Intraspecific competition in models for vegetation patterns: decrease in resilience to aridity and facilitation of species coexistence

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Abstract

Patterned vegetation is a characteristic feature of many dryland ecosystems. While plant densities on the ecosystem-wide scale are typically low, a spatial self-organisation principle leads to the occurrence of alternating patches of high biomass and patches of bare soil. Nevertheless, intraspecific competition dynamics are commonly ignored in mathematical models for vegetation patterns. In this paper, I address the impact of intraspecific competition on a modelling framework for banded vegetation patterns. Firstly, I show that in the context of a single-species model, neglecting intraspecific competition leads to an overestimation of a patterned ecosystem’s resilience to increases in aridity. Secondly, in the context of a multispecies model, I argue that intraspecific competition is a key element in the successful capture of species coexistence in model solutions representing a vegetation pattern. For both models, a detailed bifurcation analysis is presented to analyse the onset, existence and stability of patterns. Besides the intraspecific competition strengths, also the the difference between two species has a significant impact on the bifurcation structure, providing crucial insights into the complex ecosystem dynamics. Predictions on future ecosystem dynamics presented in this paper, especially on pattern onset and pattern stability, can aid the development of conservation programs.

Keywords: periodic travelling waves; wavetrains; pattern formation; spatial self-organization; numerical continuation; competitive exclusion; bifurcation analysis

1 Introduction

Approximately 40% of the Earth’s land mass are classified as drylands [32]. The development of an understanding of ecosystem dynamics in water-deprived areas is of considerable socio-economic importance as a similar proportion of the total human population lives in arid and semi-arid climate zones, where agriculture is an integral part of the economy [10]. A characteristic feature of arid ecosystems is vegetation patterns, which form an interface between continuous vegetation cover and full deserts.

A classical example of a self-organising principle in ecology, the separation into alternating patches of biomass and bare soil is induced by a positive feedback loop between local growth of vegetation and resource (water) distribution towards areas of high biomass. Several processes are the cause of such hydrological heterogeneities; for example the formation of biogenic soil crusts on bare ground that inhibit water infiltration into the soil and induce overland water flow, or the creation of soil moisture gradients due to vertically extended root systems in soil types that allow for fast water...
diffusion. A common type of pattern is regular stripes that occur on hillslopes parallel to the contours of the terrain.

Ecosystem functioning heavily depends on plant populations as they constitute basal levels of food webs. Changes to a vegetation pattern’s properties, such as wavelength or recovery time from perturbations, can provide early warning signals of desertification processes, a major threat for economies in drylands. However, the large spatial and temporal scales associated with the ecohydrological dynamics of vegetation patterns restrict the acquisition of comprehensive high-quality data to specific properties (e.g. wavelength) and to short time series. As a consequence, mathematical modelling, and in particular continuum approaches using systems of PDEs, have been established as a powerful tool to disentangle the complex ecosystem dynamics. There exist several modelling frameworks which successfully capture the self-organisation of plants into patterns and provide more insights into these processes; most notable are those by Gilad et al., Rietkerk et al. and Klausmeier (see for comprehensive reviews).

The majority of these theoretical frameworks assume that the rate of plant growth is either independent of the plant density or increasing with biomass, thus neglecting any negative impacts due to intraspecific competition for resources other than water (e.g. space). As a result of the pattern formation feedback in such models, they can admit solutions in which biomass becomes very large locally (e.g. ), a mathematically interesting but ecologically potentially irrelevant feature. A notable exception is the Gilad et al. model, in which the rate of plant growth approaches zero as biomass density increases to its maximum value, and becomes negative for higher plant densities. Nevertheless, due to differences in the various modelling frameworks, the precise impact of intraspecific competition on the ecosystem dynamics has not been addressed previously.

It is a classical result from Lotka-Volterra competition models that the interplay between intraspecific and interspecific competition can facilitate species coexistence in resource-limited ecosystems, provided intraspecific competition among all species is sufficiently stronger than interspecific competition between them (e.g. ). In the context of patterned vegetation in drylands, coexistence of herbaceous (grasses) and woody (shrubs and trees) species is commonly observed, despite the species’ competition for water. Previous theoretical studies have successfully captured species coexistence in vegetation patterns by making the assumption that only one plant type contributes to the pattern-forming feedback. Such approaches, however, are based on strong assumptions on differences between plant species, such as contrasting functional responses to soil moisture, and may thus not be applicable in a general setting. In a recent paper, I have shown that strong intraspecific competition of a species superior in its colonisation abilities can provide an alternative explanation for species coexistence that does not rely on such species-specific assumptions. I argued that a deeper understanding of the impact of intraspecific competition in spatially extended, resource-limited ecosystems can be a key ingredient in the explanation of species coexistence.

In this paper, I closely investigate the impact of intraspecific competition on solutions of a mathematical model for banded vegetation patterns in semi-arid environments. The paper is split into two major parts. Firstly, I assess the effects of intraspecific competition on pattern onset, existence and stability in the context of a single-species model by comparing results to those obtained for the corresponding model in the absence of any intraspecific competition (Sec. 2). Secondly, I extend the results presented in to provide more insights into how intraspecific competition can enable species coexistence under competition for a sole limiting resource by performing a comprehensive bifurcation analysis of a multispecies model (Sec. 3). In , I mainly focus on the impact of changes to intraspecific competition strength of either species on the existence of coexistence patterns. By contrast, in this paper, I present details on how results relate to earlier modelling studies neglecting intraspecific competition dynamics. In particular, I investigate how the bifurcation structure, especially the onset mechanisms for coexistence patterns, changes under simultaneous and separate
variations of intraspecific competition strengths of both species. Moreover, I address how the similarity between two species affects their ability to coexist. This contrasts with the analysis presented in [12] which is restricted to grass-tree coexistence, a parameter setting which corresponds to large species difference in the context of this paper. Finally, in Sec. 4 I provide an interpretation and discussion of my results.

2 Single-species model

2.1 Model

Several modelling frameworks to describe the ecohydrological dynamics in vegetation patterns have been proposed over the last two decades (see [26, 48] for reviews). One system that stands out due to its simplicity is the extended Klausmeier model [23], a phenomenological reaction-advection-diffusion system which has been the basis for many model extensions (e.g. [45, 15, 14, 13, 7, 18, 25]). To investigate the impact of intraspecific competition on the ecosystem dynamics, I adjust the plant growth rate in the Klausmeier model to account for negative effects of crowding. Suitably nondimensionalised [23, 36], the resulting model is

\[
\begin{align*}
\frac{\partial u}{\partial t} &= \text{plant growth} - \frac{u^2 w}{1 - \frac{u}{k}} - Bu + \frac{\partial^2 u}{\partial x^2}, \\
\frac{\partial w}{\partial t} &= \text{rainfall} - \text{evaporation and transpiration} - \frac{u^2 w}{\text{water uptake by plants}} + \nu \frac{\partial w}{\partial x} + d \frac{\partial^2 w}{\partial x^2},
\end{align*}
\] (2.1a, 2.1b)

where the space coordinate \( x \in \mathbb{R} \) increases in the uphill direction of the domain and time \( t \geq 0 \). The plant density is denoted by \( u(x,t) \), the water density by \( w(x,t) \). A constant amount of water is added to the system representing precipitation, while evaporation and transpiration effects occur at a constant rate. The nonlinearity in the term representing water consumption by plants accounts for part of the positive feedback between local plant growth and water redistribution towards dense biomass patches. The term is the product of the consumer density \( u(x,t) \), the resource density \( w(x,t) \), and a term that describes the enhancement of resource availability in existing biomass patches \( u(x,t) \), e.g. due to an increase in soil permeability caused by plants. Water is the limiting resource in the modelled ecosystem and thus the plants’ water consumption is directly proportional to their growth in the absence of any intraspecific competition. However, the rate of plant growth does not increase without bound as the plant density increases. Instead it is mediated by a logistic growth-type term, which accounts for intraspecific competition among the plant species. This intraspecific competition may occur due to genetic factors, such as maximum standing biomasses of single individuals [30], but does not correspond to intraspecific competition for water; those dynamics are modelled explicitly through the interactions with the water density. Finally, plant mortality occurs at a constant rate, both densities undergo diffusion, and water flow downhill is described by an advection term if the terrain is assumed to be sloped. The diffusion of water was not included in the model’s original formulation [23], but has become a well-established addition (e.g. [46, 48]), which leads to the model being referred to as the extended Klausmeier model. The

\[ k = \alpha_1 \alpha_2^{1/2} \alpha_3^{-1/2} \]

where \( \alpha_1, \alpha_2, \alpha_3 \) are the strength of the plant species’ intraspecific competition, the constant quantifying the plants’ enhancement of resource availability and the water’s evaporation rate, respectively.
parameters \( A, k, B, \nu \) and \( d \) are nondimensional parameters that can be interpreted as rainfall volume, strength of intraspecific competition, rate of plant mortality, speed of water flow downhill and the water diffusion coefficient, respectively. Typical parameter estimates (e.g. \cite{23}) suggest that \( \nu \approx 200 \) is large compared to other model parameters, as it reflects the difference between the rate of water advection and the rate of plant diffusion. The terrain’s slope, however, is not steep itself. Modelling water flow downhill by advection is only valid as long as water flow occurs as sheet flow and thus (2.1) is not valid if the terrain’s gradient exceeds a few percent.

The (extended) Klausmeier model without intraspecific competition can be obtained from (2.1) by taking \( k \to \infty \). This limiting case has been the subject of extensive mathematical analyses, in particular on the onset, existence and stability of spatial patterns \cite{43}. Onset of patterned solutions in PDE systems usually occurs at either a Hopf bifurcation of a spatially uniform equilibrium or at a homoclinic solution (but see Sec. \textit{3.4} for an exception). Typically, onset loci also form the boundaries of the parameter regions in which patterns exist, unless a fold in the solution branch occurs. At high precipitation levels, i.e. where a transition from uniform to patterned vegetation takes place, pattern onset occurs at a Hopf bifurcation of a spatially uniform equilibrium, while at low rainfall volumes, patterned solutions terminate in a homoclinic solution \cite{43}. The homoclinic solution also provides a lower bound for the pattern existence region, while the upper bound may occur at higher precipitation levels than those of the Hopf bifurcation due to the occurrence of a fold. A powerful tool in the analytical derivation of the patterns’ features is the utilisation of the size of the advection parameter \( \nu \), which allows for asymptotic approximations valid to leading order in \( \nu \) as \( \nu \to \infty \).

The addition of intraspecific competition does not have a qualitative impact on pattern onset, existence and stability in the model but noteworthy quantitative impacts are observed as detailed below. Besides the desert steady state \( v_s^D = (0, A) \), which exists and is stable in the whole parameter space, (2.1) admits a pair of vegetated spatially uniform equilibria given by

\[
\begin{align*}
\mathbf{v}_s^\pm &= \left( u^\pm, w^\pm \right) = \left( A \pm \sqrt{A^2 - 4B \left( B + \frac{A}{k} \right)}, \frac{A}{2 \left( B + \frac{A}{k} \right)} \right),
\end{align*}
\]

which exist provided

\[
A > A_{\text{min}}^G := 2B \left( \frac{1}{k} + \sqrt{1 + \frac{1}{k^2}} \right).
\]

The lower branch \( v_s^- \) is unstable, while the upper branch \( v_s^+ \) is stable to spatially uniform perturbations if \( B < 2 \). Parameter estimates consistently suggest that plant mortality \( B \) remains well below this threshold, and thus the case \( B \geq 2 \) is not considered in the analysis. As is expected, the plant density of the biologically relevant spatially uniform steady state \( v_s^+ \) decreases as the strength of intraspecific competition increases (decrease in \( k \)).

\textbf{2.2 Pattern onset, existence & stability}

Onset of spatial patterns due to a decrease in precipitation \( A \) occurs as \( v_s^+ \) loses stability to spatially nonuniform perturbations. This is referred to as a Turing-Hopf bifurcation and different methods to analytically calculate an asymptotic approximation of the rainfall threshold exist \cite{15}. In this context, this is best performed in travelling wave coordinates; patterned solutions of (2.1) are periodic travelling waves, i.e. solutions that are periodic in space and move in the uphill direction.
of the domain at a constant speed $c \in \mathbb{R}$, and motivate this approach. The transformation into a comoving frame is achieved by setting $z := x - ct$, $U(z) := u(x,t)$ and $W(z) := w(x,t)$, which yields the travelling wave ODE system

$$WU^2 \left(1 - \frac{U}{k}\right) - BU + c \frac{dU}{dz} + \frac{d^2U}{dz^2} = 0,$$

(2.2a)

$$A - W - WU^2 + (c + \nu) \frac{dW}{dz} + d \frac{d^2W}{dz^2} = 0.$$

(2.2b)

Patterned solutions of the PDE system (2.1) correspond to limit cycles of the ODE system (2.2). In the PDE setting, the patterns’ features, such as their existence, would typically be investigated in a one-dimensional parameter space of a chosen control parameter, here the precipitation volume $A$. However, the transformation into travelling wave coordinates introduces an additional parameter, the migration speed $c$. If patterns exist for a given rainfall level in (2.1), then limit cycles with a range of different migration speeds exist in (2.2) for the same precipitation volume. As a consequence, the patterns’ features need to be addressed in a two-dimensional parameter space in the travelling wave coordinates, comprised of the chosen PDE bifurcation parameter and the uphill migration speed $c$.

A convenient tool to investigate pattern onset, existence and stability is numerical continuation, but the size of the slope parameter $\nu$ also allows for an analytical derivation of some properties valid to leading order in $\nu$ as $\nu \to \infty$. A significant challenge of this approach is posed by the dependence of the parameter region in which patterns exist on the slope parameter $\nu$. In particular, the dependence of both $A$ and $c$ on $\nu$ throughout the parameter region covers several orders of magnitude. For the Klausmeier model without intraspecific competition, an extensive analysis of these dynamics exists [38, 37, 42, 43, 44]. The focus of this paper is on $c = O_s(1)$ ($x = O_s(y) \iff x = O(y)$ but not $x = o(y)$) as $\nu \to \infty$ but the pattern dynamics in (2.1) for both small and large migration speeds are expected to be qualitatively similar to those of the model without intraspecific competition.

The rainfall level the Turing-Hopf bifurcation causing pattern onset due to a destabilisation of the spatially uniform equilibrium is $A = O_s(\sqrt{\nu})$ [44]. An asymptotic approximation of this critical threshold is found by calculating the corresponding Hopf bifurcation in the travelling wave framework and determining the maximum rainfall level on the loci of Hopf bifurcations in the $(A, c)$ plane. The method follows that used for the (extended) Klausmeier model in [44, 15]. The rescaling $U = A/BU^*$, $W = B^2/3W^*$, $z = 1/\sqrt{Bz^*}$, $c = \sqrt{Bc^*}$, $\Gamma = A^2/(B^{5/2}\nu)$, $\kappa = Bk/A$ and the assumption that $A = O_s(\sqrt{\nu})$ yields

$$U' = \tilde{U},$$

(3.3a)

$$\tilde{U}' = -c\tilde{U} - WU^2 \left(1 - \frac{U}{k}\right) + U,$$

(3.3b)

$$W' = -\Gamma \left(1 - U^2W\right),$$

(3.3c)

valid to leading order in $\nu$ as $\nu \to \infty$, after dropping the asterisks for brevity. The Hopf locus in the $(A, c)$ parameter plane is calculated through a linear stability analysis. The eigenvalues $\lambda \in \mathbb{C}$ of the Jacobian matrix of (2.3) are assumed to be purely imaginary, i.e. $\lambda = i\omega$, $\omega \in \mathbb{R}$. This allows the Jacobian’s characteristic polynomial to be split into its real and imaginary parts and for $\omega$ to be eliminated. The resulting condition implicitly describes the Hopf-locus. Implicit differentiation facilitates the explicit calculation of the rainfall threshold at which the Turing-Hopf bifurcation occurs.
Investigation of this rainfall threshold shows that increases in intraspecific competition shift the Turing-Hopf bifurcation to lower rainfall levels (Fig. 2.1). The stabilisation of the spatially uniform vegetated state is caused by a reduction in plant equilibrium density under strong intraspecific competition which reduces the water requirements of the spatially uniform state.

The subset of the \((A, c)\) parameter plane in which patterned solutions of (2.1) exist can be mapped out using numerical continuation. In terms of the PDE control parameter \(A\), the pattern existence region is bounded from below by a homoclinic solution. Methods for calculating the location of homoclinic solutions exist [4], but for the analysis presented in this paper it suffices to approximate homoclinic solutions by patterned solutions of large wavelength, say \(L = 1000\). The upper precipitation bound of the pattern existence parameter region is given by either the Hopf locus or the location of a fold in the solution branch, if such a fold occurs. The impact of intraspecific competition is a reduction in the size of the parameter region in which patterns exist. As discussed above, the Hopf bifurcation occurs at lower rainfall levels if intraspecific competition is strong and the locus of the fold mimics this behaviour. By contrast, the homoclinic solution is located at higher precipitation values if intraspecific competition is strong (Fig. 2.1).

The stability of patterned solutions of (2.1) is determined through a calculation of the essential spectrum of the corresponding periodic travelling wave solution in (2.2). The essential spectrum \(S \subset \mathbb{C}\) of a periodic travelling wave describes the leading order behaviour of perturbations to it. Due to translation invariance of periodic travelling waves, the origin is excluded from the following definition of stability. If \(S\) lies entirely in \(\{z \in \mathbb{C} : \Re(z) < 0\}\), then the corresponding pattern is stable, otherwise it is unstable. The essential spectrum is calculated through a numerical continuation algorithm by Rademacher et al. [31], and I refer to [31, 39, 41] for full details on the method and to [17] for an overview of an implementation to a related system. In particular, the algorithm also facilitates the tracking of stability boundaries, such as that displayed in Fig. 2.1 based on a numerical continuation of the spectra.

An application of this algorithm to (2.1) yields that strong intraspecific competition stabilises patterned solutions at slower uphill migration speeds (Fig. 2.1). However, combined with the results on pattern existence discussed above, this also shows that the transition from patterned states to a full desert state occurs at higher rainfall levels if intraspecific competition is strong (Fig. 2.1). Thus, neglect of intraspecific competition dynamics in the model may cause an overestimation of both the patterns’ existence and stability ranges.

3 Multispecies model

3.1 Model

Species coexistence in dryland ecosystems has previously been addressed in several modelling frameworks. Both Baudena and Rietkerk [2] and Nathan et al. [30] have successfully explained tree-grass coexistence in patterned form by assuming that only one of the two species induces a pattern-forming feedback loop. The assumption that plant species significantly differ in their functional responses to the environment, however, imposes a restriction on the applicability to a general setting. To overcome this, I have introduced a modelling framework to investigate species coexistence that does not rely on such an assumption in a previous paper [16].

Without intraspecific competition being considered, this model successfully captures species coexistence as long transient states in both a spatially uniform and a vegetation pattern state, provided that species are of similar average fitness [16]. Moreover, coexistence is also possible in a spatially nonuniform savanna state (periodic travelling wave solutions in which the plant density oscillates between two nonzero biomass levels) if there is a balance between the species’ local competitiveness
Figure 2.1: **Intraspecific competition stabilises spatially uniform solutions and patterns at lower migration speeds.** Onset, existence and stability parameter regions of patterned solutions of (2.1) are shown in the \((A, c)\) parameter plane. Onset at high precipitation values occurs at a Hopf bifurcation, while onset at low values occurs at a homoclinic solution. The existence region of patterns is bounded below by the homoclinic solution and bounded above by either the Hopf bifurcation or a fold in the solution branch, if it exists. Part (a) corresponds to strong intraspecific competition, (b) to weak intraspecific competition. The loci of both the Hopf bifurcation and the fold in the patterned solution branches are shifted to lower precipitation volumes if intraspecific competition is strong, while the homoclinic solution occurs at higher rainfall levels. The relative size of the stability region is enlarged by strong intraspecific competition and includes patterns at lower migration speeds.
and their colonisation abilities [17]. If additionally intraspecific competition dynamics are taken into account, then coexistence is possible in a vegetation pattern state (periodic travelling wave solutions in which the plant density oscillates between a high biomass level and zero), provided the intraspecific competition among the superior coloniser is sufficiently large [12]. In this paper, I provide more information on the impact of intraspecific competition on the origin and existence of patterned model solutions in which species coexist.

To do so, the model used in the analysis is

\[
\frac{\partial u_1}{\partial t} = w u_1 \left( u_1 + H u_2 \right) \left( 1 - \frac{u_1}{k_1} \right) - B_1 u_1 + \frac{\partial^2 u_1}{\partial x^2},
\]

\[
\frac{\partial u_2}{\partial t} = F w u_2 \left( u_1 + H u_2 \right) \left( 1 - \frac{u_2}{k_2} \right) - B_2 u_2 + \frac{\partial^2 u_2}{\partial x^2},
\]

\[
\frac{\partial w}{\partial t} = \frac{A}{\text{rainfall}} - \frac{w}{\text{evaporation and transpiration}} - \frac{w (u_1 + u_2) (u_1 + H u_2)}{\text{water uptake by plants}} + \frac{w}{\text{water flow downhill}} + \frac{\partial w}{\partial x} + D \frac{\partial^2 w}{\partial x^2},
\]

after a suitable nondimensionalisation [12]. The model is based on the single-species model (2.1) presented in Sec. 2 and consequently all modelling assumptions are identical to those taken in the single-species model. The parameters \(B_1\) and \(k_1\) of species \(u_1\) correspond to \(B\) and \(k\) in the single-species model (2.1), while the additional parameters \(F\), \(H\), \(k_2\), \(B_2\) and \(D\) are all related to the newly introduced species \(u_2\) and represent its growth, impact on the pattern-forming feedback, strength of intraspecific competition, death rate and dispersal coefficient, respectively.

Moreover, the single species model (2.1) can be obtained from (3.1) by setting one of the plant densities to zero. In the case of \(u_1 = 0\) this further requires a rescaling. As a consequence, results presented in Sec. 2 also hold for the multispecies model (3.1) in the absence of a competitor species. The introduction of a second species nevertheless has an impact on the single-species states of the system, which is discussed below.

The model without intraspecific competition is considered in [17]. It is obtained from (3.1) by taking the limit \(k_1, k_2 \to \infty\). This limiting behaviour motivates a comparison of results presented in this paper with those in [17], to address what impact the consideration of intraspecific competition dynamics has on the modelling framework. I present results for \(k_1 = k_2\) to make such a comparison, but also discuss the effects of varying \(k_1\) and \(k_2\) separately.

The main purpose of this paper is to discuss the impact of intraspecific competition, and in general further develop the understanding of coexistence of herbaceous species and woody species in dryland ecosystems. Due to the symmetry in the model, I assume, without loss of generality, that \(u_1\) and \(u_2\) represent a grass and tree/shrub species, respectively. As detailed in [17], this yields quantitative assumptions on the model parameters. In particular, the grass species is assumed to grow at a faster rate \((F < 1)\), suffer from higher mortality \((B_1 > B_2)\), have a stronger impact on the soil’s permeability per unit biomass \((H < 1)\) and disperse faster \((D < 1)\). As a consequence, the grass species \(u_1\) is superior in its colonisation abilities and is thus referred to as the coloniser species or pioneer species. In the absence of intraspecific competition, species coexistence occurs as a state representing a savanna biome if the inferior coloniser \(u_2\) is the superior local competitor [17], quantified by the average local fitness difference \(B_2 - FB_1\) being negative [16]. In this paper, I focus on this parameter setting to explore the role of intraspecific competition and species difference in
Figure 3.1: **Linear stability of spatially uniform equilibria.** The spatially uniform equilibria of (3.1) and their stability under changes to the precipitation volume $A$ are shown. Solid lines indicate stable states, dashed lines unstable states. For high precipitation values, the coexistence equilibrium $v_{c,+}^m$ is stable because interspecific competition for water is sufficiently lower than intraspecific competition. A decrease in $A$ causes $v_{c,+}^m$ to lose stability to the single-species tree equilibrium $v_{t,+}^m$. For the parameters used in the visualisation the stability change occurs where both equilibria intersect, but this need not be the case. The grass equilibrium $v_{g,+}^m$ is unstable for all $A$, because changes in rainfall cannot change which species is of higher local average fitness. Here $k_1 = k_2 = 1000$ to keep intraspecific competition sufficiently weak. For significantly smaller values of $k_1 = k_2$ only the coexistence equilibrium is stable.

the coexistence of species in vegetation patterns. For the latter, I follow the approach of [16] and set

$$B_2 = B_1 - \chi(B_1 - \tilde{B}_2), \quad F = 1 - \chi(1 - \tilde{F}), \quad H = 1 - \chi(1 - \tilde{H}), \quad D = 1 - \chi(1 - \tilde{D}),$$

(3.2)

where $\tilde{B}_2$, $\tilde{F}$, $\tilde{H}$ and $\tilde{D}$ are typical parameter estimates for a tree species. Thus, the difference between $u_1$ and $u_2$ is quantified by a single parameter $0 \leq \chi \leq 1$. Note that the intraspecific competition strengths $k_1$ and $k_2$ are not included in this definition as their impact is addressed separately. Unless otherwise stated, I set $B_1 = 0.45$, $\tilde{B}_2 = 0.004$, $\tilde{F} = \tilde{H} = \tilde{D} = 0.01$, $k_1 = 10$, $k_2 = 10$, $d = 500$ and $\nu = 182.5$ and $\chi = 0.9$. The precipitation volume $A$ being the main bifurcation parameter of the system. The lack of detailed empirical data does not allow for an accurate parameter estimation and therefore model parameters are obtained from previous theoretical work (e.g. [46, 23]). Nevertheless, parameter estimates can still be obtained based on modelling assumptions. For example, under the assumption that biomass decreases exponentially in the absence of resources and other processes, mortality rates can be inferred from the time needed for a plant species to drop below a critical extinction threshold, starting from its maximum level [1]. Similar arguments can be applied to deduce other parameters in the model [17].

### 3.2 Stability in spatially uniform model

As for the single-species model (2.1), an understanding of patterned solutions requires knowledge of the system’s dynamics in a spatially uniform setting. The system has up to seven spatially
uniform equilibria, as visualised in Fig. [3.1]. The desert steady state \( \mathbf{v}_m^d = (0, 0, A) \) and the pair of single-species grass equilibria \( \mathbf{v}_m^{g,\pm} = (u_1^{g,\pm}, 0, u^{g,\pm}) \), where \( u_1^{g,\pm} = u^{g,\pm} \) and \( u^{g,\pm} = \pm \) and which exist provided \( A > A_m^g := A_{\text{min}} \), are identical with those of the single-species model presented in Sec. 2. Due to the symmetry in the model, (3.1) also admits a pair of single-species tree equilibria, given by

\[
\mathbf{v}_m^{t,\pm} := \left( 0, u_2^{t,\pm}, w^{t,\pm} \right) = \left( 0, \frac{FHA \pm \sqrt{(FHA)^2 - 4B_2H \left( B_2 + \frac{FHA}{k_2} \right)}}{2H \left( B_2 + \frac{FHA}{k_2} \right)}, \frac{A}{1 + H \left( \frac{u_2^{t,\pm}}{2} \right)^2} \right),
\]

which exist provided

\[
A > A_m^t := \frac{2B_2}{FH} \left( \frac{1}{k_2} + \sqrt{1 + \frac{1}{k_2^2}} \right).
\]

Finally, a pair of coexistence spatially uniform steady states \( \mathbf{v}_m^{c,\pm} := (u_1^{c,\pm}, u_2^{c,\pm}, w^{c,\pm}) \) exists, provided precipitation is sufficiently large. While it is possible to obtain a closed-form expression for \( \mathbf{v}_m^{c,\pm} \), its algebraic complexity renders any analytical approach to study its properties impracticable.

The desert steady state \( \mathbf{v}_m^d \) is always linearly stable (the eigenvalues of its Jacobian are \( -B_1, -B_2, -1 \)). The grass equilibrium \( \mathbf{v}_m^{g,\pm} \) is linearly stable for

\[
A < A^G_T := \frac{B_2^2 + k_1^2 \left( B_2 - FB_1 \right)^2}{Fk_1 \left( B_2 - FB_1 \right)},
\]

provided \( 0 < B_2 - FB_1 < FB_1 \) and \( k_1 > \sqrt{B_2(2FB_1 - B_2)(B_2 - FB_1)^{-1}} \), and unstable otherwise. The second grass equilibrium \( \mathbf{v}_m^{g,1} \) is unstable. The tree equilibrium \( \mathbf{v}_m^{t,\pm} \) is stable for

\[
A < A^T_T := \frac{F^2B_2^2 + Hk_2^2 \left( B_2 - FB_1 \right)^2}{FHk_2 \left( FB_1 - B_2 \right)},
\]

provided \( -B_2 < B_2 - FB_1 < 0 \) and \( k_2 > \sqrt{B_1FH(2B_2 - FB_1)(H(FB_1 - B_2))^{-1}} \), and unstable otherwise. The second tree equilibrium \( \mathbf{v}_m^{t,\pm} \) is unstable. Existence and stability of the coexistence equilibria \( \mathbf{v}_m^{c,\pm} \) are found using the numerical continuation software AUTO-07p [11]. The lower branch \( \mathbf{v}_m^{c,\pm} \) is always unstable, while \( \mathbf{v}_m^{c,\pm} \) is stable if intraspecific competition is sufficiently stronger than interspecific competition. In particular, the intraspecific competition of the locally superior species needs to be sufficiently strong for coexistence to be stable, while that of the locally inferior species only has a negligible effect on the stability of the equilibrium.

The upper bounds on the rainfall parameter and other constraints required for stability of the spatially uniform single-species equilibria are a crucial difference to the stability results for the single-species model [2,1]. As precipitation is increased, the single-species equilibria lose their stability to the coexistence equilibrium \( \mathbf{v}_m^{c,\pm} \), because an increase in resource availability causes a reduction in the strength of interspecific competition (Fig. 3.1). In the absence of intraspecific competition, no coexistence equilibrium exists and no upper bound on the rainfall parameter for stability of the single-species equilibria exists.

Moreover, both in [3,1] and in the absence of intraspecific competition, no bistability of the single-species equilibria can occur, as the upper precipitation bounds satisfy \( A^g_A^t < 0 \) (Fig. 3.1).
The quantity $B_2 - FB_1$, which determines the signs of $A_g^u$ and $A_t^u$, denotes the local average fitness difference between both species in the absence of any intraspecific competition [16]. A definition of local average fitness in (3.1) is not as straightforward as in the model with no intraspecific competition, but the stability thresholds $A_g^u$ and $A_t^u$ highlight that intraspecific competition cannot change which species is of higher local average fitness.

3.3 Single-species patterns

Onset and existence of single-species patterns remain independent of the introduction of a second species, i.e. results presented for the single species model (2.1) also hold for the multispecies model (3.1). By contrast, stability of single-species patterns is significantly affected by the introduction of a competitor species and is also related to the onset of coexistence patterns.

As for the single species model (2.1), patterned solutions of (3.1) are limit cycles of the corresponding travelling wave ODE system

\[
W U_1 (U_1 + HU_2) \left( 1 - \frac{U_1}{k_1} \right) - B_1 U_1 + c \frac{dU_1}{dz} + \frac{d^2U_1}{dz^2} = 0, \tag{3.3a}
\]

\[
FW U_2 (U_1 + HU_2) \left( 1 - \frac{U_2}{k_2} \right) - B_2 U_2 + c \frac{dU_2}{dz} + D \frac{d^2U_2}{dz^2} = 0, \tag{3.3b}
\]

\[
A - W - W (U_1 + U_2) (U_1 + HU_2) + (c + \nu) \frac{dW}{dz} + \frac{d^2W}{dz^2} = 0, \tag{3.3c}
\]

which is obtained from the PDE model (3.1) by setting $u_1(x, t) = U_1(z)$, $u_2(x, t) = U_2(z)$ and $w(x, t) = W(z)$ for $z = x - ct$, $c \in \mathbb{R}$. As in the single-species model (2.1), this introduces a new parameter, the uphill migration speed $c$, and the bifurcation analysis is performed in the $(A, c)$ parameter plane. However, for illustrative purposes, I fix the migration speed in the presentation of the bifurcation diagrams, but emphasise that the results do not qualitatively depend on the choice of $c$, unless otherwise stated. The transformation into the travelling wave framework enables the calculation of a pattern’s essential spectrum to determine its stability using the numerical continuation method by Rademacher et al. [31], and I again refer to [31, 39, 41] for full details on the method and to [17] for an overview on how this algorithm is implemented for (3.1) in the limit $k_1, k_2 \to \infty$.

Unlike pattern onset and existence, the stability of single-species patterns of (3.1) is affected by the second species in the system. For a single-species pattern to be stable in the multispecies model (3.1), it needs to be stable in the context of the single-species model (2.1) and stable to the introduction of the competitor species, two conditions that are independent of each other. The stability of a single-species pattern to the introduction of the competitor species is determined by a comparison of its essential spectrum in the multispecies model with that of the same solution in the single-species model (Fig. 3.2). The spectrum of the periodic travelling wave in the single-species model is a subset of that of the solution in the multispecies model. The additional elements in the latter describe the leading order behaviour of perturbations due to the introduction of the competitor species. Thus, a pattern that is stable in the corresponding single-species model may be unstable in the multispecies model (3.1) due to its interaction with a competitor species.

3.4 Onset and existence of coexistence patterns

Onset of coexistence patterns can occur through three different mechanisms. As for the single-species patterns discussed in Sec. 2 two potential causes of pattern onset are a homoclinic solution...
Figure 3.2: **Introduction of a second species affects stability of single-species patterns.** A comparison of the essential spectra of a single-species grass pattern in the single-species model (2.1) (a) and the multispecies model (3.1) (b) are shown. The spectrum in the single-species model is a subset of the spectrum in the multispecies model. The additional elements of the spectrum correspond to the leading order behaviour of perturbations in $u_2$. Note that the spectra yield that the corresponding single-species pattern is stable in the single-species model, but unstable in the multispecies model due to the introduction of species $u_2$. The vertical lines visualise the imaginary axis. The parameter values are $A = 2$ and $c = 0.25$. 
and a Turing-Hopf bifurcation of the spatially uniform coexistence equilibrium $v_{c,-}^m$. Onset of coexistence patterns can further occur on a solution branch of a single-species pattern as it loses/gains stability to the introduction of the second species. As outlined in the previous section, such a bifurcation can be detected through a comparison of the single-species pattern’s essential spectra in the context of the single-species model (2.1) and the multispecies model (3.1). The same mechanism also causes pattern onset in the absence of any intraspecific competition [17]. Onset at a homoclinic solution or at a Turing-Hopf bifurcation of a spatially uniform equilibrium, however, cannot occur if intraspecific competition dynamics are neglected, as no spatially uniform equilibria exist. In (3.1), solution branches of coexistence patterns either connect two single-species patterns (the only mechanism that occurs in the absence of intraspecific competition), a single-species pattern with the spatially uniform coexistence state, or the spatially uniform coexistence state with a homoclinic solution. The choice of which of these three mechanisms occurs depends on both the strength of intraspecific competition and the difference between both species, as is outlined below.

### 3.4.1 The role of intraspecific competition

If $k_1 = k_2$ is small and species difference is sufficiently large so that $u_1$ and $u_2$ represent a typical grass and tree species, respectively, two Hopf bifurcations on the spatially uniform coexistence equilibria occur and are the origins of coexistence pattern solution branches that connect to either of the single-species pattern branches. (Fig. 3.3a). Typically, one of the Hopf bifurcations occurs on $v_{c,-}^m$ and patterns originating there are of very large wavelength, beyond the $L = 1000$ threshold used to approximate homoclinic solutions in this bifurcation analysis. Note that the Hopf bifurcation on $v_{c,-}^m$ does not cause a stability change of the equilibrium because a third eigenvalue with positive real part exists. As $k_1 = k_2$ increases, the spatially uniform coexistence equilibrium is shifted to higher precipitation volumes and one of its biomass components may attain ecologically irrelevant negative values. Moreover, the Hopf bifurcation on $v_{c,-}^m$ moves along the solution branch, through the fold, and onto the $v_{c,+}^m$ branch (Fig. 3.3b). A further increase in $k_1 = k_2$ reduces the distance between both Hopf bifurcations, until they coincide. Beyond this threshold, no Hopf bifurcation along the spatially uniform coexistence equilibrium exists. However, coexistence patterns continue to occur. As in the analysis shown in [17] (the $k_1, k_2 \to \infty$ limit of the model in this paper), one coexistence pattern solution branch connects both single-species pattern branches for sufficiently large $k_1 = k_2$ (Fig. 3.3c). In other words, intraspecific competition shifts the existence region of both the spatially uniform coexistence equilibrium and the spatially patterned coexistence state to lower precipitation levels and enables coexistence pattern onset at a Hopf bifurcation on the spatially uniform equilibrium.

An investigation with one of the species’ intraspecific competition strengths being fixed, gives more insight into the different roles of both parameters. A decrease in intraspecific competition of the coloniser species (i.e. increase in $k_1$) reduces the size of the parameter region for which coexistence patterns occur (Fig. 3.5a). As is discussed in [12] and visualised in Fig. 3.5a and 3.5b, strong intraspecific competition among the coloniser species facilitates coexistence patterns because it shifts the upper rainfall threshold at which pattern onset occurs to higher levels, while only having a negligible impact on the onset at low precipitation volumes. This causes an increase in the size of the parameter region in which coexistence patterns exist. Variations in $k_2$, however, have a very similar effect as in the case of $k_1 = k_2$ (Fig. 3.5a and 3.5b). A reduction in intraspecific competition increases the size of the pattern existence region. In contrast to the $k_1 = k_2$ case, the Hopf bifurcation on the lower branch of the spatially uniform coexistence equilibrium has no impact on the structure of ecologically relevant solutions, as it exclusively occurs for parameter values at which one of the plant densities of the coexistence equilibrium is negative. Nevertheless, a
Figure 3.3: **Strong intraspecific competition facilitates spatially uniform coexistence and causes coexistence pattern onset at a Turing-Hopf bifurcation.** Bifurcation diagrams for different values of the carrying capacities \( k_1 = k_2 \) are shown for \( c = 0.25 \). A decrease in intraspecific competition increases the size of the precipitation interval in which coexistence patterns exist and simultaneously inhibits spatially uniform coexistence. Under strong intraspecific competition, two Hopf bifurcations along the spatially uniform coexistence equilibrium exist and cause the onset of patterns. Typically, patterns originating from the lower branch are of large wavelength and are thus omitted from the bifurcation diagram in (a). Both Hopf bifurcation loci meet in a fold as intraspecific competition is increased to a critical threshold beyond which coexistence patterns connect both single-species pattern branches ((b) and (c)). Patterned states are only shown for one value of the uphill migration speed and no stability information is provided. In (b) and (c), \( \|u_1\| \) is multiplied by \( \text{sign}(u_1) \) to visualise the occurrence of \( u_1 < 0 \).
Figure 3.4: Intraspecific competition facilitates species coexistence in vegetation patterns. Two coexistence solutions are shown. In (a), intraspecific competition is strong and the solution represents a vegetation pattern, while in (b) a solution corresponding to a savanna state is visualised, which occurs due to weak intraspecific competition. Note the different values of the precipitation parameter. A decrease in intraspecific competition destabilises the coexistence state at lower rainfall volumes. The species difference parameter is $\chi = 0.3$. 

(a) $A = 2, k_1 = k_2 = 10$

(b) $A = 3.75, k_1 = k_2 = 100$
transition to a bifurcation structure in which the coexistence pattern solution branch connects both single-species patterns occurs as follows. As $k_2$ increases the $u_1$ density of the spatially uniform coexistence equilibrium decreases and becomes negative after intersecting the single-species tree equilibrium. Consequently, the Hopf bifurcation on the equilibrium occurs for lower densities of $u_1$ as $k_2$ increases (Fig. 3.5a). At a critical threshold, the Hopf bifurcation crosses $u_1 = 0$, where it coincides with the Hopf bifurcation on the single-species tree equilibrium. For $k_2$ larger than this threshold, ecologically relevant patterns connect the Hopf bifurcations on the single-species equilibria and do not extend to the Hopf bifurcation on the coexistence equilibrium solution branch, as this occurs for $u_1 < 0$ (Fig. 3.5b).

3.4.2 Transition from a savanna to a patterned vegetation state

Strong intraspecific competition also changes the solution behaviour by facilitating species coexistence in a state representing vegetation patterns. As discussed above, increases in intraspecific competition strength shift the parameter interval in which coexistence patterns occur to lower precipitation volumes (Fig. 3.3). Associated with this is a transition from a solution-type that represents a savanna biome to a solution type that represents a vegetation pattern. Both these solution types are periodic travelling waves, but the biomass components of the former oscillate between two non-zero levels, while those of the latter oscillate between a nonzero plant density and zero (Fig. 3.4a and 3.4b). In general, the transition between the two solution types is a gradual process. However, it may be accelerated by a destabilisation and associated change in wavelength of a pattern. The savanna state patterned solution also occurs in the $k_1, k_2 \rightarrow \infty$ limit as discussed in [17].

3.4.3 The role of species difference

The difference between both plant species, quantified by the parameter $\chi$ in the parameter setting (3.2), also has a significant impact on the bifurcation structure of the system. In the results presented above, the difference between both species is set to a large value so that $u_1$ and $u_2$ represent a grass and tree species, respectively. Under this assumption, the onset of coexistence patterns at the lower precipitation bound for pattern existence always occurs along the single-species grass pattern. Decreases in the species difference $\chi$, corresponding to simultaneous changes in parameters of species $u_2$ that make it more similar to species $u_1$, cause the pattern onset locus to move along the single-species pattern branch in a decreasing precipitation direction towards the homoclinic solution of $u_1$. At a critical threshold of $\chi$, the homoclinic $u_1$ solution coincides with the homoclinic coexistence solution and a transition of the pattern onset type occurs. For lower values of the species difference parameter $\chi$, onset at low precipitation values thus occurs at the homoclinic solution (Fig. 3.6).

3.5 The effects of plant dispersal

As is discussed in [12], the ratio of the plant species’ diffusion coefficients $D$ has a significant impact on the model solutions. Plant components of the patterned model solutions are not exactly in phase. Depending on the parameters in the system, the uphill edges (and to a lesser extent the downhill edges) of the travelling wave solutions are dominated by one species, while its competitor is mostly confined to narrow regions in the centre of the bands. This behaviour can be quantified
Figure 3.5: **Strong intraspecific competition of the coloniser species and weak intraspecific competition of the locally superior species promote patterned coexistence.** Bifurcation diagrams under changing intraspecific competition of one-species only are shown. Both strong intraspecific competition among the coloniser species $u_1$ and weak intraspecific competition among the locally superior species $u_2$ increase the size of the parameter region in which coexistence patterns exist. The insets in (a) and (b) (axes limits: $A \in [6.75, 7.75], \pm \|u_1\| \in [-0.1, 0.1]$) show the onset of coexistence patterns close to $u_1 = 0$ to highlight the transition from onset at the spatially uniform coexistence equilibrium to onset at the single-species $u_2$ pattern as intraspecific competition among $u_2$ decreases. The inset in (c) (axes limits: $A \in [3.2, 3.5], \pm \|u_1\| \in [7.1, 7.3]$) shows a blow-up of the parameter region in which coexistence pattern exist. The pattern migration speed is $c = 0.25$. In (a) and (b), $\|u_1\|$ is multiplied by $\text{sign}(u_1)$ to visualise the occurrence of $u_1 < 0$. For an interpretation of colours and linestyles used in the visualisation, see the legend of Fig. 3.3.
Figure 3.6: A transition from coexistence pattern onset at a single-species pattern to onset at a homoclinic solution occurs due to increases in species similarity. Bifurcation diagrams for different values of the species difference parameter $\chi$ are shown in (a) and (b). A transition from coexistence pattern onset at a homoclinic solution to onset at the single-species grass pattern occurs as species difference increases. The type of onset point and the precipitation level at which onset occur are tracked in (c). The pattern migration speed is $c = 0.25$. For an interpretation of colours and linestyles used in (a) and (b), see the legend of Fig. 3.3.
through the linear correlation

\[ \rho(U_1, U_2) = \frac{\text{cov}(\tilde{U}_1, \tilde{U}_2)}{\sigma(\tilde{U}_1)\sigma(\tilde{U}_2)}, \]

between both plant densities, where \( \text{cov}(\cdot, \cdot) \) denotes the covariance of two vectors, and \( \sigma(\cdot) \) the standard deviation. The vectors \( \tilde{U}_1 \) and \( \tilde{U}_2 \) are obtained by discretising the spatial domain and evaluating the plant densities \( u_1 \) and \( u_2 \) on this mesh. Note that the linear correlation takes values \( -1 \leq \rho(U_1, U_2) \leq 1 \), and a larger correlation corresponds to a more in-phase-like appearance of both plant patterns.

An exhaustive calculation of the linear correlation in the parameter space can be performed, as numerical continuation allows for an easy generation of model solutions. The ratio of the plant species’ diffusion coefficients \( D \) has the most significant impact on the correlation (Fig. 3.7). To specifically focus on the coexistence of grasses and trees, I have outlined in [12] that if the species with slower growth rate also disperses at a slower rate (i.e. \( (F - 1)(D - 1) > 0 \)), then larger differences in the diffusion coefficients yield smaller spatial correlations, as the uphill edge of each vegetation band features a high density of the faster disperser only. In this parameter setting, that species can be referred to as the pioneer species, as it is responsible for the colonisation of the bare ground in the uphill direction, before its competitor species utilises the increased resource availability in the newly colonised ground. Increases in the similarities of the species’ dispersal behaviour causes an increase in the spatial correlation. In particular, the correlation attains its maximum value close to \( D = 1 \), i.e. where both plant species diffuse at the same rate. For \( D = 1 \), the solution profile shows both plant species to be approximately in phase (Fig. 3.7a).

By contrast, if the assumption that one species both grows and disperses at a faster rate is dropped (i.e. \( (F - 1)(D - 1) < 0 \)), then the correlation between the plant species does not decrease significantly from its maximum close to \( D = 1 \) (Fig. 3.7b). However, the solution changes significantly. Instead of occurring in a patterned configuration with its competitor, the faster dispersing species attains a spatially uniform state, while the faster growing species (and slower disperser) remains in a patterned state (Fig. 3.7a).

4 Discussion

The inclusion of intraspecific competition dynamics in the modelling framework of the Klausmeier model for dryland vegetation patterns has a significant impact on the model solutions. In the context of the single-species model (2.1), neglecting intraspecific competition among plants leads to an overestimation of the precipitation range in which patterns occur, while in the multispecies model (3.1), intraspecific competition is a key ingredient in the successful capture of species coexistence in a solution type that represents patterned vegetation.

In the single-species Klausmeier model, the rate of plant growth grows without bound as the plant density increases [23]. One possible motivation for this simplistic description is the type of ecosystem the modelling framework is describing. Dryland vegetation is limited by the low volumes of precipitation in arid ecosystems and thus total biomass in generally low. Thus, any negative density-dependent effects on the rate of plant growth caused by intraspecific competition are generally neglected in the Klausmeier model and similar modelling frameworks [23, 33, 22]. However, even though total biomass on the ecosystem-wide scale is low, the spatial self-organisation of plants leads to the occurrence of localised patches in which biomass is high, thus raising a potential issue for the assumption to neglect intraspecific competition.
Figure 3.7: Plant dispersal influences spatial species distribution and enables coexistence of a spatially uniform fast disperser with a patterned slow disperser. The spatial correlation between plant species is shown in (b) and some example solutions are displayed in (b). Note that the spatial correlation peaks close to $D = 1$ and only decreases slightly for $D > 1$. In this parameter setting, coexistence of the locally superior species (which also disperses faster) in a spatially uniform state with a patterned state of the superior coloniser (but slower disperser) is possible. The species difference is set to $\chi = 0.3$ and the wavelength $L$ is fixed to $L = 25$ in the numerical continuation with the uphill migration speed allowed to vary.
Figure 4.1: Large species difference inhibits coexistence onset from desert. Grass density $u_1$ and tree density $u_2$ of a model solution of (3.1) are shown in the $(t, x)$ under increasing precipitation volume $A$. Initially, both biomass densities are set to zero, apart from a region in the centre of the domain. The tree species becomes extinct and onset of a single-species grass pattern occurs. Onset of a coexistence pattern is only possible after a reintroduction of species $u_2$ at $t = 1000$, following a sufficient increase in precipitation $A$. A further increase in $A$ causes a transition from the single-species grass pattern to a spatially uniform single-species state, but the coexistence pattern eventually invades. The parameter values are consistent with the bifurcation diagram shown in Fig. 3.6b.
Indeed, model solutions of the Klausmeier model and its extensions typically undergo several wavelength changes in their transition from a uniformly vegetated state to a desert state along the precipitation gradient. Towards the lower end of the rainfall range supporting stable patterns, the solutions' wavelength become large and biomass may locally increase to biologically unrealistic levels [3]. The consideration of intraspecific competition dynamics in the single-species model (2.1) presented in this paper does now allow for such solutions due to the existence of an upper bound, the maximum standing biomass, on the plant density at every space point. As a consequence, the patterned state loses stability (and existence) to the desert equilibrium at higher precipitation volumes than in the model without intraspecific competition (Fig. 2.1). Hence, it can be concluded that models without intraspecific competition overestimate the resilience of vegetation patterns to increasing aridity and that an understanding of intraspecific competition dynamics is essential to make predictions on desertification processes in ecosystems.

A characteristic feature of banded vegetation is the uphill migration of vegetation stripes [9]. Model solutions of the Klausmeier model consistently predict a reduction in uphill migration speed before a destabilisation due to increasing aridity occurs [3, 40], a property that can be used for early detection of degradation processes. While the introduction of intraspecific competition to the single-species Klausmeier model decreases the size of the rainfall range supporting stable patterns, it stabilises patterned solutions with slower uphill migration speeds (Fig. 2.1). This further emphasises the importance of taking intraspecific competition dynamics into account when developing methods of predicting future ecosystem developments, as they have a significant impact on ecologically important properties of model solutions.

The impact of intraspecific competition in the framework of the multispecies model (3.1) is even more significant, because it stabilises species coexistence both in a spatially uniform state and in a state representing vegetation patterns (i.e. oscillations between a high level of biomass and zero). In the absence of intraspecific competition dynamics, species coexistence can only occur in a spatially nonuniform savanna-type state (i.e. oscillations between two nonzero biomass levels) [17]. The main mechanism that enables coexistence both in (3.1) and the model neglecting intraspecific competition is the spatial self-organisation of vegetation, which causes heterogeneities in the environmental conditions. Coexistence is possible if the species which is locally inferior is superior in its colonisation abilities. The latter allows the species to utilise the spatial heterogeneities in the resource availability to colonise new ground, before eventually being outcompeted locally by a second species [17]. In the absence of intraspecific competition dynamics, such a balance is only maintained for relatively high volumes of precipitation, thus giving rise to the savanna-type model solution. As precipitation decreases, the coexistence state loses its stability to a single-species state of the coloniser species, as the beneficial effects of the coloniser's ability to self-organise itself into patterns tips the balance in its favour [17]. If intraspecific competition of the coloniser species is sufficiently strong, however, its advantages due to its self-organisation abilities decline as the maximum density in single plant patches declines. This stabilises the coexistence state at lower rainfall volumes at which it represents a vegetation pattern state (Fig. 3.5). This stabilisation of coexistence is related to classical results from nonspatial Lotka-Volterra competition models which state that coexistence is possible if intraspecific competition among all species is stronger than interspecific competition between them (e.g. 5). The crucial difference is that due to the spatial self-organisation in the system, strong intraspecific competition of one species only suffices to explain species coexistence [12].

Variations in the strength of intraspecific competition of both species further have an impact on the system's bifurcation structure, and in particular on the onset of patterns. Decreases in intraspecific competition strength cause a transition of the pattern onset mechanism at high precipitation levels from a Hopf bifurcation of the spatially uniform coexistence equilibrium to a stability change
of a single-species pattern to the introduction of a second species (Fig. 3.3b and 3.3c). As a consequence, model results predict that under weak intraspecific competition no transition from a spatially uniform coexistence state to a patterned state can occur. Instead, one species’ biomass decreases to zero as aridity increases causing a transition to a spatially uniform single-species state. Only a reintroduction of the extinct species after a further decrease in precipitation can result in a patterned coexistence state.

The mechanism causing onset of coexistence patterns at the lower end of the precipitation range supporting their existence mainly depends on the difference between both species. If species are sufficiently similar, onset occurs at a homoclinic solution, while otherwise onset occurs due to a stability change of a single-species pattern to the introduction of a competitor (Fig. 3.6). This has significant ecological consequences as this predicts that the introduction of two significantly differing species into a desert state under sufficiently high precipitation volumes will not result in a successful invasion of the coexistence state. Instead, one species will become extinct and only a single-species pattern will prevail (Fig. 4.1). A transition to a coexistence state only becomes possible after a further increase in rainfall and a reintroduction of the second species. This, combined with the insights into ecosystem resilience presented above, highlights that mathematical modelling can be a powerful aid for the development of conservation programs in drylands.

The various hypotheses proposed by both (3.1) and (2.1) could be tested using empirical data. However, the acquisition of data from vegetation patterns that are of sufficiently high quality and quantity is a significant challenge yet to be addressed by ecologists. Exceptions, for example on the uphill migration speed of vegetation stripes in various sites worldwide, exist [9] but in isolation such datasets are not sufficient to provide empirical tests for the models presented in this paper. Methods for data collection (in particular image processing) are expected to improve and thus such tests may become possible in the future.

The intraspecific competition dynamics among plant species are incorporated into the modelling framework in a general way by combining them into one single variable, the maximum standing biomass, for each species. The significant impact of strong intraspecific competition proposed by the results presented in this paper motivates a more detailed investigation of its details in the future. A promising option is the explicit modelling of toxic soil compounds produced by plants which inhibit their growth [27]. The impact of toxicity on multispecies ecosystems has been shown to be significant even in the absence of competition for water [24] and thus forms a promising first step for a model extension that applies to dryland ecosystems.

The modelling framework presented in this paper is very general and provides a deliberately simple description of a self-organisation principle in ecology. Moreover, results presented in this paper only depend on basic species properties but do not rely on any species-specific assumptions. This suggests that results may be extended to a host of different consumer-resource ecosystems in which coexistence of consumer species occurs. Indeed, the significant impact of self-organisation in such ecosystems has been addressed in recent years through both empirical and theoretical approaches [8 6], which emphasise that pattern formation can play a significant role in species coexistence and suggest more detailed theoretical studies of the phenomenon in the future to advance our understanding of species coexistence.
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