.3 (c), to a pattern of a different wavelength occurs. The multistability of patterned states implies that the newly attained state is not necessarily close to destabilisation. Hence, such transitions cannot typically be reversed by simply increasing/decreasing the precipitation volume back to its original level.

A change in wavelength is not the only possible result of a pattern's destabilisation. If intraspecific competition of the coloniser species is strong, a large range of coexistence patterns lose their stability to a single-species pattern (of the coloniser) with the same wavelength as precipitation decreases. In such a case, destabilisation results in an extinction event, despite the stability of coexistence patterns at different wavelengths for the same environmental conditions (Fig. 3.2 (a) and (b) and Fig. 3.3). Thus, species richness in the system not only depends on precipitation volume and species properties but also on past states of the ecosystem. In particular, the resilience of coexistence patterns to increases in aridity depends on their wavelength and uphill migration speed. The phenomena outlined above are examples of hysteresis, a well-known feature of theoretical models of vegetation patterns and other patterned ecosystems [39].

Spatially uniform equilibria and regular spatio-temporal patterns are not the only stable outcomes of the model system (2.3). In the absence of strong intraspecific competition, no direct switch from regular coexistence pattern to a uniform state of the locally superior species occurs (Fig. 3.2 (d)). Instead, this transition takes place via a coexistence state, which lacks any regularity in space and time (example solution plot is shown in the supplementary material). Currently, I am unable to make any conclusive statements about this type of model solution and its ecological implications, but note that it relies on the intraspecific competition dynamics of both species being weak.

Similar to the spatially uniform states discussed in Sec. 3.1, stable patterned model outcomes of (2.3) are also complemented by unstable solutions. While in this context, unstable states do not have any ecological relevance, they are essential to understand the full solution structure of the mathematical model. Examples of bifurcation diagrams as well as more information on the bifurcations that occur in the system are given in the supplementary material.

3.3 Plant species' distribution

Depending on system parameters, the multispecies model (2.3) captures the spatial species distribution within vegetation stripes. In other words, the uphill edge of a single vegetation band is dominated by one species, while its competitor is mostly confined to a narrow region in the centre of the band.

The ratio of the plant species' diffusion coefficients D has the most significant impact on the correlation between both plant species (Fig. 3.4). If the species with slower growth rate also disperses at a slower rate, then the correlation between both species is small, as the uphill edge of each vegetation band features a high density of the faster disperser only. As the difference between the plant species' diffusion coefficients becomes smaller, the correlation between the plant densities increases. For $D = 1$, i.e. when both plant species diffuse at the same rate, both species feature near the top edge of each stripe at a high density. Nevertheless, solution components are not exactly in phase due to the faster growth and mortality dynamics of the coloniser species. (Fig. 3.4b).

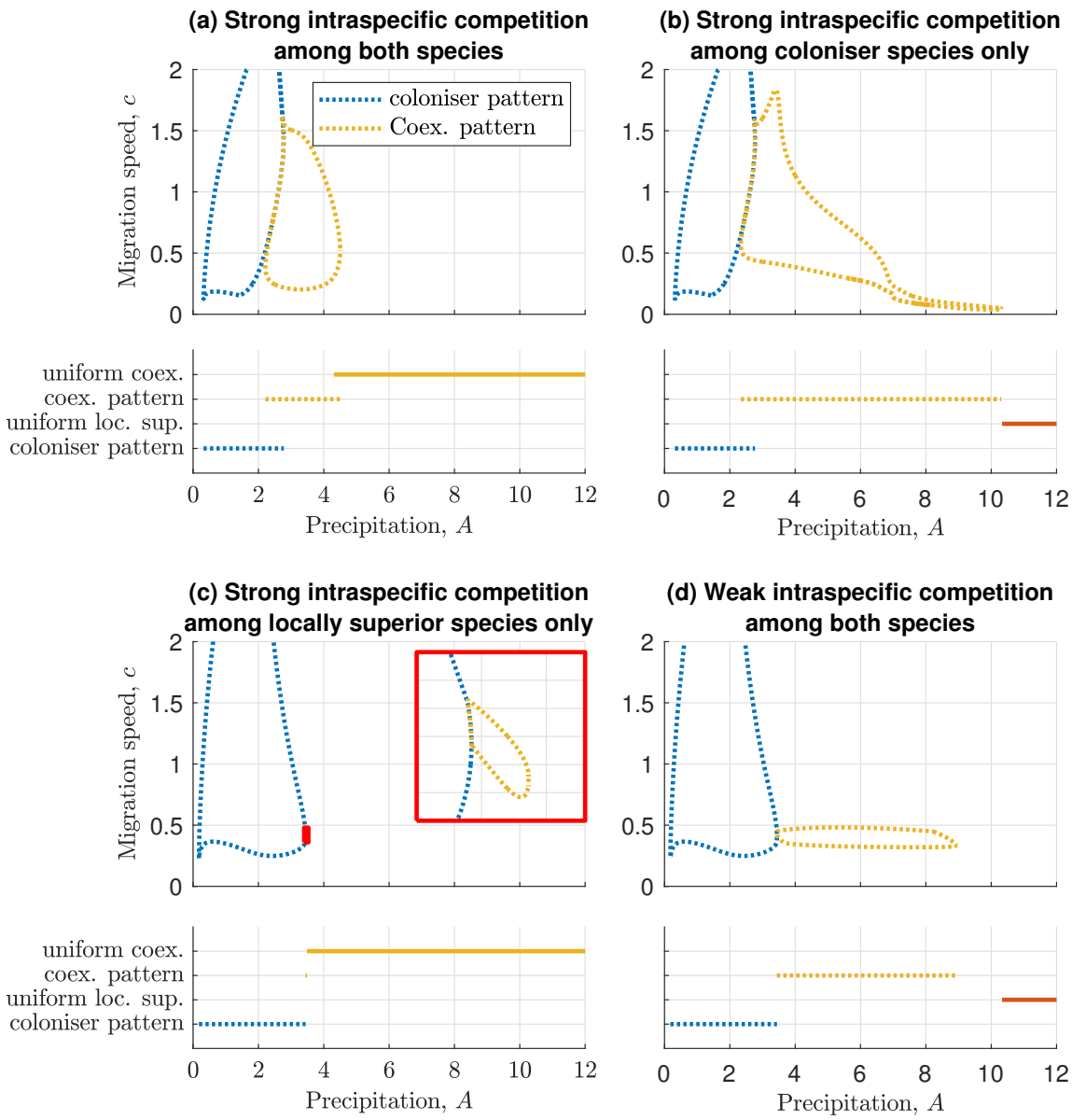
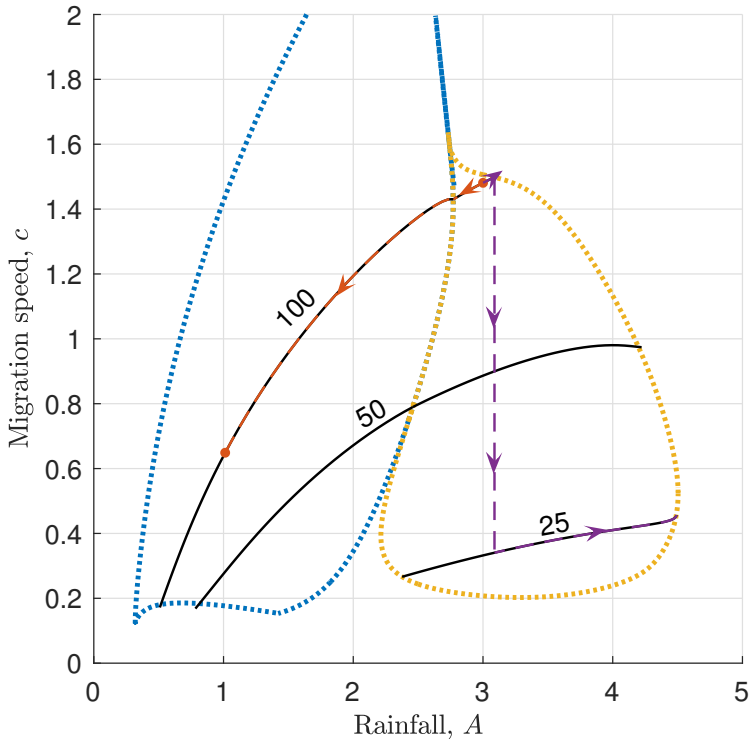
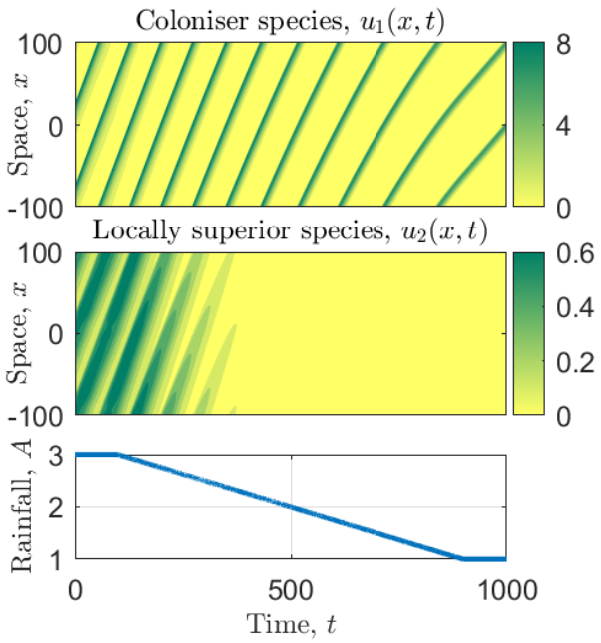


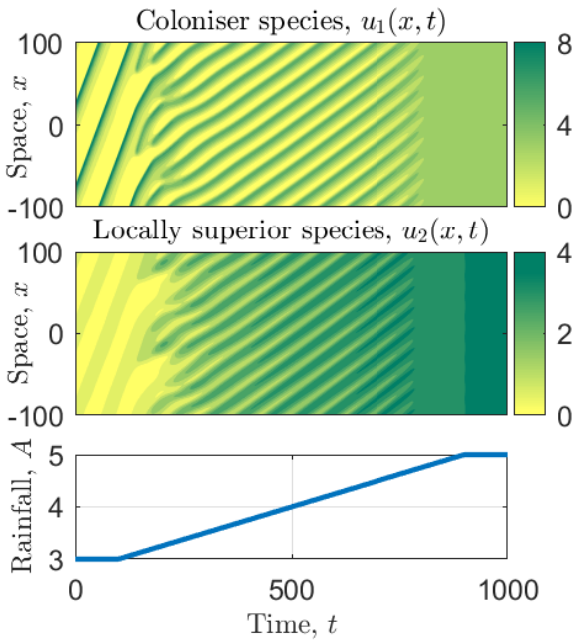
Figure 3.2: Overview of stable model outcomes for different combinations of species' intraspecific competition strengths. The lower panel in each quadrant provides a visualisation of the precipitation ranges in which spatially uniform (solid lines) and spatially patterned solutions (dotted lines) are stable model solutions. The top panel shows the stability boundaries of the patterned states in the (A, c) parameter plane and thus also provides information on the uphill migration speed of stable patterns. Increases in intraspecific competition strength of the locally superior species stabilises spatially uniform coexistence for lower precipitation volumes, while strong intraspecific competition among the coloniser species promotes patterned coexistence. The intraspecific competition strengths are $k_1 = k_2 = 10$ in (a), $k_1 = 10, k_2 = 10^4$ in (b), $k_1 = 10^4, k_2 = 10$ in (c) and $k_1 = k_2 = 10^4$ in (d), while other parameter values are $B_1 = 0.45$, $B_2 = 0.05$, $F = H = 0.11$, $\nu = 182.5$ and $d = 500$ in (a)-(d).



(a) Wavelength contours of stable patterns.

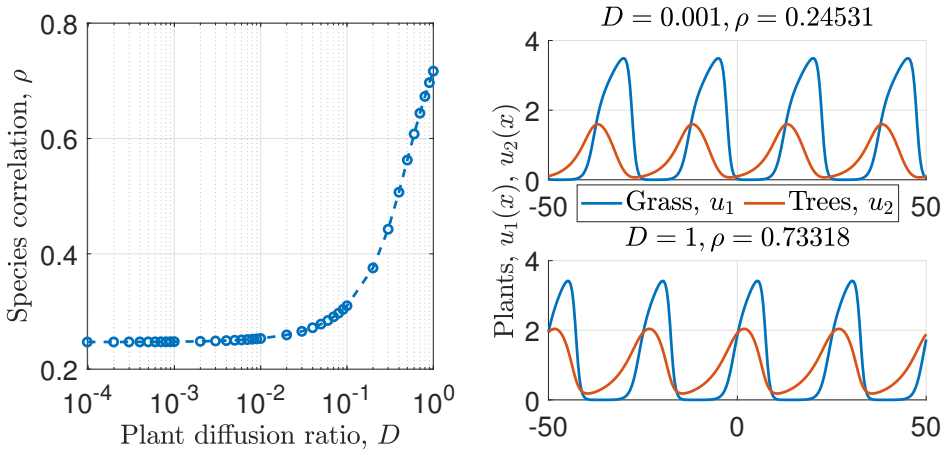


(b) Transition to single-species pattern.



(c) Transition to uniform coexistence.

Figure 3.3: State transitions under changing precipitation. Transitions from patterned coexistence to a single-species pattern (b) and a uniform coexistence state (c) under changing precipitation volumes are shown. Both model solutions are initiated at rainfall volume $A = 3$ and a wavelength of $L = 100$. Solutions follow wavelength contours (solid black curves in (a)) until they are destabilised and a pattern of a new stable wavelength is chosen. Red dashed lines in (a) indicate the dynamics of the solution shown in (b); purple dashed lines that of the model outcome visualised in (c). Parameter values correspond to those used in Fig. 3.2 (a).



(a) Correlation between species

(b) Numerical PDE simulations

Figure 3.4: The spatial correlation between the two plant species components of model solutions under changes in the diffusion coefficient D are shown in (a). Part (b) visualises solution profiles (u_1,u_2 only) for specific values of D. Correlation increases as dispersal behaviour becomes more similar. Other parameter values are $B_1 = 0.45$, $B_2 = 0.05$, $F = H = 0.11$, $\nu = 182.5$, $d = 500$, $k_1 = k_2 = 5$ and $A = 2$.

4 Discussion

The exploration of coexistence mechanisms that prevent competitive exclusion in resource limited ecosystems has been a common research topic in theoretical ecology for many decades [7, 31, 41, 47]. The importance of considering intraspecific competition dynamics has been established early in the history of coexistence theory (e.g. [26]). Self-limitation of species enables coexistence because it keeps their abundances sufficiently low to prevent resource monopolisation by any one species [7, 41]. More recently, heterogeneities caused by spatial self-organisation in otherwise homogeneous environments have been singled out as an alternative potential explanation of species coexistence under competition for a sole limiting resource [10, 21]. Interestingly, these processes are typically associated with opposite impacts on population growth in general: intraspecific competition corresponds to negative density-dependence in population growth, but spatial self-organisation involves local facilitation.

In the context of dryland vegetation, a classical example of a self-organisation principle in ecology, pattern formation on its own has been unable to explain species coexistence across a wide range of the precipitation (resource input) gradient [21, 34]. In this paper, I show that the combination of facilitative self-organisation and self-limiting intraspecific competition in a theoretical framework provides more insights into the coexistence of a coloniser species with a locally superior species in states ranging from spatially uniform savannas to regular stripe patterns.

A widely applicable result of coexistence theory is that coexistence of two species can occur if each species' intraspecific competition is stronger than its impact on the competitor species (e.g. [7, 31]). Interestingly, the combination of intraspecific competition with spatial self-organisation dynamics show that different species' self-limitation is the facilitator of coexistence at opposite ends of the resource input spectrum. This phenomenon arises despite the assumption that both species do not qualitatively differ from each other in any of their functional responses to the environment. Under high resource availability, for which spatially uniform plant cover is possible, strong intraspecific competition of the locally superior species facilitates coexistence (Fig. 3.1). If self-limitation of the locally superior species is sufficiently strong, it cannot utilise

all of the available resource and can thus allow for coexistence with a second species [31]. In this context, local superiority corresponds to a higher local average fitness, which is determined by the stability of spatially uniform single-species equilibria. While in the multispecies model presented in this paper, the stability regions of these steady states do not overlap, complications in the definition of the locally superior species may arise in other modelling frameworks if bistability of single-species states occurs.

The impact of intraspecific competition changes significantly if resource availability is low. Under such environmental conditions, the spatial self-organisation principle destabilises spatially uniform states and leads to pattern formation. Firstly, species coexistence requires the locally superior species to be inferior in its colonisation abilities [21]. This balance enables species coexistence due to spatial heterogeneities in the environment, caused by the spatial self-organisation. The potential of intercepting resource run-off in uncolonised regions is high, which can be exploited by the coloniser. The redistribution of water towards areas of high biomass consequently facilitates the growth of the second species. Eventually, the locally superior species locally outcompetes the superior coloniser, thus creating a balance that facilitates coexistence. Secondly, coexistence in patterned form is facilitated by strong intraspecific competition of the coloniser species (Fig. 3.2 (b)). In contrast to the coexistence mechanism which applies under high resource availability and is discussed above, the intraspecific competition's impact on resource availability is not the cause of coexistence. Instead, coexistence under severe resource scarcity is enables by the strengthening of the facilitative balance between the two species' colonisation abilities and local competitiveness. In the absence of intraspecific competition, the coloniser is able to tip that balance in its favour by being able to colonise new areas faster than being outcompeted locally by its competitor. Strong self-limitation prevents this and thus facilitates coexistence.

A different important aspect in the understanding of species coexistence in self-organised ecosystems highlighted by the results presented in this paper is hysteresis. As is common with pattern-forming systems, multistability of stable states occur. In other words, given any set of parameters describing plant species and environmental conditions, no conclusive statement about the model outcome can be made. Instead, information about a pattern's history is required to obtain more information about its future dynamics. In particular, extinction events, i.e. the transition from a coexistence state to a single-species state, cannot be pinned down to a specific level of resource without having information about the ecosystem's current and past states (Fig. 3.3). Theoretical studies of history dependence in patterned vegetation in the context of only one species highlight that this property could be of crucial importance to advance our understanding of the ecosystem dynamics in general, not only of the transitions between coexistence and single-species states [12, 39]. Hysteresis is believed to be of crucial importance in many ecosystems [43], but empirical evidence of history dependence in patterned ecosystems is challenging to detect [14] and only limited empirical data on the phenomenon exists [42].

A novelty of results presented in this paper is the proposal of a coexistence mechanism for dryland vegetation patterns that does not rely on species-specific assumptions. Previous theoretical models on the subject suggest that species coexistence in vegetation patterns is only possible if only one species contributes to the system's pattern-forming feedback loop [3, 33] or if plant species adapt to different soil moisture niches [6, 44]. By contrast, the coexistence mechanism presented in this paper exclusively relies on comparative assumptions (e.g. one species being superior in its colonisation abilities while having a lower local average fitness than its competitor). As a consequence, it applies to a wider combination of plant species and may be extended to other consumer-resource systems governed by self-organisation principles, for example shellfish reefs [8].

It is worth emphasising that the coexistence mechanism attributed to spatial self-organisation presented in this paper differs from that proposed in a different class of model: rock-paper-

scissor-type systems. In those models, coexistence is facilitated by competitive hierarchies of three or more species that follow the idea of the well-known children's game of the same name. Under such assumptions, spatial self-organisation occurs due to spatial segregation and leads to each coexisting species occupying its own habitat in a larger spatial domain [2, 23, 25, 36]. By contrast, the ecohydrological model presented in this paper captures species coexistence within single patches of vegetation, in agreement with field observations [38, 45]. Moreover, it also captures both the uphill movement of vegetation stripes and the spatial species distribution within vegetation bands (Fig. 3.4b). Field observations of banded vegetation patterns report that the top edge of each stripe is dominated by annual grasses [38], thus coined to be the *coloniser species*, while other species are mostly confined to the centre and lower regions of each stripe. The comprehensive analysis of spatial correlation between both plant species in coexistence solutions of (2.3) shows that the spatial species distribution in a single vegetation band mainly depends on the plant species' dispersal behaviour. The faster the diffusion of the coloniser species in relation to its competitor, the more pronounced is its presence at the uphill edge of the stripe. This confirms the empirical hypothesis that the pioneering character of grasses in grass-tree coexistence is indeed caused by the faster dispersal of the coloniser species [38].

In the model presented in this paper, all intraspecific dynamics are combined into one single parameter for each species. To gain a better understanding of how the balance between intraspecific and interspecific competition enables species coexistence, more information on these dynamics is needed. Promising first steps have been made through the explicit inclusion of (auto-)toxicity effects on interacting plant species [27]. These suggest potential avenues of further exploration in both the context of vegetation patterns and more general modelling frameworks for species coexistence within ecosystems in which both spatial self-organisation and intraspecific competition dynamics play a significant role.

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