Species coexistence facilitated by intraspecific competition in a model for dryland vegetation patterns

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Abstract

The exploration of mechanisms that enable species coexistence under competition for a sole limiting resource is widespread across ecology. One classical example is the coexistence of herbaceous and woody species in self-organised dryland vegetation patterns. Previous theoretical investigations have explained this phenomenon by making strong assumptions on the differences between grasses and trees (e.g. contrasting dispersal behaviours or different functional responses to soil moisture). Motivated by classical theory on competition models in population dynamics, I argue that the interplay between interspecific and intraspecific competition of a single species can explain species coexistence without relying on such assumptions. I use an ecohydrological reaction-advection-diffusion system that captures the interactions of two plant species with an explicitly modelled resource to show that coexistence is facilitated by strong intraspecific competition of one species only. Crucially, the inclusion of spatial self-organisation principles yields significant differences from the nonspatial case. In a spatially extended system, coexistence is facilitated by strong intraspecific dynamics of the species superior in its colonisation abilities if its competitor species has a higher local average fitness. In the nonspatial case, 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; periodic travelling waves; ecosystem engineering.

1 Introduction

Species coexistence in resource-limited ecosystems is a widespread phenomenon. One classical example is vegetation patterns, a characteristic feature of drylands [21]. 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 [34]. Depending on plant species' and soil properties, a range of different mechanisms are the cause of this feedback loop. For example, the formation of biogenic soil crusts on bare soil can inhibit water infiltration and induce overland water flow, or the combination of laterally extended root systems with a soil type that facilitates fast water diffusion can cause resource redistribution below-ground [30]. Dense biomass patches hence act as resource sinks. This drives further plant growth and thus closes the feedback loop.

Vegetation patterns occur in a range of different shapes, including regular stripes parallel to contours of gentle slopes [41]. 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 that causes upslope expansion and downslope contraction of single bands [11].

Coexistence of herbaceous (*grasses*) and woody (*shrubs* or *trees*) species is commonly observed in dryland vegetation patterns [41]. In the context of migrating vegetation stripes, grass species dominate the upslope edges of each band, whereas tree species are mostly confined to the centre and downslope regions of the stripes [36]. It is thus argued that grasses are the driving force of the bands' uphill migration and they are therefore referred to as *pioneer species*.

With observations of patterned vegetation being reported from all continents except Antarctica [12, 24, 41], a understanding of their ecosystem dynamics is of considerable global importance. In particular, changes to pattern properties, such as wavelength or recovery time from perturbations, can provide valuable early warning signals of catastrophic irreversible desertification processes [35]. Ecosystem degradation is a significant socio-economic issue, as agricultural resources are a major contributor to economies in drylands [39].

Due to the large temporal and spatial scales involved in the ecosystem-wide processes, the acquisition of high-quality data for vegetation patterns is limited to a small number of properties. For example, data on terrain topography, pattern wavelength and uphill migration speed can be obtained through remote sensing techniques [3, 13], but other essential information, such as a pattern's species composition can currently not be acquired in a similar way. As a consequence, a number of theoretical frameworks have been developed over the last three decades [6, 28, 43]. Continuum approaches using partial differential equations (PDEs), in particular, have been established as a powerful tool to disentangle the complex ecohydrological dynamics in patterned vegetation [31]. These theoretical studies provide valuable insights into the impact of various processes, such as grazing regimes [20, 37, 38] or secondary seed dispersal through overland water flow [10], on patterned vegetation. One aspect commonly ignored in these modelling frameworks is species richness, as most models do not distinguish between different plant species in their description of the ecohydrological dynamics.

Notable exceptions are the theoretical studies by Baudena and Rietkerk [4], Nathan et al. [33], and Ursino and Callegaro [7, 40], which have successfully reproduced species coexistence in vegetation patterns. These are based on the assumption that only one plant species induces the formation of spatial patterns, thus facilitating the growth of a second, non-pattern-forming species [4, 33], or on the hypothesis that plant species are adapted to different resource niches [7, 40]. These approaches, however, rely on the presumption that the plant species fundamentally differ in their interaction with the environment and are thus not applicable to a general setting. Mathematical models based on spatial self-organisation of plants in drylands neglecting such a distinction have to date been unable to suggest a mechanism for stable species coexistence. Instead, such approaches have proposed that species coexistence in patterned form occurs as long transient states [18] or have only successfully captured species coexistence for higher precipitation volumes under which solutions represent a savanna state (i.e. continuous vegetation cover without bare ground regions) [19].

In this paper, I argue that sufficiently strong intraspecific competition of one species only can generate species coexistence in banded vegetation patterns. I present an extension of a multispecies model to investigate the role of intraspecific competition in the coexistence of a *pioneer species* (i.e. superior coloniser) with a species that is locally superior (i.e. of higher local average fitness). The model is based on the assumption that plant species only differ in their basic parameters (such as growth and mortality rates), but not in any of their functional responses (such as the responses to different soil moisture levels). This allows the investigation to focus on basic ecological processes that apply in a general setting, instead of providing results based on species-specific properties. I highlight the importance of spatial self-organisation in the process by showing key differences in the effects of intraspecific competition between a nonspatial and spatially extended system. Model solutions presented in this paper successfully

reproduce species distribution of grasses and trees in a single vegetation band and I establish the main driving force behind this spatial distribution.

Results presented in this paper complement separate work in which the impact of intraspecific competition dynamics on both single-species and multispecies vegetation patterns are addressed through a comparison with corresponding models neglecting such dynamics [15]. Moreover, the extent to which two plant species differ from each other is singled out as an additional important factor affecting the bifurcation structure of the system. This provides additional insights beyond the parameter regimes for tree/shrub - grass coexistence considered in this paper.

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 [23]. This phenomenological model stands out due to its deliberate simplicity and thus provides a rich framework for model extensions (e.g. [5, 10, 14, 16, 17, 27, 37]). One recent extension has introduced a second plant species to the system, based on the assumption that plant species only differ in their basic parameters but not in any of their functional responses [18, 19]. This model forms the basis of the theoretical framework presented below.

2.1 Model details

To investigate the effects of intraspecific competition on species coexistence in banded vegetation, I include density-dependent inhibition effects in the growth rates of both plant species in the multispecies model presented in [18, 19]. Suitably nondimensionalised (see supplementary material), the model is

$$\frac{\partial u_1}{\partial t} = \overbrace{w u_1 \left(u_1 + H u_2\right)\left(1 - \frac{u_1}{k_1}\right)}^{\text{plant growth}} - \overbrace{B_1 u_1}^{\substack{\text{plant}\\\text{mortality}}} + \overbrace{\frac{\partial^2 u_1}{\partial x^2}}^{\text{plant dispersal}} , \tag{2.1a}$$

$$\frac{\partial u_2}{\partial t} = \overbrace{F w u_2 \left(u_1 + H u_2\right)\left(1 - \frac{u_2}{k_2}\right)}^{\text{plant growth}} - \overbrace{B_2 u_2}^{\substack{\text{plant}\\\text{mortality}}} + \overbrace{D\frac{\partial^2 u_2}{\partial x^2}}^{\text{plant dispersal}} , \tag{2.1b}$$

$$\frac{\partial w}{\partial t} = \underbrace{A}_{\text{rainfall}} - \underbrace{w}_{\substack{\text{evaporation and}\\\text{transpiration}}} - \underbrace{w\left(u_1 + u_2\right)\left(u_1 + H u_2\right)}_{\text{water uptake by plants}} + \underbrace{\nu \frac{\partial w}{\partial x}}_{\substack{\text{water flow}\\\text{downhill}}} + \underbrace{d\frac{\partial^2 w}{\partial x^2}}_{\substack{\text{water}\\\text{diffusion}}} , \tag{2.1c}$$

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 (2.1) thus represent a transversal cut along the gradient of the terrain.

The water density is denoted by $w(x,t)$ and the plant densities by $u_1(x,t)$ and $u_2(x,t)$, respectively. 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 consumed by plants, represented by the third term on the right hand side of (2.1c). 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 (e.g. through increased soil permeability). The latter is represented by $u_1 + H u_2$, where the nondimensional constant H accounts for the different contributions to this feedback by both species. Similarly, the rate of plant growth depends on both the resource density (w) and the

enhancement of water uptake in vegetated areas ($u_1 + Hu_2$). Species differ in their efficiency to convert water into biomass and this is accounted for by the nondimensional constant F. In contrast to the model in [18, 19], plant growth is also assumed to be limited by intraspecific competition, here modelled through a logistic growth-type term with maximum standing biomass k_i for species u_i. In this context, this 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]. 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 [41]. 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 herbaceous (*grass*) and woody (*tree/shrub*) species, respectively. A number of theoretical models on dryland vegetation have been proposed over the last three decades and therefore all parameter values in (2.1) are obtained from previous models. Details on parameter estimation for models of dryland vegetation are presented in [1, 23, 29]. The distinction between herbaceous and woody species yields qualitative assumptions on the model parameters [19]. The grass species both grows and dies at a faster rate ($F < 1, B_1 > B_2$), has a stronger impact on the soil's permeability per unit biomass ($H < 1$) and disperses faster ($D < 1$). The assumptions on both growth and diffusion rates yield that the grass species u_1 is superior in its colonisation abilities and is thus referred to as the *coloniser species*. In the absence of intraspecific competition, species coexistence in a state representing a savanna biome is possible if the inferior coloniser u_2 is the *superior local competitor* [19], i.e. the species of higher local average fitness, and parameters are chosen accordingly throughout this paper [18].

2.2 Model analysis

Both single-species solutions and coexistence solutions of (2.1) 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 (2.1) into a travelling wave framework, in which the 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).

Numerical simulations of the PDE system (2.1) 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 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 (2.1) 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 species of higher local average fitness 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). 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 the locally superior species is unable to utilise all of the available resource. This creates a resource niche for 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.

3.2 Patterned species coexistence

Bifurcation analysis of (2.1) establishes two different mechanisms as the cause of coexistence pattern onset; a Hopf bifurcation of the spatially uniform coexistence equilibrium, and a stability change of a single-species pattern due to the introduction of a competitor species. As a consequence, a coexistence pattern connects a single-species pattern to either the spatially uniform coexistence equilibrium (Fig. 3.2a and 3.2c) or the single-species pattern of its competitor (Fig. 3.2b) in the parameter space.

The onset of spatial patterns via a Hopf bifurcation of a spatially uniform equilibrium is a classical result of bifurcation theory (e.g. [32]). Coexistence pattern onset at such a bifurcation is inhibited (i.e. shifted to lower precipitation volumes) by both weak intraspecific competition of the superior coloniser and strong intraspecific competition of the locally superior species. As discussed in Sec. 3.1, this stabilisation of spatially uniform coexistence occurs due to the creation of a resource niche for the locally inferior species by these changes in intraspecific competition.

To understand the onset of coexistence patterns from a single-species pattern, information on the latter's stability is required. The stability properties can be split into two distinct and independent mechanisms. To be stable, a single-species pattern requires to be both stable in the absence of a second species and stable to the introduction of its competitor. Onset of

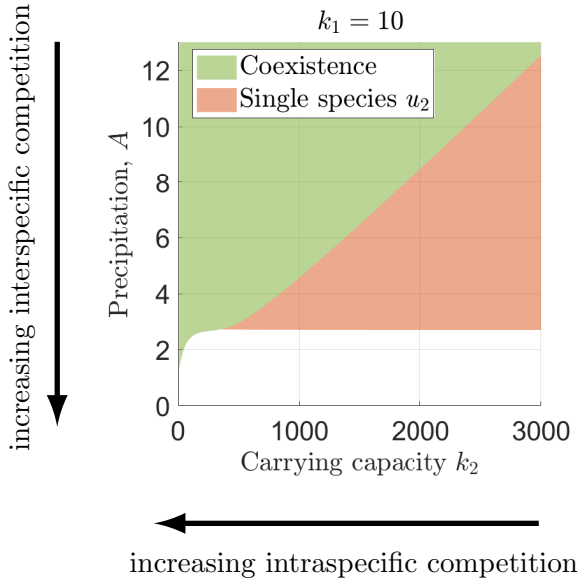


Figure 3.1: Linear stability of spatially uniform equilibria in the nonspatial model. Stability regions of the coexistence equilibrium and the equilibrium of the locally superior species are shown under changes to interspecific (rainfall parameter A) and intraspecific (carrying capacity k_2) competition.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

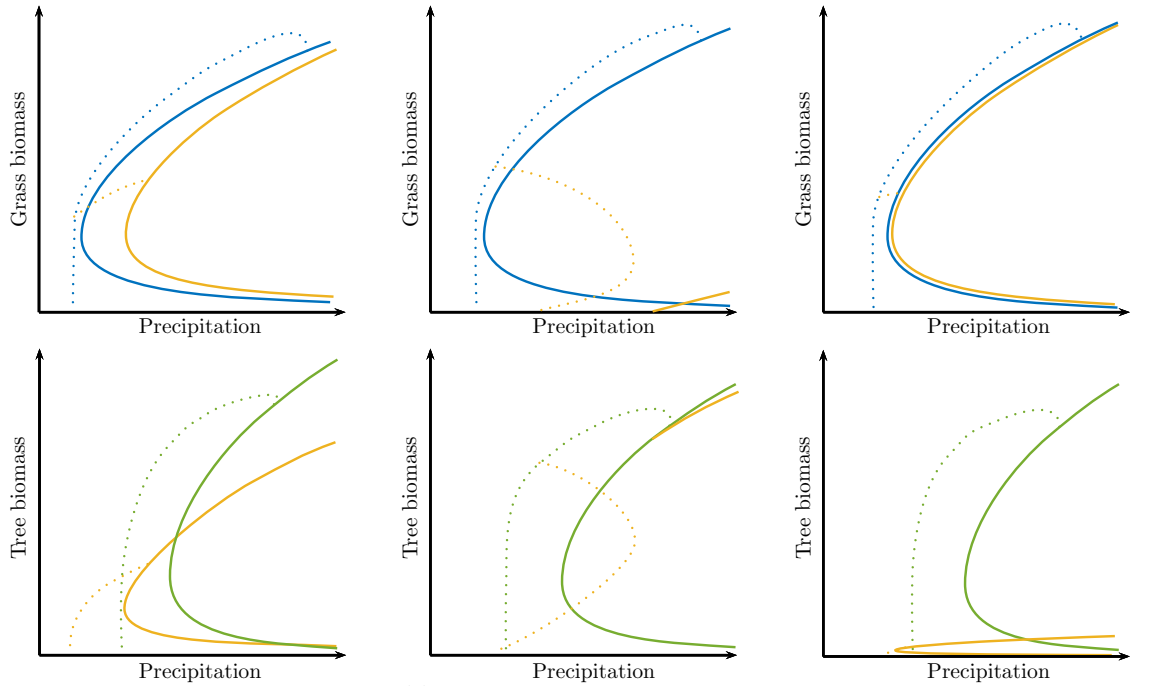
coexistence patterns occurs if a single-species pattern loses/gains stability to the introduction of the second species [19].

A transition between the two mechanisms occurs if intraspecific competition of the locally superior species decreases. Such a decrease reduces the biomass of the locally inferior species in the coexistence equilibrium, and leads to an intersection of the coexistence equilibrium with the single-species equilibrium of the locally superior species. In particular, the Hopf bifurcations on both equilibria coincide for a critical level of the locally superior species' intraspecific competition. This intersection causes a switch in the onset mechanism of coexistence patterns, which hence connect both single-species solution branches for sufficiently weak intraspecific competition of the locally superior species (Fig. 3.2b).

The precipitation range in which patterned coexistence occurs is significantly influenced by the strengths of intraspecific competition of both species. Species coexistence in patterned form is promoted by strong intraspecific competition among the coloniser species and weak intraspecific competition among the locally superior species (Fig. 3.2). This is at odds with the results for the spatially uniform setting reported in Sec. 3.1. The inclusion of spatial dynamics allows the locally inferior species to tip the balance arising from the creation of a resource niche in its favour if intraspecific competition among the locally superior species is strong. The reason for this is the associated differences in biomass that do not enable the locally superior species to outcompete the coloniser at the same rate as the latter colonises new areas.

3.3 Plant species' distribution

Depending on system parameters, the multispecies model (2.1) 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.



(a) Strong intraspecific competition among both species

(b) Strong intraspecific competition among coloniser species only

(c) Strong intraspecific competition among locally superior species only

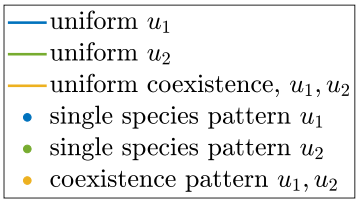
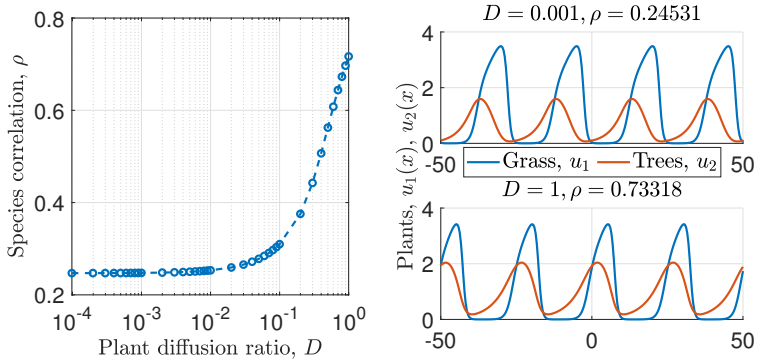


Figure 3.2: Sketches of bifurcation diagrams for different strengths of intraspecific competition among both species are shown. Solid lines correspond to spatially uniform states and dotted lines to spatial patterns. No stability information is shown. Strong intraspecific competition among the coloniser species promotes species coexistence in patterned form, while strong intraspecific competition among the locally superior species has an inhibitory effect on coexistence patterns. Bifurcation diagrams including full details can be found in the supplementary material.



(a) Correlation between species (b) Numerical PDE simulations

Figure 3.3: 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 $A = 2$.

The ratio of the plant species' diffusion coefficients D has the most significant impact on the correlation between both plant species (Fig. 3.3). 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 grass species. (Fig. 3.3b).

4 Discussion

It is a well-known classical result (e.g. [8]) that in the context of two-species competition models in population dynamics, species coexistence is possible if each species' intraspecific competition is stronger than its competitive impact on the second species. In this paper, I show, using patterns of vegetation as a case study, that if competition dynamics for a sole limiting resource are explicitly modelled, then sufficiently strong intraspecific competition among one species only is sufficient to enable species coexistence, and that spatial self-organisation plays a key role in this coexistence mechanism.

Indeed, the inclusion of spatial dynamics in the ecohydrological modelling framework changes which species' intraspecific competition is the facilitator of species coexistence. In a nonspatial setting, a common approach to model coexistence of herbaceous and woody species in savannas [42], strong intraspecific competition of the (locally) superior species (trees) creates a resource niche for a second species (grasses) and thus facilitates coexistence (Fig. 3.1). (Local) average fitness is determined by the stability of 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.

Requirements for species coexistence change significantly if spatial dynamics are considered; these are motivated by a self-organisation principle due to a positive feedback between local vegetation growth and water redistribution towards areas of dense biomass. Firstly, species coexistence requires the locally superior species (trees) to be inferior in its colonisation abilities

[19]. This balance enables species coexistence due to spatial heterogeneities in the environment, caused by the water redistribution feedback loop. Resource availability in uncolonised regions is high, which can be exploited by the superior coloniser (grasses). The redistribution of water towards areas of high biomass consequently facilitates the growth of the second species. Eventually, the locally superior species (trees) locally outcompetes the superior coloniser (grasses), thus creating a balance that facilitates coexistence. Secondly, effects of intraspecific competition on species coexistence under consideration of spatial dynamics are significantly different from those in the spatially uniform setting. Coexistence in patterned form is facilitated by strong intraspecific competition of the coloniser species (grasses) (Fig. 3.2b) and inhibited by strong intraspecific competition of the locally superior species (trees) (Fig. 3.2c). The latter in particular provides a stark contrast to theory on classical nonspatial competition models in which strong intraspecific competition generally promotes species coexistence. Both strong intraspecific competition among the locally superior species (trees) and weak intraspecific competition among the coloniser species (grasses) increase the coloniser's (grasses') biomass at the coexistence equilibrium. The resulting large difference between the equilibrium densities of both species does not allow the locally superior species (trees) to outcompete the coloniser species (grasses) at the same rate as the latter colonises new areas. Unlike in the spatially uniform setting, in which the creation of a resource niche for the locally inferior species (grasses) facilitates species richness, this inhibits coexistence.

The 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 [4, 33] or if plant species adapt to different soil moisture niches [7, 40]. 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 [9].

Model results also suggest that coloniser species (grasses) can act as *ecosystem engineers* in the system. An ecosystem engineer is a species that facilitates other species due to alterations of environmental conditions [22]. The bifurcation analysis presented in this paper shows that species coexistence can occur in parameter regions in which the locally superior species (trees) cannot exist in the absence of a competitor species (Fig. 3.2). The coloniser species (grasses) creates heterogeneities in resource availability by increasing the water infiltration into the soil and thus facilitates its competitor. In the context of grass-tree coexistence this agrees with previous theoretical [4, 19] and empirical [2, 25] studies.

Field observations of banded vegetation patterns in which herbaceous and woody species coexist report that the top edge of each stripe is dominated by the grass species [36], thus coined to be the *pioneer species* as vegetation stripes typically move in the uphill direction over time [13]. The model presented in this paper captures both these behaviours (Fig. 3.3b). In particular, a comprehensive analysis of spatial correlation between both plant species in coexistence solutions 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 (grasses) 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 herbaceous species.

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 [26] which suggest potential avenues of further exploration in both the context of vegetation patterns and more general modelling frameworks for species coexistence in competition models.

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