Cambridge Prisms: Drylands

www.cambridge.org/dry

Research Article

Cite this article: Randhawa T, Rajendra D, Patnaik S and Guttal V (2025). Higher trait diversity in savanna tree species may reduce bistability in favour of woodlands. *Cambridge Prisms: Drylands*, **2**, e4, 1–12
https://doi.org/10.1017/dry.2025.1

Received: 11 June 2024
Revised: 10 January 2025
Accepted: 23 January 2025

Keywords:
alternative stable states; individual variation; bistability; trait diversity; species functional diversity

Corresponding author:
Vishwesha Guttal;
Email: guttal@iisc.ac.in

© The Author(s), 2025. Published by Cambridge University Press. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (http://creativecommons.org/licenses/by/4.0), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

Higher trait diversity in savanna tree species may reduce bistability in favour of woodlands

Tanveen Randhawa, Dharanish Rajendra, Swastik Patnaik and Vishwesha Guttal

Centre for Ecological Science, Indian Institute of Science, Bengaluru, 560012, Karnataka, India

Abstract

Over the last decade, several studies have shown the importance of trait diversity in natural populations. Theoretical ecological studies are beginning to incorporate trait variations in models but they continue to be largely ignored in the context of ecosystems that exhibit alternative stable states. Here, we begin with a mean-field model of bistable savanna-woodland system and then introduce trait variation in functional and demographic traits of savanna trees and saplings in the model. Our study reveals that higher trait variation reduces the extent of bistability in the system, such that the woodland state is favoured; that is, woodland occurs over a wider range of driver values compared to the grassland state. We find that the shift from one state to another can become less or more drastic, depending on the trait which exhibits variation. Interestingly, we find that even if the overall tree and grass cover remain insensitive to different initial conditions, the steady-state population trait distribution exhibits sensitivity to initial conditions. Our model findings suggest that in dryland ecosystems, and potentially in a broader class of bistable ecosystems, historical contingency has a stronger impact at the population level rather than at the ecosystem level when trait diversity is considered.

Impact statement

Dryland ecosystems support unique biodiversity of flora and fauna and many human populations for crucial ecosystem services. Dryland vegetation can exhibit multiple stable states, such as savannas and woodlands. They can also sometimes abruptly switch between these states, even with little environmental changes, making them difficult systems to predict and manage. Mathematical models have played a crucial role in elucidating insights into dynamics of such systems, but to date, they all have ignored a key biological reality: Individuals both within and among species vary from each other in their phenotype (or traits).

In this study, we fill this major gap. Our model analyses, which incorporate diversity in plant demographic and functional traits, reveal that these variations in savanna species favour woodlands over grasslands, that is, grasslands exist over a smaller range of rainfall levels. Depending on which trait is varied, trait variations can make the transition from one state to another more, or less, abrupt. Our study also shows that changes in tree cover and community composition could be decoupled due to strong impacts of historical contingency effects, such that differing community compositions can coexist for the same tree cover. Our modelling study suggests that the management of savannas could benefit from a trait-based dynamics approach.

Introduction

Savannas are intriguing systems where grasses and trees coexist without competitively excluding each other (Scholes and Archer, 1997). Savannas differ from woodlands in that they have a continuous layer of grass with a discontinuous layer of trees, giving rise to a predominantly grassy and fire-prone state. In contrast, in woodlands, trees form a continuous layer alongside a discontinuous grassy layer, giving rise to a high canopy cover (as referred to in Walker and Noy-Meir, 1982; Wilcox et al., 2018). These states differ not only in their physiognomy but the fire regimes they experience. As a consequence of these complex interactions, savannas and woodlands can coexist as alternative stable states under the same environmental conditions (Walker and Noy-Meir, 1982; Dublin et al., 1990; Van Langevelde et al., 2003; Beckage et al., 2009; Warman and Moles, 2009; Hirota et al., 2011; Staver et al., 2011). Systems with two alternative stable states – also known as bistable systems – show complex dynamics in response to changes in external conditions or driver (Holling, 1973; May, 1977). Their response can be nonlinear and discontinuous rather than linear and continuous. Such a response to external conditions, which may also vary stochastically with time, can result in an abrupt shift from one stable state to another (Scheffer et al., 2001; Guttal and Jayaprakash, 2007; Chen et al., 2018). In the context of savanna-woodland ecosystems, studies show that rainfall is a key driver of ecosystem states (Sankaran et al., 2005; Hirota et al., 2011; Staver et al., 2011; Eby et al., 2017). While grassland and savannas are found to occupy regions with low rainfall, woodlands occupy regions with high

https://doi.org/10.1017/dry.2025.1 Published online by Cambridge University Press

rainfall. Interestingly, both biome states can be found at intermediate levels of rainfall. When rainfall exceeds a certain threshold value, the system can abruptly shift from a grassy state to a woody state. Such shifts may dramatically alter biodiversity, ecosystem function and the services they provide to large human populations that depend on savanna ecosystems (Solbrig et al., 1996; Jackson et al., 2002; Bond and Parr, 2010). In this broad context, our goal is to investigate the role of trait diversity, an important feature of real systems, on the bistability of the savanna-woodland system.

Mathematical models (Higgins et al., 2000; D'Odorico et al., 2006; Meyer et al., 2009; Baudena et al., 2010; Yatat et al., 2014; Majumder et al., 2019; Djeumen et al., 2021) have proved to be important tools for understanding ecosystems with alternative stable states, where manipulative experiments, such as long-term fire manipulation experiments (Biggs et al., 2003; Higgins et al., 2007) or landscape-scale fire-exclusion experiments (Andersen et al., 2005) are difficult to test various hypotheses at large scales. While the literature is replete with models describing such complex systems and their dynamics, very little is known about how trait diversity affects the dynamics of bistable systems (Dakos et al., 2019). It is well known that variation between species can be high; however, for certain traits, variation between individuals of a species can be comparable to variation among individuals of different species (Des Roches et al., 2018). For example, in a meta-analysis of various plant communities, intraspecific variation in plant height was found to be as high as 67% of the total within-community trait variance (Siefert et al., 2015). These differences between individuals can be more or less pronounced depending on the scale or level at which these comparisons are made (Messier et al., 2010). Intraspecific or interspecific trait variation can have a stronger effect on ecological responses if they influence these responses indirectly or directly, respectively (Des Roches et al., 2018). However, these trait differences are often obscured in studies that treat all individuals as identical to each other or use only the mean value of the trait (Moran et al., 2016). While this assumption is convenient for simplifying study design and modelling, such assumptions could potentially limit our understanding of how communities and ecosystems persist and how they respond to changes in their environment (Bolnick et al., 2011).

In this context, it is pertinent to ask how trait variation can affect ecosystem structure, function, and dynamics. A few experimental (Agashe, 2009; Becks et al., 2010), meta-analytic (González-Suárez et al., 2015) and theoretical studies (Hart et al., 2016; Crawford et al., 2019; Baruah, 2022) have used phenomenological models to show how trait variation affects species diversity, community structure and (or) ecosystem processes. Recent articles have also speculated on the role of individual variation in vector-borne disease dynamics (Cator et al., 2020), tipping points in ecosystems (Dakos et al., 2019), and tritrophic food chains (DeAngelis, 2013). Cator et al. (2020) stressed the importance of using trait-based mechanistic models over phenomenological ones as the latter do not account for the underlying mechanism and can be unreliable over longer timescales. How significant are these individual differences to the various processes and patterns we see in nature is a question of paramount importance (Funk et al., 2017).

In the context of savanna-woodland bistable systems, it is unclear whether trait diversity would increase or decrease the chances of abrupt shifts (or "tipping events") and how easily these ecosystems/biome states can be restored to the previous state after a tipping event. For instance, in the case of mutualistic networks, Baruah (2022) showed that trait variation may increase the occurrence of tipping events. Similarly, a model of shallow lake considers trait evolution and reveals that the resilience of the system increases through adaptive evolution (Chaparro Pedraza et al., 2021). Another recent study (Limberger et al., 2023) showed that depending on the functional trait that was varied, the resilience of the system with alternative stable states increased, decreased or exhibited no change. However, the effect of trait variation on savanna-woodland dynamics remains understudied.

Here, we consider a well-studied model of savanna-woodland bistable ecosystem (Staver and Levin, 2012) and incorporate trait variation to analyse its effects on the ecosystem dynamics. We introduce heritable variation in two demographic traits (the death rates of savanna saplings and the death rates of savanna trees) and in a functional trait that nonlinearly determines the transition of savanna saplings to adults, referred to as sapling resistance to fire. We look at how these trait variations affect the state of the system and the qualitative nature of these shifts at the ecosystem level, for traits that vary linearly (death rate of savanna sapling and trees) and non-linearly (sapling resistance to fire) with growth rates. We also look at the distribution of traits in the system and which individuals comprise the steady-state population.

Model and methods

Savanna-woodland model with no trait variations

We begin by introducing the model developed by Staver and Levin (2012) which describes the dynamics of the ecosystem consisting of grasses, savanna tree saplings and savanna tree adults. This model does not incorporate trait variations and thus serves as a baseline model for our study. Here, the proportion of grass cover, savanna saplings and adult trees are denoted by G, S and T, respectively, which together add up to unity. The model incorporates how these three components of the ecosystem interact differently with fires: Fire spread and frequency of the fire depend on the grass cover; at high grass cover, the system experiences frequent fires that spread across the landscape. During fires, grasses and savanna tree saplings lose their aboveground biomass (Higgins et al., 2000). However, when the saplings reach a certain height such that they can escape the flame zone, they become resistant to subsequent fires (Hoffmann et al., 2012). This fire-resistant stage is termed as the savanna tree adult. In this way, fire limits the transition of savanna tree saplings to adults.

The above nonlinear/threshold behaviour of savanna saplings to fire frequency is captured by the rate constant $\omega(G;\theta)$, which is a nonlinear function of the grass cover as shown in Figure 1(A). At high values of grass cover G, due to the higher frequency and spread of fires, the transition of savanna tree saplings to adult savanna trees occurs at a very low rate, while it occurs at a higher rate for low grass cover. The value of the parameter θ can be used to determine the approximate value of grass cover at which nonlinearity kicks-in and can be used as a proxy to determine the resistance of the sapling to fire. We note that the fire is modelled implicitly, the model is deterministic and nonspatial (also referred to as mean-field models). We relax some of these assumptions in our second version of the trait diversity model.

Other key parameters of the model are as follows: trees produce saplings at a rate β, with saplings replacing grasses as they are assumed to be competitively superior to grasses. Saplings and adult trees die at a constant intrinsic death rate μ and ν, respectively. The grasses spread instantaneously and cover the space previously

https://doi.org/10.1017/dry.2025.1 Published online by Cambridge University Press

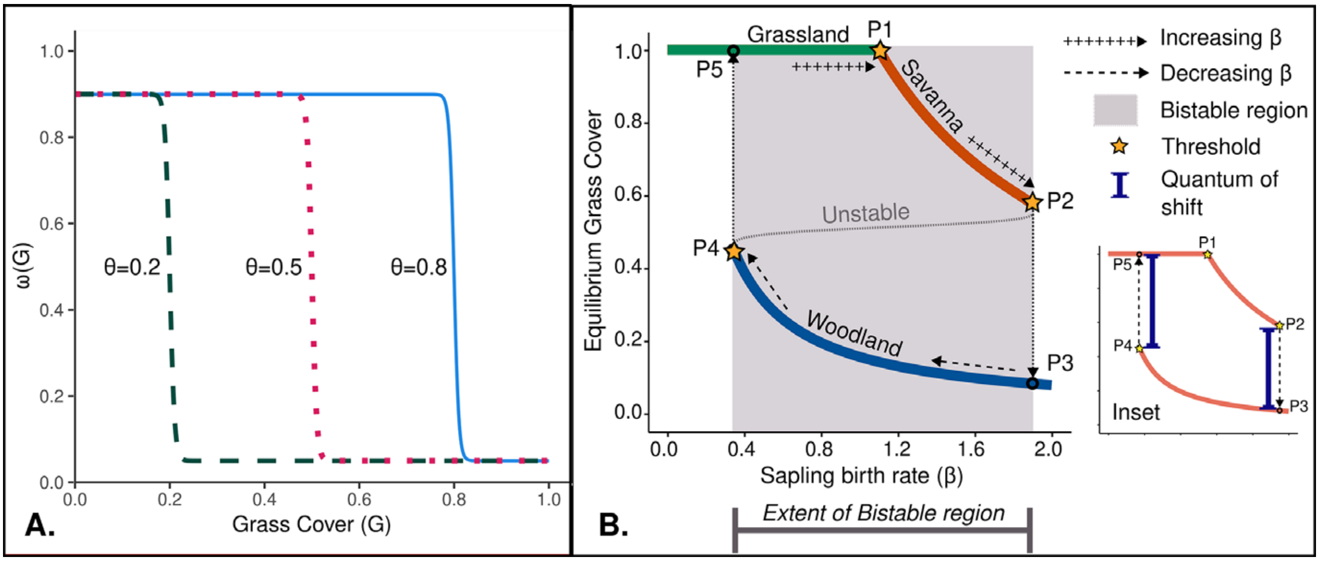

Figure 1. (A) Savanna sapling to tree transition rate (ω) for different values of sapling resistance fire (θ). ω varies as a function of Grass cover (G) and θ. At low values of grass cover and thus low fire frequency, saplings have a high rate of transition to adult trees and vice versa. Saplings with high θ value ($\theta = 0.8$, denoted by blue solid line) transition to trees even at high grass cover while those with low θ ($\theta = 0.3$, denoted by green dashed line) value remain at the sapling stage even at low grass cover. (B) Stability or bifurcation diagram of the savanna-woodland model with no trait variations (*no variation model*). The figure depicts how the steady-state grass cover changes as a function of sapling birth rate (β), different stable states (grassland in green, savanna in orange and woodland in blue), threshold points (denoted by star – **P1**, **P2**, **P4**), the extent of bistable region (grey region) and the quantum of shift at threshold points (Inset). Parameters: sapling resistance to fire $\theta = 0.5$, tree death rate $\nu = 0.1$ and sapling death rate $\mu = 0.5$.

occupied by saplings or trees. Putting these processes in a mathematical form yields the model described by three coupled ordinary differential equations (Staver et al., 2011) (see Table 1).

In savanna-woodland systems, rainfall is often the key environmental driver of the vegetation states. Here, we assume that the savanna sapling birth rate (β) increases with rainfall (Wilson and Witkowski, 1998). Thus, a smaller value of β corresponds to a higher aridity stress on the system. We characterise the bifurcation diagram which illustrates how the steady states (grass cover) change as a function of the driver value (β; see Figure 1(B)), identifying their stability. In this system, we define three ecosystem states: the term grassland state refers to a system entirely occupied by grasses (~100% grass cover), whereas a system with more than 50% tree cover is referred to as the woodland state. The state with a grass cover less than 100% but greater than 50% is termed a savanna state.

Figure 1(B) shows that at low sapling birth rates (high aridity), the system exists only in the grassland state; we refer to this as the *monostable grassland state.* In contrast, at high sapling birth rates, the steady state of the system is woodland, also referred to as *monostable woodland state.* At intermediate β values (denoted by the grey region, $0.34 < \beta < 1.9$), we find the existence of alternative stable states, also called a *bistable region.* In this region, we find either the coexistence of grassland and woodland states (for $0.34 < \beta < 1.1$) or savanna and woodland states (for $1.1 < \beta < 1.9$). In the bistable region, depending on the initial value of the grass cover, the system will reach one of the two alternative states. The range of parameters over which the system is bistable is referred to as the *extent of bistability* (grey horizontal bar in Figure 1(B)).

In this system, we observe several types of transitions from one stable state to another. Figure 1(B) shows that at the bifurcation or the threshold point marked **P1** in the upper branch, the system exhibits a continuous transition from a grassland to a savanna state as a function of the increasing sapling birth rate β; we refer to this as a *gradual regime shift.* In addition, at a higher β value, marked **P2** in Figure 1(B), the system exhibits a discontinuous transition from a savanna state to a woodland state; we refer to such transitions as *abrupt regime shifts.* We see another abrupt regime shift at the threshold point **P4**, from a woodland to a grassland state as a function of decreasing β values. We can quantify the transitions for each of these regime shifts by the difference in grass cover between the two stable states at the threshold point; we term this as the *quantum of shift.* For a gradual regime shift, this quantity will be zero whereas it will be a nonzero number for abrupt transitions. Larger the quantum of shift, more drastic the regime shift.

Trait variation models

In this manuscript, our goal is to understand how the dynamics at the *ecosystem level* and *population level* are affected by trait diversity. At the *ecosystem level*, we investigate the total vegetation cover (grass, tree or sapling) which is obtained by summing over proportions of all traits of that vegetation type. Specifically, we first obtain the bifurcation diagram which captures the relationship between the state variable of the ecosystem (e.g. grass cover or tree cover) and the birth rate of the sapling (β); as remarked before, the parameter β can be thought of as a proxy of annual rainfall, a key driver of vegetation in semi-arid ecosystems. This will reveal how properties of the bifurcation diagram such as the extent of bistability (i.e. grey region in Figure 1(B)), qualitative nature of transitions, as well as the quantum of shifts (inset of Figure 1(B)) at the threshold point vary when we introduce trait variations in the model. Next, we also look at the consequences of trait variation at the *population level*, that is, we not only focus on total grass or tree cover, but also how the population of each of the traits evolves over time, and which tree and sapling traits constitute the steady-state population.

https://doi.org/10.1017/dry.2025.1 Published online by Cambridge University Press

Table 1. Symbols and descriptions of the model and model variables and parameters

Symbol	Description	Range or value
	Deterministc model with no trait variation	
S	Savanna sapling cover	0–1
T	Savanna tree cover	0–1
G	Grass cover	$1-S-T$
$\frac{dS}{dt}=\beta GT-\omega(G;\theta)S-\mu S$	ODE for sapling dynamics	
$\frac{dT}{dt}=\omega(G;\theta)S-v$	ODE for tree dynamics	
$\frac{dG}{dt}=\mu S+vT-\beta GT$	ODE for grass dynamics	
$\omega(G;\theta)=\omega_0+\frac{\omega_1-\omega_0}{1+e^{(-G+\theta)/s}}$	Sapling to tree conversion rate	0.05–0.9
β	Sapling birth rate	0–2
μ	Death rate of sapling	0–1
v	Death rate of trees	0–1
θ	Half-saturation constant of ω for saplings	0–1
s	Slope of the function near θ	0.005
ω_0	Upper limit of ω	0.9
ω_1	Lower limit of ω	0.05
	Deterministc model with discrete trait variations in μ	
i	Denotes ith type (e.g. species)	
S_i,T_i,G_i	Vegetation covers of type i	0–1
$\frac{dS_i}{dt}=\beta GT_i-\omega(G;\theta)S_i-\mu_i S_i$	Sapling population dynamics for type i when varying μ	
$\frac{dT_i}{dt}=\omega(G;\theta)S_i-vT_i$	Tree population dynamics for type i when varying μ	
$\frac{dG}{dt}=\sum_{i=1}^{k}p_i\mu_i S+vT-\beta GT$	Grass population dynamics when varying μ	
μ_i	Death rate of sapling of type i	0–1
p_i	Proportion of type i	0–1
All other parameters	Same as the previous model	
	Stochastic model with continuous traits	
$\mathcal{S}$	Savanna sapling individual	–
$\mathcal{T}$	Savanna tree individual	–
$\mathcal{G}$	Grass individual	–
S,T,G	Same as the deterministic model	0–1
β,μ,v,ω	Same as the deterministic model	

To investigate these questions, we consider two modelling approaches. First, we use the deterministic modelling framework of Staver and Levin (2012) and include discrete variations in three traits of the model. Second, we use a stochastic agent-based modelling framework where the same three traits are considered, but are now assumed to vary continuously and evolve via demographic stochastic processes. Both modelling approaches assume clonal inheritance of traits.

Deterministic discrete trait variation model

We describe an extension of the model of Staver and Levin (2012) to include trait variations in two demographic traits (sapling death rate (μ), tree death rate (v)) and one functional trait (sapling resistance to fire – θ; defined below). First, we define θ, which appears in the sapling-to-tree transition rate function $\omega(G;\theta)$, as the trait that determines the resistance of the sapling to fire. Although the original model treats $\omega(G;\theta)$ as a sapling trait that is entirely dependent on the ecosystem-level properties of fire governed by the grass cover, we treat θ to capture how resistant individual saplings are to fires. Saplings with a high value of θ can transition to adult trees even when fires are frequent, whereas saplings with a low value of θ can transition to trees only if the frequency of the fire is low (Figure 1(A)). This trait, for example, could be correlated with the height of the saplings such that taller saplings survive topkill during fires and thus transition to adult trees at a higher rate (Higgins et al., 2000, 2012).

We now introduce variations in demographic traits – tree death rate (μ) and sapling death rate (v) – which result from a combination of a suite of traits rather than one specific plant trait. For example,

https://doi.org/10.1017/dry.2025.1 Published online by Cambridge University Press

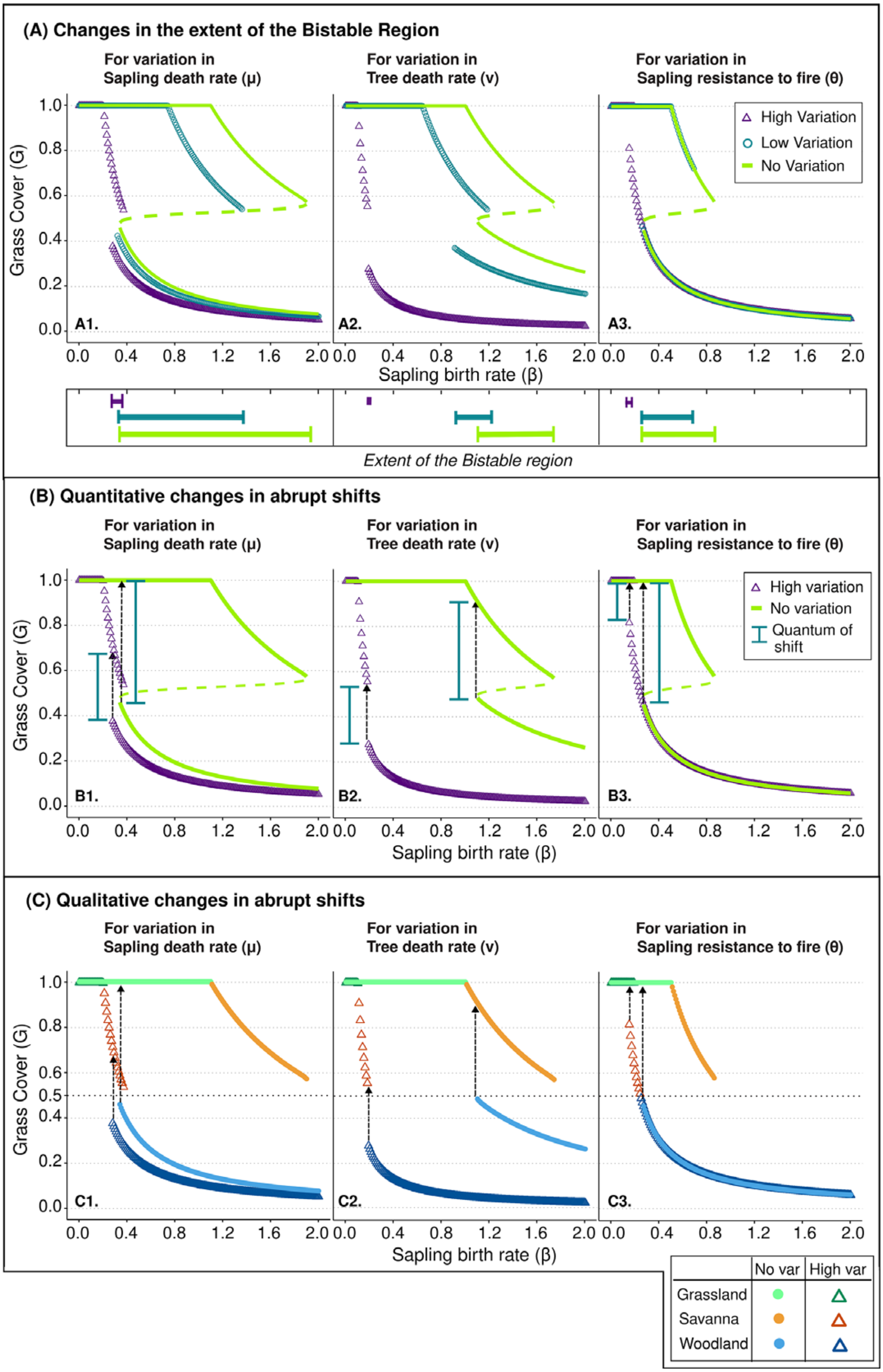

Figure 2. Ecosystem-level properties such as bistable region and nature of regime shifts can depend on trait variations. For each bifurcation diagram, we assume that only one trait (mentioned in the title of that diagram) exhibits variations keeping other traits constant. (Row A) shows that the extent of bistable region reduces with increasing trait variation (see the panels below each subfigure). Extent of grassland reduces, while that of woodland increases, with increasing trait variations. (Row B) shows that the quantum of abrupt shift reduces with increasing trait variation. (Row C) shows how nature of transition changes with trait variations: In (C1), whereas the no variation case (denoted by closed circles) exhibits a transition from woodland to grassland, the high variation case (denoted by open triangles) shows a transition from woodland to savanna. In (C2), the qualitative nature of transitions remains same for both no and high variations. In (C3), while the no variation case shows a transition from woodland to grassland, the high variation case shows a transition from savanna to grassland. Parameters: (A1–C1) sapling resistance to fire $\theta = 0.5$ and tree death rate $\nu = 0.1$. (A2–C2) $\theta = 0.5$ and sapling death rate $\mu = 0.05$. (A3–C3) $\nu = 0.1$ and $\mu = 0.2$.

https://doi.org/10.1017/dry.2025.1 Published online by Cambridge University Press

tree death in savannas can occur due to megaherbivores such as elephants (Vanak et al., 2012), which plants may resist by investing in spiny or toxic stems (Sheil and Salim, 2004). Another major factor for tree or sapling deaths is drought (Fensham et al., 2009; Sankaran, 2019). Trees with low drought resistance mediated by traits such as low cavitation resistance, low hydraulic safety margins and low wood density experience high mortality during droughts (Sankaran, 2019) and thus have high tree death rate (ν) values. In addition, saplings that invest in bark thickness and stem diameter are more likely to survive in the sapling stage (Hoffmann and Solbrig, 2003). Some of the traits that help saplings survive from background death processes may also help survive fires, and hence be correlated with θ, a point we ignore for the study since we only vary one trait at a time. We emphasise a key difference between the functional and demographic traits we have chosen to vary: whereas the trait θ representing sapling resistance to fire affects the growth rate of trees via nonlinear frequency dependence on grass cover as shown in Figure 1(A), the sapling death rate (μ) and tree death rate (ν) are independent of frequency of any of the ecosystem states (grass cover, sapling or tree covers) and affect the corresponding growth rate term linearly.

For simplicity, we assume that each trait follows a discrete uniform distribution (see Sensitivity Analysis for other distributions), by considering a finite number k of trait types, which could represent different tree species at one extreme or a continuous trait approximated as discrete types for mathematical convenience. We assume that the traits are clonally inherited, with no mutations. If we consider trait variations in only one of the traits keeping the other traits fixed, the corresponding mathematical equations will be in the form of $2k+1$ ordinary differential equations (Table 1).

In the Results section, we present results for two levels of trait variations – a ‘low variation’ case and a ‘high variation’ case, keeping the mean trait value the same. The low trait variation is implemented as a smaller range of the trait values (0.3–0.7), while the high trait variation corresponds to a larger range (0–1). We use a combination of analytical methods and numerical simulations, details of which are presented in Supplementary Material Section 1; see Table 1 for the description and values of parameter values.

Sensitivity analysis

To test the robustness of our results, we perform sensitivity analyses. First, we consider different number of discrete trait types (k) to be 10, 100 or 1000. In addition, we also consider different trait distributions – unimodal beta and bimodal beta distributions, in addition to the case of uniform distribution already discussed. Finally, we also consider a model variation in which Forest trees are included, as in the full model of (Staver and Levin, 2012) thus making the total vegetation types to four (see Supplementary Material Section 2 for model details).

Stochastic continuous trait variation model

To further test the robustness of our conclusions on our choice of discrete trait types, we employ an agent-based stochastic dynamical model. This is an alternative and complementary modelling strategy that helps us relax some major assumptions of the model in the previous section: by modelling traits as continuous (rather than discrete) and by including stochastic birth – death processes (rather than deterministic). Specifically, here too, we consider three types of individuals: grass ($\mathcal{G}$), savanna saplings ($\mathcal{S}$) and savanna trees ($\mathcal{T}$). A tree i with trait value x_i (can be either μ_i, ν_i or θ_i) can give rise to a sapling offspring having the same trait value, that is, clonal inheritance, replacing a grass ‘individual’. A sapling individual can grow into a tree individual, maintaining the trait value. Both tree and sapling individuals can die at their respective death rates (μ_i and ν_i) and will be replaced by grass. These processes, in the notation of chemical kinetics, can be represented as:

$$\mathcal{T}(x_i)+\mathcal{G} \xrightarrow{\beta_i} \mathcal{T}(x_i)+\mathcal{S}(x_i) \tag{1}$$

$$\mathcal{S}(x_i) \xrightarrow{\omega(G,\theta_i)} \mathcal{T}(x_i) \tag{2}$$

$$\mathcal{S}(x_i) \xrightarrow{\mu_i} \mathcal{G} \tag{3}$$

$$\mathcal{T}(x_i) \xrightarrow{\nu_i} \mathcal{G} \tag{4}$$

Each reaction is a random process whose rate depends on the trait values of the individuals. We highlight an important contrast with a typical reaction kinetic framework of population models, where the rates of reactions are constant. In our model, each individual i has their own rates of transitions (μ_i, ν_i or θ_i – which we interpret as traits) and the distribution of these rates change over time. We use the Gillespie algorithm (Gillespie, 1976) to simulate this process for a population size of $N=1000$ and for 1,000 time units. We note that the system reaches a steady state typically within 200 time units.

Results

Ecosystem-level dynamics of the deterministic model

We first present the results of the deterministic trait variation model at the ‘ecosystem-level’. We do this by investigating the grass cover, tree cover (and sapling cover) at steady-state for various possible variations in traits. Specifically, we consider how properties of the bifurcation diagram change with trait variations (no, low and high variation, as already described). In Figure 2, we display how the bifurcation diagram changes with trait variations. We reveal four major effects: First, we find that with an increase in variation in any of the three traits, the grassland state (i.e. the state with $G=1$ and $T=0$) exists for a shorter range of the sapling birth rate (β); in particular, the grassland state will be found for lower values of β (row A, Figure 2). In contrast, trait variations have the opposite impact on the woodland state: woodlands can occur for a larger range of sapling birth rates and even at lower values of β (i.e. at higher aridity levels). In other words, trait variations seem to reduce bistability in favour of woodland state.

Second, we find that increasing trait variations leads to a reduction in the bistable region in the system, that is, the region of parameter space where the two alternative states are stable (see the bottom panels of row A, Figure 2). For example, in the no variation case for the sapling death rate μ (Figure 2(A1)), the bistable region ranges between 0.34 and 1.90 units of β. This reduces to a range of 0.28–0.37 units of sapling birth rate (β) for the high-variation case. This is true for all the three cases of trait variation we studied (Figure 2(A1), (A2), (A3)).

Third, we observe qualitative changes in the nature of regime-shifts with increasing trait variation, but these patterns differ between traits in which variation exists (Figure 2, row C). For instance, when there is no variation in the sapling death rate (μ; Figure 2(C1)), we find an abrupt shift from a woodland to a grassland state as a function of decreasing β value, whereas, with high trait variation, we find an abrupt shift from a woodland to a savanna state. No qualitative change in regime shifts is observed when we introduce variations in tree death rate (v); the system shifts from a woodland state to a savanna state as a function of decreasing β for both no and high variation cases (Figure 2(C2)). In contrast, for the high variation in the resistance of the saplings to fire (θ), we observe an abrupt shift from savanna to grasslands (Figure 2(C3)).

Fourth and finally, we also observe changes in the quantum of shifts in grass cover at the threshold point, with increasing trait variations (Figure 2, row B). The quantum of shift decreases across all the cases of increasing variation in μ, v and θ (Figure 2(B1)–(B3)). Thus, with higher trait variation in the system, regime shifts become less drastic compared to the no-variation case.

Population-level dynamics of the deterministic model

We now consider population-level dynamics, which we define as explicit consideration and analysis of trait distributions for various scenarios (Figure 3). Specifically, we compare the initial and final distribution of the traits in each of the three regimes (monostable grassland, bistable and monostable woodland as previously described), to understand the population composition at steady state. We begin by noting that the bifurcation diagram, that is, steady states denoted by grass cover and tree cover, of the no trait variation model was independent of initial grass cover G_0 or the distribution of traits in the monostable woodland regime. However, in the trait variation model, despite the ecosystem-level property being independent of initial conditions, we find that population-level states can depend on initial values: When we consider the variation in the resistance of the saplings to fire (θ; Figure 3, column C), we find that the proportion of each persisting tree trait depends on the initial grass cover (G_0), highlighting that the dynamics of the population level can depend on the initial conditions. Thus, woodlands with equivalent ecosystem-level tree cover can have different compositions of tree (and sapling) types in the population, depending on their initial conditions. However, we find that when the sapling or tree death rates vary (Figure 3, columns A and B, respectively) only trees and saplings with the lowest trait value survive, while others get eliminated. This is true for all initial values of grass cover (rows representing different initial grass cover; also see Supplementary

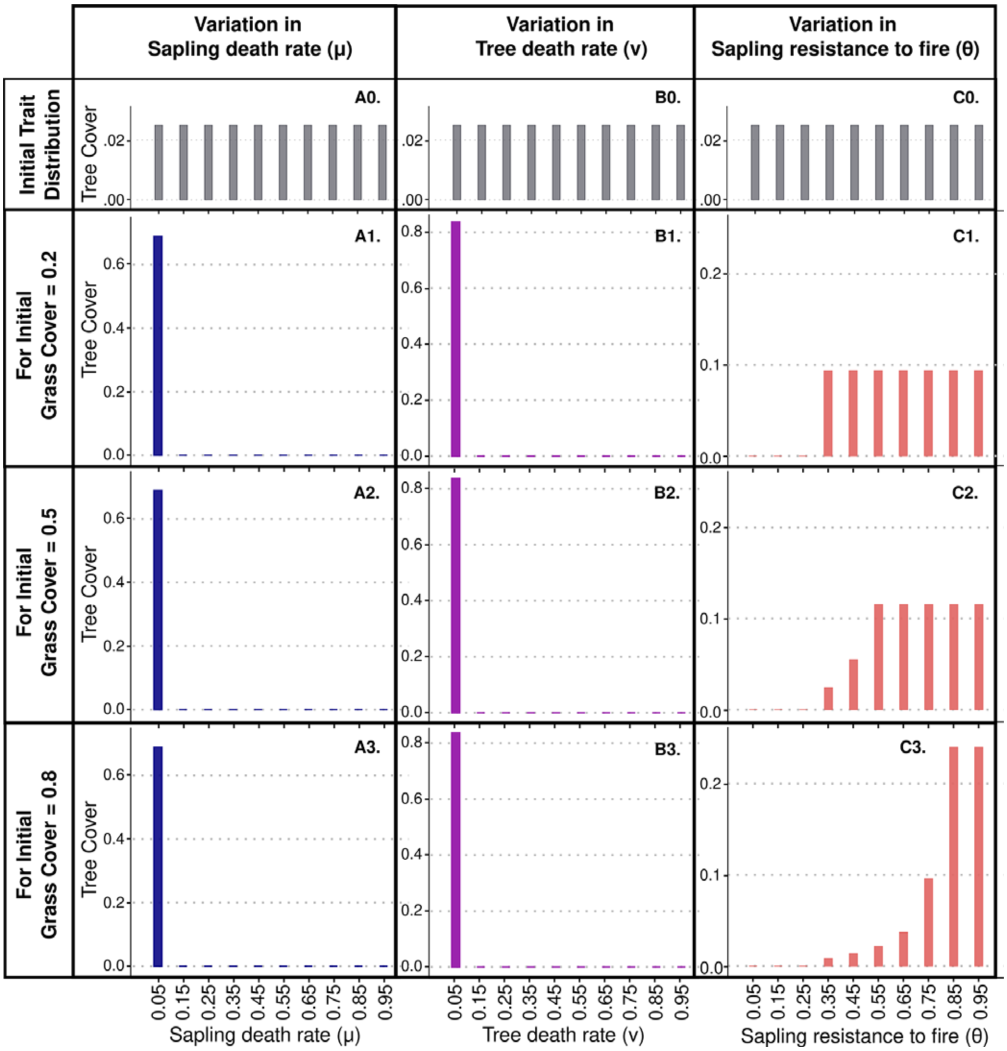

Figure 3. Population-level dynamics can be sensitive to initial conditions, for $\beta = 0.45$ which corresponds to monostable woodland regime. Specifically, we show how the uniform initial trait distribution (shown in the top most row) evolves for different initial values of grass cover (across rows). We find that for variations in sapling death rate (μ; A1–A3) and tree death rate (v; B1–B3), only the sapling and trees with the least death rates (thus, higher survival) survive. However, for variation in sapling resistance to fire (θ; C1–C3), we find that the steady-state distribution depends on the initial grass cover, with mean value of θ increasing as initial grass cover increases.

https://doi.org/10.1017/dry.2025.1 Published online by Cambridge University Press

Figure S4 for more values of initial grass cover, and S5 and S6 for different initial distributions). This exclusion of individuals with higher death rates results in a final population with no variation, as expected. Unlike the monostable woodland regime, results from the bistable regime do not show a strong pattern (see Supplementary Figure S7) while the monostable grassland regime has no tree population.

Our analysis of temporal evolution further reveals the importance of trait variations (Figure 4). Whereas the system with no variation case yields a grassland state (Figure 4(A)), the system with trait variation in sapling resistance to fire (θ) reaches a woodland state (Figure 4(B)). A closer examination of the dynamics at the trait level (Figure 4(C)–(E)) further reveals that not all the initial tree/sapling types survive. At $t = 0$, trees with high θ values start increasing in proportion, as their saplings immediately transition to adults, resulting in a sharp decline in the corresponding sapling cover. Consequently, sapling cover of these trees increases, reducing the grass cover. With the decline in grass cover, other sapling types with lower θ eventually transition to trees, while types with low θ values decline to zero asymptotically due to death processes at sapling death rate μ. Trait variation also results in the system reaching a stable state earlier than when no variation is present.

Robustness of results to parameter variations and model variations

Our analysis with alternative trait distributions (unimodal beta, Supplementary Figure S1; bimodal beta, Supplementary Figure S2) and increasing the number of trait types (Supplementary Figure S3) shows that our conclusions on how trait diversity affects the ecosystem level dynamics are robust. In addition, our simulations of the stochastic continuous trait variation model (Supplementary Figure S8) and the extended model that includes forest trees (Supplementary Figure S11) too confirm our findings. In all these cases, as trait variation increases, the extent of grassland decreases and that of the woodland increases. Further, the quantum of the jump in the abrupt transition also reduces as trait variation

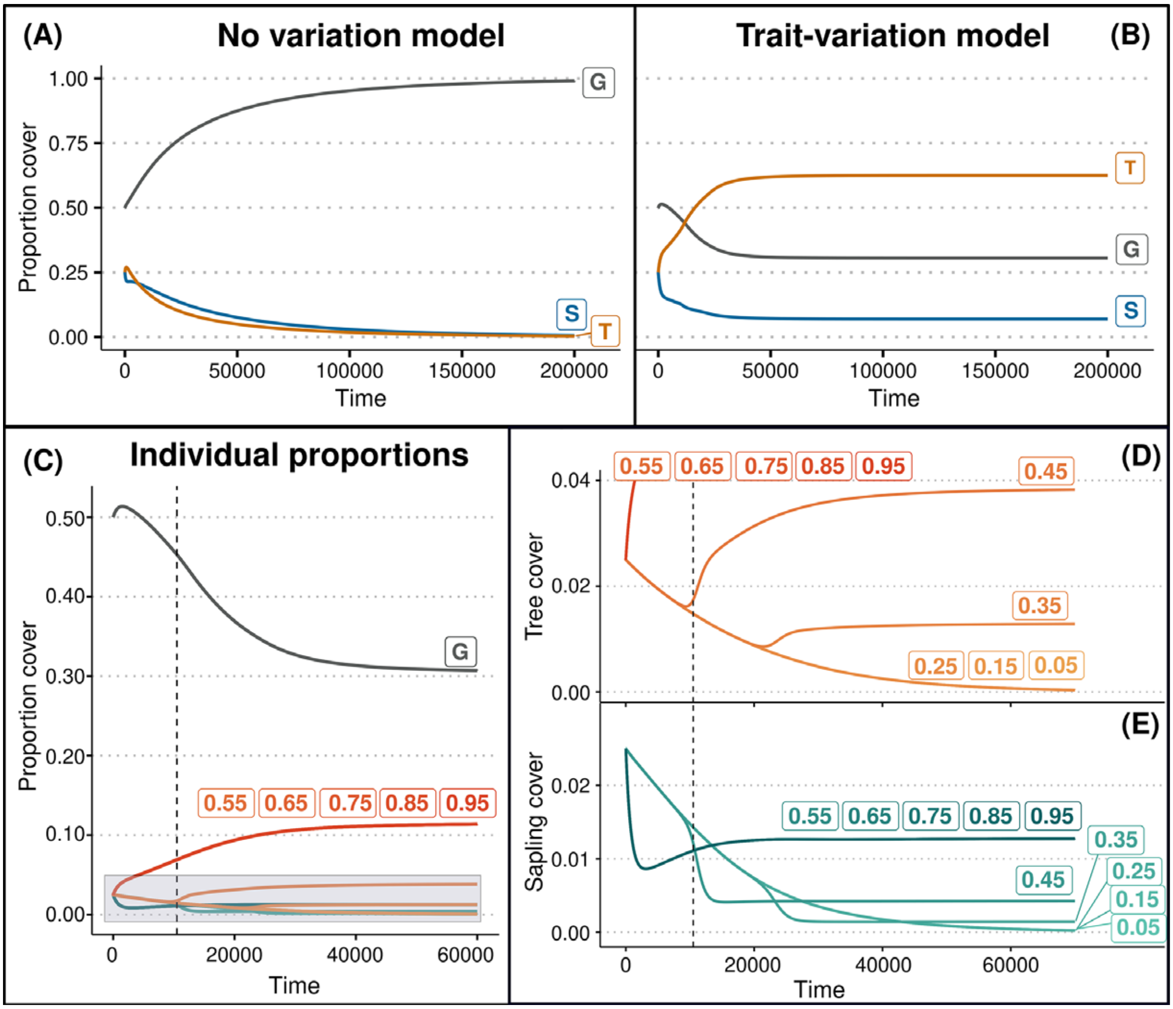

Figure 4. A comparison of time series for the no variation and the trait variation model with variation in sapling resistance to fire (θ), at a fixed value of sapling birth rate. Lines in red and blue hues represent tree cover (T) and sapling cover (S), respectively, while the dark grey line represents Grass cover (G). (A) shows that the system exists in a grassland state for the model with no variation. (B) shows that the system exists in a woodland state for the model with trait variation. (C) shows the individual proportions of different tree and sapling types for the trait variation model in (B). The red and blue bubbles above the lines determine the θ value of the specific tree and sapling type, respectively. (D) and (E) show a zoomed-in view of the grey region in (C), showing only tree and sapling cover, respectively. Parameter values at $t = 0$ are: total tree cover = total sapling cover = 0.25, while individual tree and sapling cover = 0.025. $\nu = 0.1$, $\mu = 0.2$, $\beta = 0.45$, $\theta = [0.05, 0.15, 0.25, \ldots, 0.95]$.

https://doi.org/10.1017/dry.2025.1 Published online by Cambridge University Press

increases. In the stochastic model, we note that the bistable region naturally shrinks due to the stochasticity, as expected from previous studies on stochastic bistable systems (Guttal and Jayaprakash, 2007). Furthermore, we find that the population-level dynamics exhibit qualitatively similar historical contingency effect irrespective of the trait distributions chosen (Supplementary Figures S4–S6), including the case of the stochastic continuous trait model (Supplementary Figures S9 and S10) and the model that includes forest trees (Supplementary Figure S12).

Discussion

Our model study shows that trait diversity can influence the bistable savanna-woodland system in several interesting ways. We find a general pattern across three traits that we studied: the range of bistability reduces when the trait variation increases. More specifically, a higher trait variation leads to a larger parameter range where woodlands persist. Consequently, the parameter range of stability for the grassland reduces. Furthermore, we find that the qualitative nature of transitions and the quantum of transitions can change, making them less drastic, due to trait variations. At the population level, we find a novel result that the steady-state distribution of traits depends on the initial conditions of the ecosystem; this is true even when the steady-state ecosystem state (e.g. tree cover or grass cover) is identical. Broadly, this suggests that historical contingency has a stronger impact at the population level rather than at the ecosystem level when trait diversity is considered.

Different trait variations may also affect the dynamics at the population and ecosystem levels differently. When we considered trait variations in death rates, we found that the ecosystem in steady state consists of trees (or saplings) with the lowest death rates, as expected. However, in the case of sapling resistance to fire, we find that trait types that are above a threshold value survive, while others are eliminated from the population (Figure 3(C1)–(C3)). This is because saplings with θ values below that threshold fail to transition to trees due to fire. Therefore, saplings with a value of θ lower than the threshold experience strong selection, while those with θ above the threshold experience weak or no selection pressure, leading to high variation in the trait in steady state. A similar finding of certain traits being absent in the steady-state population has been reported by Dantas et al. (2013) in the Cerrados of eastern Brazil where fire prevents certain species from colonising the savannas. We argue that the response of the trait sapling resistance to fire is different from sapling and tree death rates possibly due to the nonlinear relationship between the trait and survival from fire (Moran et al., 2016); this result is also broadly consistent with the effect predicted by Jensen's inequality (Ruel and Ayres, 1999).

Interestingly, we find that communities with similar environmental conditions can be very dissimilar in their community composition, not only as a result of complexity resulting in alternative stable states but also due to historical contingency even when there are no multiple stable states. In the woodland regime, the steady-state tree cover for different cases of initial conditions was identical, yet the population compositions differed for trait θ (Figure 3(C1)–(C3)). This difference results from the influence of initial grass cover on steady-state distribution. When grass cover (which governs the frequency of fire) is reduced, even saplings with lower θ find conditions favourable for them to transition to trees (Figure 4(C)–(E)); note that this interplay is possible only because of initial trait diversity. Thus, even in the absence of bistability, the community shows a strong impact of historical legacy of grasses. This impact of entirely different taxa (i.e., grasses) on tree community trait assemblage is mediated by disturbance frequency experienced by the system. In this way, historical disturbance regimes would have a signature on the current community composition.

Potential practical implications

We discuss some potential practical insights from our study. Across continents, tropical grasslands and savannas are at risk of woody encroachment (O'Connor and Crow, 1999; Ratnam et al., 2011; Stevens et al., 2017; Buisson et al., 2019). One method employed for grassland restoration includes prescribed fires and mechanical removal of trees (or tree thinning) (Brockway et al., 2002; Cuevas and Zalba, 2010). Tree thinning is expected to achieve the effect of reduced resistance to fire, but requires careful consideration of the dynamics of the system as the restoration efforts can also lead to an undesirable state (Smit, 2004). In fact, our model analyses show that the removal of highly fire-resistant saplings (i.e. high θ values (0.65–0.95) in the steady-state population represented by Figure 3(C1)) is insufficient to revert a woodland to a grassland state. To restore a grassland, it is necessary to also remove saplings with high resistance to fires (either manually or through controlled prescribed burning). In other words, restoration efforts can be made more efficient by focusing on the removal of both tree and sapling types. Our work adds credence to the idea that understanding the dynamics of grassland systems, along the role of trait diversity, is an important research gap for achieving better grassland restoration (Török et al., 2021).

While most studies look at the coarse-grained properties of the system, our trait diversity model can be used to gain insights on community composition. We find that changes in tree cover and plant diversity are decoupled in the monostable woodland regime when the resistance of the saplings to fire trait (θ) exhibits variability. Such decoupling was also observed by Pardo et al. (2013) for one of the Pyrenean treeline ecotones as even with no significant change in tree cover, vegetation composition changed significantly. In the literature on savanna forest ecosystems, remotely sensed tree cover is often used as a state variable that can be used to assess ecosystem resilience as well. Changes in community composition, which arise from historical contingency and other local factors, do not affect the tree cover, but can in turn increase the vulnerability of the overall ecosystem due to changes in trait distributions. Therefore, our study cautions that resilience metrics that use tree cover alone (or their derivative properties such as variance or correlations (Génin et al., 2018; Dakos et al., 2019)), without accounting for trait diversity and community composition, could have serious limitations as indicators of ecosystem stability (Baruah et al., 2020). At a very broad level, owing to differences in the predictions of no trait variations model and the more realistic trait variation model (Figure 1(B) and Figure 2), an important take away for ecosystem modellers is to consider trait diversity, not just mean trait values (Wakeling et al., 2011), in ecosystem modelling.

Future directions and concluding remarks

We have adopted a simple model in which we investigated variation in one trait at a time. Future studies can incorporate variations in multiple traits simultaneously. There could be interesting tradeoffs, for example, a higher resistance to fire (θ) through bark/stem properties can result in a slower growth rate of saplings to trees (Corrêa Scalon et al., 2020). Or, there could be positive correlations between different traits (e.g. a higher resistance to fire may also lead to better survival to other background abiotic stressors). Intriguingly, even in the deterministic version of the trait variation

https://doi.org/10.1017/dry.2025.1 Published online by Cambridge University Press

model, we predict coexistence of a diverse trait distribution of sapling resistance at steady state. These variations can be attributed to nonlinear response of vegetation to climate (rainfall) and disturbances (fires through grass cover). Naturally, including additional mechanistic factors that act as the source of trait variation (e.g. demographic stochasticity and dispersal) as well as external stochastic factors (e.g. seasonal and interannual rainfall variability) offer some interesting avenues for future work.

On the modelling front, any system with multiple competing traits is essentially an eco-evolutionary dynamical system, for which many alternative and mathematical rigorous formulations are available. These include, but are not limited to, parsing the interactions via game theoretic pay-off matrices and constructing suitable replicator-mutator equations or an adaptive dynamics approach (Geritz et al., 1997; Lion, 2018; Wickman et al., 2023; Bhat and Guttal, 2025). In addition, mutations and spatial structure to the model of trait diversity are known to have impact on ecological dynamics especially in the context of dryland ecosystems (Hirota et al., 2011; Staver et al., 2011; Sankaran et al., 2019; Goel et al., 2020; Bennett et al., 2023). Another important area in the context of systems with bistable dynamics is the ability to obtain early warning signals of potential abrupt transitions (Scheffer et al., 2001; Génin et al., 2018). How do trait variations affect, do they enhance or reduce the intensity of signals, could be a question of important practical consideration.

In summary, we have shown some potential effects that trait variations can have on dryland ecosystems with alternative stable states. Trait diversity may promote woodlands, make regime shifts less catastrophic and lead to the establishment of a community assembly that may crucially depend on the historical composition of the community. Finally, beyond dryland ecosystems, a diverse range of ecosystems are hypothesised to exhibit alternative stable states. Our research suggests that incorporating trait diversity in mathematical models could open up new avenues to gain insights on the basic ecological understanding of ecosystems and potentially offers new perspectives for management and restoration.

Supplementary material. To view supplementary material for this article, please visit http://doi.org/10.1017/dry.2025.1.

Data availability statement. All codes necessary to reproduce the results of this manuscript are available via our Git-hub `repository:` https://github.com/tee-lab/trait-variation/ .

Acknowledgements. We are grateful to three anonymous reviewers for many helpful constructive criticisms which substantially improved the manuscript.

Author contribution. T.R. and V.G. conceived the idea. T.R. and D.R. developed the models, conducted simulations and analysed the results. S.P. performed model analyses. T.R. and V.G. wrote the manuscript, with inputs from other coauthors.

Financial support. We acknowledge funding from the Department of Biotechnology (BT/PR29719/FCB/125/19/2018), Department of Science and Technology (NGP-GS08/IISc-B/KA/2023 and Science and Engineering Research Board (MTR/2022/000273) to V.G. and a PhD scholarship to T.R. via Ministry of Education and Prime Ministers Research Fellowship, all from the Government of India.

Competing interest. The authors declare no competing interests.

References

Agashe D (2009) The stabilizing effect of intraspecific genetic variation on population dynamics in novel and ancestral habitats. *The American Naturalist* **174**(2), 255–267.

Andersen AN, Cook GD, Corbett LK, Douglas MM, Eager RW, Russell-Smith J, Setterfield SA, Williams RJ and Woinarski JC (2005) Fire frequency and biodiversity conservation in australian tropical savannas: implications from the kapalga fire experiment. *Austral ecology* **30**(2), 155–167.

Baruah G (2022) The impact of individual variation on abrupt collapses in mutualistic networks. *Ecology Letters* **25**(1), 26–37.

Baruah G, Clements CF and Ozgul A (2020) Eco-evolutionary processes underlying early warning signals of population declines. *Journal of Animal Ecology* **89**(2), 436–448.

Baudena M, D'Andrea F and Provenzale A (2010) An idealized model for tree–grass coexistence in savannas: the role of life stage structure and fire disturbances. *Journal of Ecology* **98**(1), 74–80.

Beckage B, Platt WJ and Gross LJ (2009) Vegetation, fire, and feedbacks: a disturbance-mediated model of savannas. *The American Naturalist* **174**(6), 805–818.

Becks L, Ellner SP, Jones LE and Hairston NGJr (2010) Reduction of adaptive genetic diversity radically alters eco-evolutionary community dynamics. *Ecology Letters* **13**(8), 989–997.

Bennett JJ, Bera BK, Ferré M, Yizhaq H, Getzin S and Meron E (2023) Phenotypic plasticity: a missing element in the theory of vegetation pattern formation. *Proceedings of the National Academy of Sciences* **120**(50), e2311528120.

Bhat AS and Guttal V (2025) Eco-evolutionary dynamics for finite populations and the noise-induced reversal of selection. *The American Naturalist* **205**(1), 1–19.

Biggs R, Biggs H, Dunne T, Govender N and Potgieter A (2003) Experimental burn plot trial in the kruger national park: history, experimental design and suggestions for data analysis. *Koedoe* **46**(1), 1–15.

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VH, Schreiber SJ, Urban MC and Vasseur DA (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* **26**(4), 183–192.

Bond WJ and Parr CL (2010) Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. *Biological Conservation* **143**(10), 2395–2404.

Brockway DG, Gatewood RG and Paris RB (2002) Restoring grassland savannas from degraded pinyon-juniper woodlands: effects of mechanical overstory reduction and slash treatment alternatives. *Journal of Environmental Management* **64**(2), 179–197.

Buisson E, Le Stradic S, Silveira FA, Durigan G, Overbeck GE, Fidelis A, Fernandes GW, Bond WJ, Hermann J-M, Mahy G, et al. (2019) Resilience and restoration of tropical and subtropical grasslands, savannas, and grassy woodlands. *Biological Reviews* **94**(2), 590–609.

Cator LJ, Johnson LR, Mordecai EA, Moustaid FEl, Smallwood TRC, LaDeau SL, Johansson MA, Hudson PJ, Boots M, Thomas MB, Power AG and Pawar S (2020) The role of vector trait variation in vector-borne disease dynamics. *Frontiers in Ecology and Evolution* **8**:189.

Chaparro Pedraza PC, Matthews B, de Meester L and Dakos V (2021) Adaptive evolution can both prevent ecosystem collapse and delay ecosystem recovery. *The American Naturalist* **198**(6), E185–E197.

Chen N, Jayaprakash C, Yu K and Guttal V (2018) Rising variability, not slowing down, as a leading indicator of a stochastically driven abrupt transition in a dryland ecosystem. *The American Naturalist* **191**(1), E1–E14.

Corrêa Scalon M, Domingos FMCB, da Cruz WJA, Júnior BHM, Marimon BS and Oliveras I (2020) Diversity of functional trade-offs enhances survival after fire in neotropical savanna species. *Journal of Vegetation Science* **31**(1), 139–150.

Crawford M, Jeltsch F, May F, Grimm V and Schlägel UE (2019) Intraspecific trait variation increases species diversity in a trait-based grassland model. *Oikos* **128**(3), 441–455.

Cuevas YA and Zalba SM (2010) Recovery of native grasslands after removing invasive pines. *Restoration Ecology* **18**(5), 711–719.

D'Odorico P, Laio F and Ridolfi L (2006) A probabilistic analysis of fire-induced tree-grass coexistence in savannas. *The American Naturalist* **167**(3), E79–E87.

Dakos V, Matthews B, Hendry AP, Levine J, Loeuille N, Norberg J, Nosil P, Scheffer M and De Meester L (2019) Ecosystem tipping points in an evolving world. *Nature Ecology & Evolution* **3**, 355–362.

https://doi.org/10.1017/dry.2025.1 Published online by Cambridge University Press

Dantas VdL, **Pausas JG**, **Batalha MA**, **Paula Loiola Pd and Cianciaruso MV** (2013) The role of fire in structuring trait variability in neotropical savannas. *Oecologia* **171**, 487–494.

DeAngelis DL (2013) Intraspecific trait variation and its effects on food chains. *Mathematical Biosciences* **244**(2), 91–97.

Des Roches S, **Post DM**, **Turley NE**, **Bailey JK**, **Hendry AP**, **Kinnison MT**, **Schweitzer JA and Palkovacs EP** (2018) The ecological importance of intraspecific variation. *Nature Ecology & Evolution* **2**, 57–64.

Djeumen IY, **Dumont Y Doizy A and Couteron P** (2021) A minimalistic model of vegetation physiognomies in the savanna biome. *Ecological Modelling* **440**, 109381.

Dublin HT, **Sinclair AR and McGlade J** (1990) Elephants and fire as causes of multiple stable states in the serengeti-mara woodlands. *The Journal of Animal Ecology* **59**(3), 1147–1164.

Eby S, **Agrawal A**, **Majumder S**, **Dobson AP and Guttal V** (2017) Alternative stable states and spatial indicators of critical slowing down along a spatial gradient in a savanna ecosystem. *Global Ecology and Biogeography* **26**(6), 638–649.

Fensham R, **Fairfax R and Ward D** (2009) Drought-induced tree death in savanna. *Global Change Biology* **15**(2), 380–387.

Funk JL, **Larson JE**, **Ames GM**, **Butterfield BJ**, **Cavender-Bares J**, **Firn J**, **Laughlin DC**, **Sutton-Grier AE**, **Williams L and Wright J** (2017) Revisiting the Holy Grail: using plant functional traits to understand ecological processes. *Biological Reviews* **92**(2), 1156–1173.

Génin A, **Majumder S**, **Sankaran S**, **Danet A**, **Guttal V**, **Schneider FD and Kéfi S** (2018) Monitoring ecosystem degradation using spatial data and the r package spatialwarnings. *Methods in Ecology and Evolution* **9**(10), 2067–2075.

Geritz SA, **Metz JA**, **Kisdi É and Meszéna G** (1997) Dynamics of adaptation and evolutionary branching. *Physical Review Letters* **78**(10), 2024.

Gillespie DT (1976) A general method for numerically simulating the stochastic time evolution of coupled chemical reactions. *Journal of Computational Physics* **22**(4), 403–434.

Goel N, **Guttal V**, **Levin SA and Staver AC** (2020) Dispersal increases the resilience of tropical savanna and forest distributions. *The American Naturalist* **195**(5), 833–850.

González-Suárez M, **Bacher S and Jeschke JM** (2015) Intraspecific trait variation is correlated with establishment success of alien mammals. *The American Naturalist* **185**(6), 737–746.

Guttal V and Jayaprakash C (2007) Impact of noise on bistable ecological systems. *Ecological modelling* **201**(3–4), 420–428.

Hart SP, **Schreiber SJ and Levine JM** (2016) How variation between individuals affects species coexistence. *Ecology Letters* **19**(8), 825–838.

Higgins SI, **Bond WJ**, **Combrink H**, **Craine JM**, **February EC**, **Govender N**, **Lannas K**, **Moncreiff G and Trollope WS** (2012) Which traits determine shifts in the abundance of tree species in a fire-prone savanna? *Journal of Ecology* **100**(6), 1400–1410.

Higgins SI, **Bond WJ**, **February EC**, **Bronn A**, **Euston-Brown DI**, **Enslin B**, **Govender N**, **Rademan L**, **O'Regan S**, **Potgieter AL**, et al. (2007) Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* **88**(5), 1119–1125.

Higgins SI, **Bond WJ and Trollope WS** (2000) Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology* **88**(2), 213–229.

Hirota M, **Holmgren M**, **Van Nes EH and Scheffer M** (2011) Global resilience of tropical forest and savanna to critical transitions. *Science* **334**(6053), 232–235.

Hoffmann WA, **Geiger EL**, **Gotsch SG**, **Rossatto DR**, **Silva LC**, **Lau OL**, **Haridasan M and Franco AC** (2012) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. *Ecology Letters* **15**(7), 759–768.

Hoffmann WA and Solbrig OT (2003) The role of topkill in the differential response of savanna woody species to fire. *Forest Ecology and Management* **180**(1–3), 273–286.

Holling CS (1973) Resilience and stability of ecological systems. *Annual Review of Ecology, Evolution, and Systematics* **4**(1), 1–23.

Jackson RB, **Banner JL**, **Jobbágy EG**, **Pockman WT and Wall DH** (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* **418**(6898), 623–626.

Limberger R, **Daugaard U**, **Gupta A**, **Krug RM**, **Lemmen KD**, **Van Moorsel SJ**, **Suleiman M**, **Zuppinger-Dingley D and Petchey OL** (2023) Functional diversity can facilitate the collapse of an undesirable ecosystem state. *Ecology Letters* **26**(6), 883–895.

Lion S (2018) Theoretical approaches in evolutionary ecology: environmental feedback as a unifying perspective. *The American Naturalist* **191**(1), 21–44.

Majumder S, **Tamma K**, **Ramaswamy S and Guttal V** (2019) Inferring critical thresholds of ecosystem transitions from spatial data. *Ecology* **100**(7), e02722.

May RM (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* **269**(5628), 471–477.

Messier J, **McGill BJ and Lechowicz MJ** (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**(7), 838–848.

Meyer KM, **Wiegand K and Ward D** (2009) Patch dynamics integrate mechanisms for savanna tree–grass coexistence. *Basic and Applied Ecology* **10**(6), 491–499.

Moran EV, **Hartig F and Bell DM** (2016) Intraspecific trait variation across scales: implications for understanding global change responses. *Global Change Biology* **22**(1), 137–150.

O'Connor T and Crow V (1999) Rate and pattern of bush encroachment in eastern cape savanna and grassland. *African Journal of Range and Forage Science* **16**(1), 26–31.

Pardo I, **Camarero JJ**, **Gutiérrez E and García MB** (2013) Uncoupled changes in tree cover and field layer vegetation at two pyrenean treeline ecotones over 11 years. *Plant Ecology & Diversity* **6**(3–4), 355–364.

Ratnam J, **Bond WJ**, **Fensham RJ**, **Hoffmann WA**, **Archibald S**, **Lehmann CE**, **Anderson MT**, **Higgins SI and Sankaran M** (2011) When is a 'forest'a savanna, and why does it matter? *Global Ecology and Biogeography* **20**(5), 653–660.

Ruel JJ and Ayres MP (1999) Jensen's inequality predicts effects of environmental variation. *Trends in Ecology & Evolution* **14**(9), 361–366.

Sankaran M (2019) Droughts and the ecological future of tropical savanna vegetation. *Journal of Ecology* **107**(4), 1531–1549.

Sankaran M, **Hanan NP**, **Scholes RJ**, **Ratnam J**, **Augustine DJ**, **Cade BS**, **Gignoux J**, **Higgins SI**, **Le Roux X**, **Ludwig F**, et al. (2005) Determinants of woody cover in african savannas. *Nature* **438**(7069), 846–849.

Sankaran S, **Majumder S**, **Viswanathan A and Guttal V** (2019) Clustering and correlations: Inferring resilience from spatial patterns in ecosystems. *Methods in Ecology and Evolution* **10**(12), 2079–2089.

Scheffer M, **Carpenter S**, **Foley JA**, **Folke C and Walker B** (2001) Catastrophic shifts in ecosystems. *Nature* **413**(6856), 591–596.

Scholes RJ and Archer SR (1997) Tree-grass interactions in savannas. *Annual Review of Ecology, Evolution, and Systematics* **28**(1), 517–544.

Sheil D and Salim A (2004) Forest tree persistence, elephants, and stem scars. *Biotropica* **36**(4), 505–521.

Siefert A, **Violle C**, **Chalmandrier L**, **Albert CH**, **Taudiere A**, **Fajardo A**, **Aarssen LW**, **Baraloto C**, **Carlucci MB**, **Cianciaruso MV**, et al. (2015) A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**(12), 1406–1419.

Smit G (2004) An approach to tree thinning to structure southern african savannas for long-term restoration from bush encroachment. *Journal of Environmental Management* **71**(2), 179–191.

Solbrig OT, **Medina E**, **Silva JF**, et al. (1996) Biodiversity and tropical savanna properties: a global view. *Scope-Scientific Committee on Problems of the Environment International Council of Scientific Unions* **55**, 185–211.

Staver AC, **Archibald S and Levin SA** (2011) The global extent and determinants of savanna and forest as alternative biome states. *Science* **334**(6053), 230–232.

Staver AC and Levin SA (2012) Integrating theoretical climate and fire effects on savanna and forest systems. *The American Naturalist* **180**(2), 211–224.

Stevens N, **Lehmann CE**, **Murphy BP and Durigan G** (2017) Savanna woody encroachment is widespread across three continents. *Global Change Biology* **23**(1), 235–244.

Török P, **Brudvig LA**, **Kollmann J**, **Price JN and Tóthmérész B** (2021) The present and future of grassland restoration. *Restoration Ecology* **29**(S1), e13378.

Van Langevelde F, **Van De Vijver CA**, **Kumar L**, **Van De Koppel J**, **De Ridder N**, **Van Andel J**, **Skidmore AK**, **Hearne JW**, **Stroosnijder L**, **Bond WJ**, et al.

https://doi.org/10.1017/dry.2025.1 Published online by Cambridge University Press

(2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* **84**(2), 337–350.

Vanak AT, **Shannon G**, **Thaker M**, **Page B**, **Grant R and Slotow R** (2012) Biocomplexity in large tree mortality: interactions between elephant, fire and landscape in an african savanna. *Ecography* **35**(4), 315–321.

Wakeling JL, **Staver AC and Bond WJ** (2011) Simply the best: the transition of savanna saplings to trees. *Oikos* **120**(10), 1448–1451.

Walker BH and Noy-Meir I (1982) Aspects of the stability and resilience of savanna ecosystems. In Huntley BJ and Walker BH (eds.), *Ecology of Tropical Savannas*. Berlin, Heidelberg: Springer, pp. 556–590.

Warman L and Moles AT (2009) Alternative stable states in australia's wet tropics: a theoretical framework for the field data and a field-case for the theory. *Landscape Ecology* **24**, 1–13.

Wickman J, **Koffel T and Klausmeier CA** (2023) A theoretical framework for trait-based eco-evolutionary dynamics: population structure, intraspecific variation, and community assembly. *The American Naturalist* **201**(4), 501–522.

Wilcox BP, **Birt A**, **Fuhlendorf SD and Archer SR** (2018) Emerging frameworks for understanding and mitigating woody plant encroachment in grassy biomes. *Current Opinion in Environmental Sustainability* **32**, 46–52.

Wilson T and Witkowski E (1998) Water requirements for germination and early seedling establishment in four african savanna woody plant species. *Journal of Arid Environments* **38**(4), 541–550.

Yatat VD, **Dumont Y**, **Tewa JJ**, **Couteron P and Bowong S** (2014) Mathematical analysis of a size structured tree-grass competition model for savanna ecosystems. *Biomath* **3**(1), 1404212.

https://doi.org/10.1017/dry.2025.1 Published online by Cambridge University Press