Mechanisms behind facilitation-competition transition along rainfall gradients

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Abstract

Woody cover is rapidly changing due to mortality, shrub encroachment, and afforestation, reshaping herbaceous communities and ecosystem functioning worldwide. Often, trees and shrubs promote herb growth in dry sites but suppress it in wetter ones, as predicted by the classical Stress Gradient Hypothesis. However, explanations for the facilitation-to-competition transition remain verbal and contested, lacking a clear link to resource competition theory. Here, we present a mechanistic framework consisting of two submodels: (i) canopy shading that reduces photosynthesis and evapotranspiration, and (ii) root effects, including water uptake and increased moisture via hydraulic redistribution. We elucidate the conditions under which interactions shift from facilitation to competition. The models reproduce this reversal only when water is not the sole limiting factor at high rainfall or when woody density increases with precipitation. Moreover, the reversal can occur across any aridity gradient, including those driven by evaporative demand influenced by temperature and humidity. The two pathways leave distinct signatures: canopy shading produces a hump-shaped pattern with maximum facilitation at intermediate stress, while the root pathway predicts a shift from positive to negative interactions as water availability increases. By translating a classic idea into a quantitative framework, this model enhances ecosystem management in a changing world.

1 Introduction

Global climate and land-use changes are rapidly reshaping woody vegetation worldwide [1,2]. These shifts are especially common in drylands, which cover about 40% of Earth's land surface [3,4]. Many water-limited systems are losing woody cover due to widespread drought and fire [5]. Conversely, other dry regions show woody expansion, driven by shrub encroachment [2,6] and large-scale afforestation aimed at climate mitigation [1,7]. In these ecosystems, woody plants (hereafter, trees) strongly shape microclimate and resource availability, thereby influencing the abundance and distribution of herbaceous plants (hereafter, herbs) that sustain forage production and biodiversity in drylands [2,6].

Trees are ecosystem engineers, altering the environment beyond simply consuming light and water [8]. They can facilitate herb growth through **canopy and root mechanisms**. The canopy suppresses light availability, which reduces carbon assimilation (photosynthesis) but also lowers evapotranspiration and therefore water loss [9]. This reduction in evapotranspiration also results from microclimatic buffering: slower wind speeds, higher humidity, and lower temperatures beneath the canopy [10]. Tree roots not only extract water, thereby drying the soil, but can also increase soil moisture by enhancing infiltration [11] and redistributing water from deeper to shallower soil layers through hydraulic lift [12,13].

Rainfall amount often mediates the balance between these positive and negative effects. Meta-analyses find that trees typically benefit herbs at low rainfall but hinder them as rainfall increases [14–16]. Even so, some studies report inconsistent neighbor effects along similar gradients [17], pointing to hidden thresholds or additional factors that alter the expected pattern.

Over the past three decades, the transition from facilitation to competition has largely been investigated through the lens of the Stress Gradient Hypothesis (SGH). This conceptual framework was proposed to explain why facilitation dominates under high abiotic stress (low rainfall), whereas competition prevails under benign conditions [18–23]. The original explanations emphasized plant responses along water-stress gradients [20], but the hypothesis has since been applied to many other stress types [24,25]. The primary argument is that tree-mediated relief of water stress dominates under low rainfall, whereas shading-induced inhibition dominates under low stress (high rainfall) [9]. These verbal arguments were later extended using phenomenological models that embedded spatial–temporal dynamics [26] and biodiversity feedbacks [27].

Despite its prominence, the SGH has been questioned both mechanistically and in terms of predicted patterns [9,28–31]. Some studies argue that species interactions become more strongly negative with rainfall [14], whereas others report a unimodal (hump-shaped) pattern in which facilitation peaks at intermediate stress and weakens under both severe aridity and benign conditions [29]. Resolving these discrepancies calls for quantitative models that explicitly represent resource dynamics and make assumptions transparent, allowing specific processes such as shading or water uptake to be identified as drivers that generate, sustain, or limit facilitation along the gradient.

Consumer-resource theory is the leading modeling framework for mechanistic explanations of species interactions [32–35]. Yet, it has only recently been applied to the SGH [36,37]. These recent applications yielded insights into the role of trees in elevating resource availability during early succession [36] and into the joint effects of drought and grazing [37]. However, they focused exclusively on root mechanisms and did not consider canopy shading, the mechanism emphasized in the classical conceptual hypothesis [20]. Crucially, and contrary to the SGH's prediction of a facilitation-to-competition shift, these consumer-resource models produced an interaction sign that remained constant (either positive or negative) along the rainfall gradient, rather than a transition from facilitation to competition.

Here, we develop a minimal consumer–resource framework that generates the classic shift from facilitation to competition as rainfall (resource supply rate) increases. The model clarifies the

conditions under which this transition emerges for both canopy and root mechanisms (Fig. 1) and reconciles contrasting predictions regarding how facilitation strength varies along precipitation gradients.
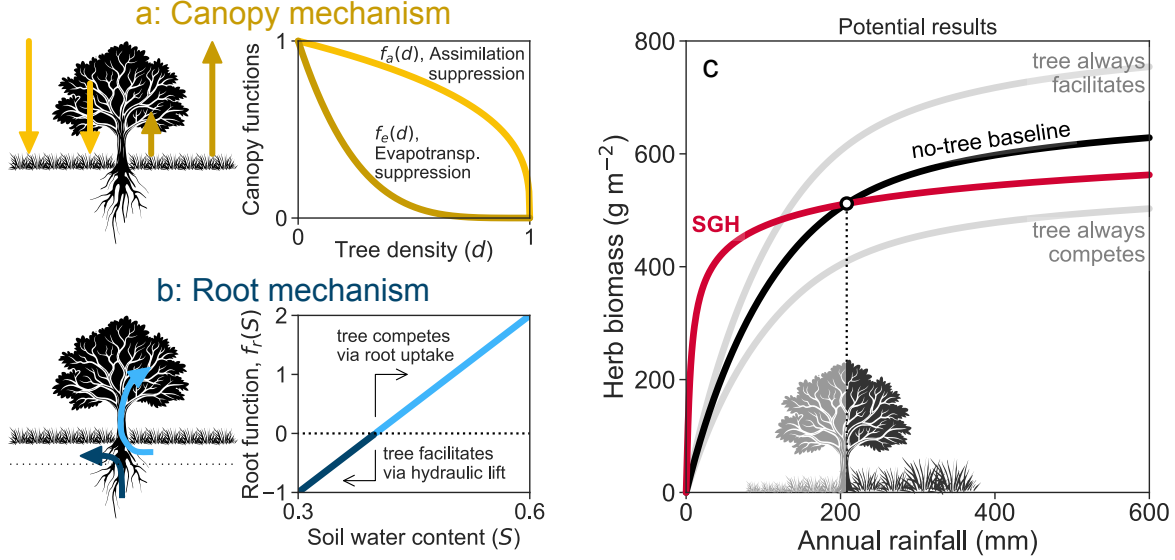

Figure 1: **Assumptions of the two submodels (a, b) and potential model outcomes (c).** (a) The canopy mechanism assumes that tree density suppresses both photosynthetic assimilation (yellow) and water loss by evapotranspiration (brown). However, the reduction in evapotranspiration with increasing tree density is greater than the reduction in photosynthesis, which is a necessary condition for facilitation under shading. (b) The root mechanism focuses on water uptake (light blue) and hydraulic lift (dark blue), where water from deep layers is transported upward by the tree and increases moisture in shallow soil. The curve reflects the net effect of these two opposing processes: when the soil is dry, steep water potential gradients between deep and shallow layers favor upward water movement throught the roots, producing negative net uptake (a gain to the upper soil). As soil moisture increases, water extraction by roots becomes more efficient, and uptake outweighs hydraulic lift, resulting in higher (more positive) net uptake values. (c) Potential model outcomes are illustrated by comparing rainfall–biomass relationships with and without trees (black line). In the two simple scenarios (grey), trees either consistently facilitate or consistently inhibit herb growth across the rainfall gradient, whereas the Stress Gradient Hypothesis (SGH; red line) predicts a transition from facilitation to competition, marked by the intersection between the black and the red lines.

2 Results

We developed a consumer-resource model that describes the coupled dynamics of herbs' biomass and soil moisture as follows:

$$\text{herb biomass:} \qquad \frac{dB}{dt} = \overbrace{a\,f_a(d)\,f_k(B)B\,S}^{\text{growth}} - \overbrace{m\,B}^{\text{mortality}} \tag{1a}$$

$$\text{soil water:} \qquad \underbrace{nz_r}_{\substack{\text{active} \\ \text{soil depth}}}\frac{dS}{dt} = \underbrace{p}_{\text{precipitation}} - \underbrace{q_s S^\gamma}_{\text{drainage}} - \underbrace{e_0\,f_e(d)B\,S}_{\text{evapotranspiration}} - \underbrace{f_r(S,d)}_{\text{tree root}}. \tag{1b}$$

The first equation tracks the change in herb biomass (B) over time, which is governed by growth and mortality processes. The second equation represents the dynamics of soil moisture (S), which is influenced by gains from precipitation (p) and losses due to drainage, evapotranspiration, and a tree-root effect. Due to their much slower dynamics, trees are represented as a constant parameter for tree density (d representing canopy cover or root density). This parameter affects both the canopy-suppression factors on herb growth ($f_a(d)$) and on evapotranspiration ($f_e(d)$), as depicted in Fig. 1a. The impact of the root mechanism $f_r(S,d)$ on soil water is depicted in Fig. 1b. We further assumed that when water and light are ample, other factors such as nutrients or genetic limits constrain herb growth, represented by a carrying capacity term $f_k(B) = 1 - B/k$. For simplicity, we investigated each mechanism separately: when examining canopy effects, we removed root effects, and vice versa.

When water is the main limiting factor and tree density is constant, our model, like previous mechanistic models [36;37], shows that the interaction between trees and herbs remains either facilitative or competitive along the entire precipitation gradient. However, a key finding is that introducing a new limiting factor ($f_k(B)$ in the model), which can represent nutrient limitation, or a genetic size limit, is a **necessary condition** for the Stress Gradient Hypothesis transition to occur (see Supplementary Section **??**). When this condition is met, both the canopy and root mechanisms can produce a clear shift from facilitation to competition as precipitation increases. The following explores how each of these mechanisms drives this transition.

In the **canopy mechanism**, in the absence of trees, herb biomass increases with precipitation, showing a saturation pattern as the curve's slope decreases (black line in Fig. 2a). With some trees (light curve), herb biomass is higher than the no-tree baseline at low precipitation but is reduced at higher precipitation levels, showing a clear transition from facilitation to competition. At very high tree density (dark curve), herb biomass is suppressed across the entire precipitation gradient.

This pattern is a result of a tug of war between two opposing forces exerted by the trees. First, trees facilitate growth by providing shade, which reduces evapotranspiration and conserves soil water. This effect is represented by the function $f_e(d)$, leading to greater soil water availability relative to a no-tree environment (see Fig. 2c). Second, trees inhibit herb's growth by reducing light availability through the function $f_a(d)$. This factor, along with other limiting elements like nutrients or grazing (captured by the carrying capacity term, $f_k(B)$), down-regulates herb assimilation. The combined effect is represented by the product $f_a(d)f_k(B)$.

At low precipitation, herb biomass is low, so the carrying capacity term $f_k(B)$ is very weak (close to 1). In this dry scenario, the tug of war is mainly between the water-saving benefit of $f_e(d)$ and the light reduction effect of $f_a(d)$. When tree density is low, the extra soil water overpowers the minor loss in light, facilitating herb growth (light curve in Fig. 2a). However, when tree cover is high, the reduction in light becomes too strong, suppressing the herbs (dark curve). As precipitation increases, herb biomass also rises. This strengthens the carrying capacity term $f_k(B)$ (making it closer to zero) and tips the balance. The combined competitive effect of reduced light and carrying capacity ($f_a(d)f_k(B)$) becomes stronger than the facilitative effect of water conservation. In other words, under high rainfall, water is no longer the limiting factor, and therefore, the benefit of reduced water loss is not enough to compensate for the reduction in photosynthesis, leading to a transition from net facilitation to net competition.
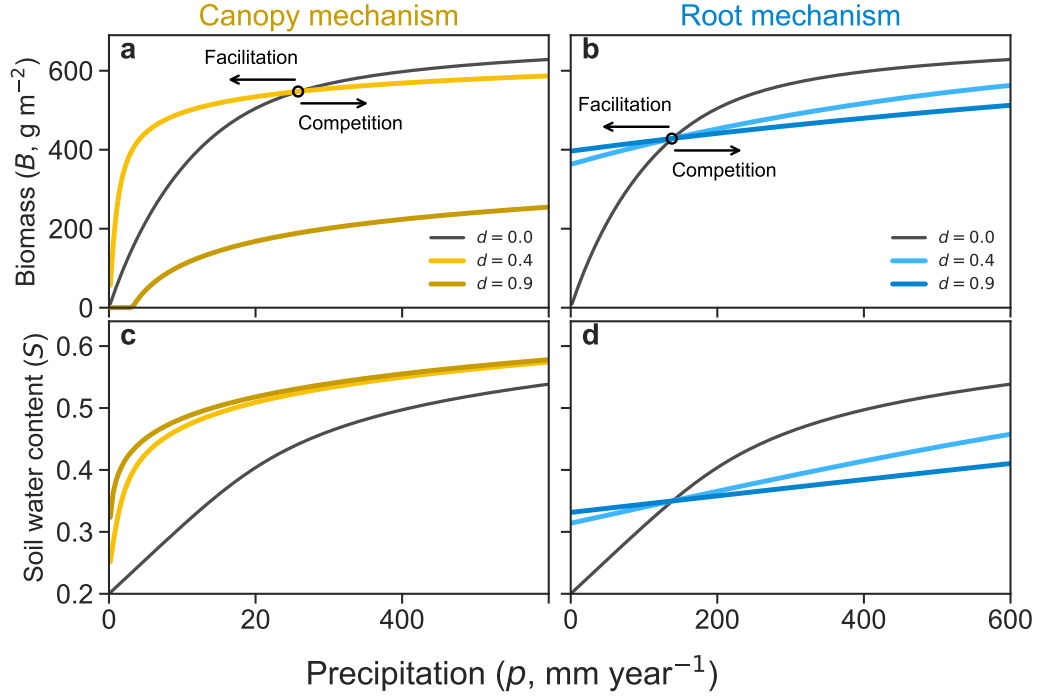
Figure 2: **The transition from facilitation to competition is produced by two different mechanisms.** Herb biomass and soil water solutions of (Eqs. (1)) are shown for the canopy mechanism (panels a,c) and the root mechanism (panels b,d). Black lines give the no-tree baseline ($d = 0$), light solid curves show moderate tree density ($d = 0.4$) and dark solid curves high tree density ($d = 0.9$). Facilitation (competition) occurs when the herb biomass solid curves are above (below) the baseline curve. Other parameter values are as reported in Table 1.

For the **root mechanism**, all non-zero tree densities show a similar transition pattern: herb biomass is higher than the baseline at low precipitation and lower at high precipitation (see Fig. 2b). As tree density increases, both effects intensify along the precipitation gradient. This is because the tug of war between facilitation and competition is expressed by a single function, $f_r(S, d)$, which represents the net effect of tree roots on soil water available in the herb root zone.

This function captures the tipping of the balance as soil water content changes. At low soil water levels, tree roots can lift water from deeper soil layers to the herb root zone, facilitating growth. As soil water content increases, hydraulic lift is no longer possible. Beyond this point, roots begin to compete with herbs by taking up water from the same soil layer. Counterintuitively, the root term $f_r(S, d)$ by itself does not produce a facilitation-to-competition switch (see Supplementary Section **??**). With water as the only limiting resource (i.e., $f_k(B) = 1$), the equilibrium soil moisture $S^\star$ is set by the consumer and is independent of the precipitation supply p (R* logic;[33]). Because f_r acts through S rather than directly through p, the sign of the interaction is fixed by whether $S^\star$ lies below or above the hydraulic switching range, so it does not change along the rainfall gradient. However, when a second growth constraint is introduced through the carrying-capacity term $f_k(B)$, the outcome changes: as p increases, biomass approaches its limit and cannot deplete water further, so $S^\star$ rises. This upward shift in $S^\star$ carries the system across the hydraulic threshold, turning facilitative lift into competitive uptake and yielding the observed transition. Put simply, $f_k(B)$ caps biomass at high rainfall, weakening consumption and allowing soil water to accumulate, which moves $S^\star$ into the competitive domain of $f_r(S, d)$.

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Notably, the two mechanisms produce very different biomass responses at low precipitation. In the canopy mechanism, precipitation is the only water source, so all curves must start from the origin, zero biomass at zero rainfall. A small initial increase in precipitation leads to stronger facilitation, which is visible as a widening gap between the low-tree-density curve and the no-tree baseline (light and black curves in Fig. 2a, respectively). This facilitative gap eventually narrows before disappearing at the transition to competition. In contrast, the root mechanism includes an additional water source: hydraulic lift from deeper soil layers during dry surface conditions. This allows herb biomass to persist even without precipitation. The gap between tree-density curves and the baseline shrinks steadily as precipitation increases, until it reaches the transition point. This distinct pattern in the biomass gap is key to understanding the contrasting responses in interaction intensity between the two mechanisms.

For the canopy mechanism, the interaction intensity based on the absolute difference is unimodal (see Fig. 3a). This pattern directly results from the widening and eventual vanishing of the gap between the biomass curve with trees and the no-tree baseline curve, as previously discussed. However, when using the relative log response ratio (see Fig. 3c), the interaction intensity decreases monotonically for p below the transition threshold. In contrast, the root mechanism yields monotonically-decreasing positive interaction intensities, regardless of whether absolute difference or relative log response ratio is used. A broader discussion of the canopy mechanism's interaction intensity in the full (p, d) parameter space is given in Supplementary Section **??**.
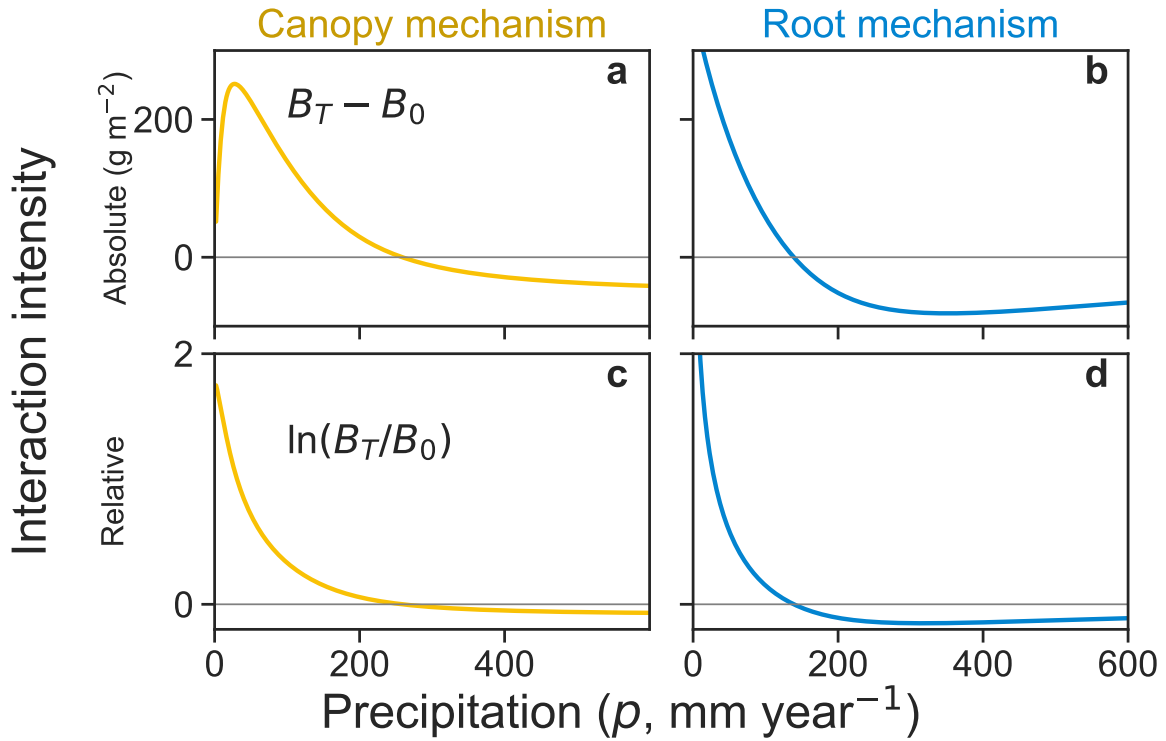

Figure 3: **Interaction intensity patterns depend on both mechanism and metric.** The gray lines represent zero interaction. Positive interactions indicate facilitation by trees; negative interactions indicate competition. Panels a and b show the absolute interaction intensity, $B_T - B_0$, where B_0 and B_T denote herb biomass in the absence and presence of tree density, respectively. Panels c and d show the relative log response ratio, $\ln(B_T/B_0)$. Parameters: $d = 0.0$ and $d = 0.3$ were used to compute B_0 and B_T, respectively; other parameters are given in Table 1.

3   Discussion

The Stress Gradient Hypothesis has guided decades of work but has largely been articulated in verbal or phenomenological terms[9;19;20;26;27;29;30]. We show that a minimal consumer-resource model linking canopy shading or root water redistribution to herb biomass generates the observed shift from facilitation to competition along rainfall gradients. Our model also specified when the shift should and should not arise. Finally, the framework also clarifies the expectation on interaction intensity, with a mid-gradient peak in the facilitation under shading and a monotonic decline from positive to negative effect under the root pathway.

Our aim is to provide general insight and testable predictions rather than site-specific accurate description. Accordingly, the model is intentionally simple yet mechanistic: water balance is explicit, and interaction signs emerge from the equations rather than being imposed a priori. This simplicity enables a thorough understanding of each parameter (See Supplementary Section ??).

The model focuses on the primary pathways through which woody plants influence herbs: canopy shading and root water redistribution. It keeps tree density fixed while examining steady-state contrasts. Other processes, such as grazing protection, nutrient supply, or spatial patterns[31;36–38] can be incorporated where they are expected to matter (see the Supplementary Sections ?? and ?? for transient dynamics and varying tree density). We therefore view this framework as a baseline for systems where water and light competition dominate, and as a foundation for targeted extensions that incorporate additional mechanisms.

The stress gradient hypotheses have been invoked for many stress types[9;18–23]. Yet, as Maestre et al.[29] noted, "Stress is not a precise concept, and therefore it is difficult to apply quantitatively to communities or ecosystems". Here we focus on mechanisms tied directly to plant water balance, while recognizing that other stressors such as freezing, toxicity, or salinity, are likely to require different model structures. The same framework can also be applied to evaporative demand, another driver of aridity, which is influenced by temperature and humidity. This driver can change the magnitude of facilitation and competition and shift the transition point along the gradient. Still, the model consistently predicts a shift from net facilitation to net competition as water limitation relaxes (see Figure in Supplementary Section ??).

The model resolves the empirical question whether stress should be represented by resource supply rate (precipitation) or by resource abundance (soil water content)[9;36;37;39]. It shows that precipitation or evaporative demand are the appropriate measures for quantifying water stress in such systems (see Supplementary Section ??). Soil water content, in contrast, is not an independent driver but an emergent outcome of interacting processes including precipitation, evapotranspiration, biotic uptake, and substrate properties[9;36;39]. Treating soil water as externally fixed cuts off these mechanistic links and removes the causal connection between resource supply and species interactions. Only when stress is parameterized as a supply rate can the facilitation–competition interplay characteristic of the SGH be captured[9;36;37;39].

3.1   Canopy mechanism

Shading is a ubiquitous factor plant growth and community dynamics[40–43]. This mechanism is central in conceptual models that generate the transition from facilitation to competition[9;20]. Our findings indicate that shading can simultaneously enhance and constrain growth, with implications far beyond tree–herb interactions.

In the model, shading acts solely by reducing light, so any reduction in radiation, whether caused from trees, slope aspect, buildings, or solar panels, should generate similar responses. In dry conditions, shaded hillslopes, north-facing in the northern hemisphere and the reverse in the southern hemisphere, should be more productive than sun-exposed slopes. In wet conditions, the pattern should reverse. Variation with slope aspect is a long-standing observation in botany[44;45], yet we are not aware of a mechanistic model that explains this global pattern. The same logic applies to urban ecosystems, where buildings cast shade, and to agricultural settings, with the co-location of solar panels and crops (agrivoltaics) being on the rise over the last two decades[46].In such settings, the model predicts when agrivoltaics will increase or decrease productivity depending on environmental conditions

The model highlights several conditions that have seldom been investigated in empirical studies along gradients. First, a necessary condition for facilitation under shading is that the proportional reduction in evapotranspiration with increasing shade exceeds the proportional reduction in photosynthesis. Although this likely holds for many plants, there are clear exceptions, such as species that require high light and are sensitive to shade. We therefore suggest that empirical tests of the shading mechanism begin by verifying this assumption.

For the transition from facilitation to competition to occur without a change in tree cover, another condition must be met. Under high rainfall, water must cease to be the main limiting factor (the carrying capacity effect). This implies that a qualitative switch is less likely when moving from an arid to a semiarid system if both remain water-limited. Instead, a switch is expected only when crossing into a system limited by another resource, such as nutrients (see Supplementary Section **??**, which shows that carrying capacity is equivalent to an additional essential resource). This result may explain empirical studies that do not observe a shift along precipitation gradients[17;29;47;48] and underscores that the transition should not be viewed as inevitable.

Alternatively, shading can lead to a facilitation-to-competition transition without introducing carrying capacity, but only when tree density increases with rainfall (See Supplementary Section **??**). This occurs because at high tree cover, light becomes the primary limiting factor and offsets the positive effects of shading on water balance. This density effect can be further enhanced by photoinhibition, where excessive light inhibits photosynthesis. We therefore recommend that future empirical studies quantify how tree density changes along the gradient and manipulate tree cover directly, or mimic shading with shade cloth. Such an approach is necessary to determine whether interaction outcomes change under a constant shade level (Fig. 2), or arise from shifts in canopy density along the gradient (Supplementary Section **??**).

3.2   Root mechanisms

Root-mediated effects in natural settings can be highly variable because they depend on root architecture and soil properties[11;49]. In the canopy mechanism, we used a two-layer simplification in which deep tree roots do not change the soil water available to herbs[50]. By contrast, in the root mechanism, we assumed partial overlap in rooting depth so that trees and herbs draw from the same near-surface water. We further assumed hydraulic lift, whereby trees move water upward from deeper layers when the surface is dry and draw water from the herb layer when it is wet.

When trees increase soil moisture under dry conditions and reduce it under wet conditions, a transition from facilitation to competition can occur. Although we initially expected this transition to arise inevitably from the root mechanism, we found that it occurs only when another factor limits biomass at high rainfall; otherwise, equilibrium soil moisture remains constant along the gradient. Notably, although there is empirical evidence for hydraulic lift[13], its strength and prevalence remain uncertain, so we treat it as secondary to shading for broad-scale patterns. Alternatively, a more common way

trees may increase soil moisture is by enhancing infiltration[11]. While infiltration alone does not cause a facilitation-to-competition transition[37], our model shows that it can do so when combined with shading: under low precipitation, the positive effects of increased infiltration dominate, whereas at high rainfall, the negative effects of shading prevail (Supplementary Section **??**).

3.3 Concluding Remarks

Our findings help reconcile conflicting reports on interaction strength along rainfall gradients by showing that the expected pattern depends first on the mechanism. Under the canopy pathway, the absolute difference in biomass is hump-shaped, with maximum facilitation at intermediate rainfall, whereas under the root mechanism, the interaction declines monotonically from positive to negative. A second source of variation is the metric, and this sensitivity applies to shading in particular: only the absolute measure yields a unimodal pattern, whereas relative measures decline with rainfall, consistent with earlier suggestions[9].

Importantly, tree density further modulates these patterns of interactions along aridity gradients (Supplementary Section **??**). Hence, empirical patterns can only be interpreted accurately when tree density is quantified. Under low precipitation, facilitation peaks at intermediate density, while low and high tree densities weaken it. As precipitation increases, progressively lower densities are sufficient to shift the balance from facilitation to competition. Eventually, at high rainfall, even near-zero tree density reduces herb performance, so further changes in density no longer cause a qualitative shift.[9].

Many empirical studies report a shift from facilitation to competition[14–16], and many do not[9;28–31]. In the lens of our framework, cases without a shift arise when (i) other pathways dominate, for example, protection from herbivory, or (ii) when the conditions for a shift are not met, for example, when shade suppresses photosynthesis more than evapotranspiration. This perspective moves the discussion from whether the hypothesis holds to which mechanism operates. It also points to practical tests, pairing shade manipulations with canopy and soil water measurements, and reporting both absolute and proportional changes.

Looking ahead, climate change is exacerbating water limitations in many regions[51–54], while woody cover is changing due to drought, fire, shrub encroachment, afforestation, and altered land use[1;2;5–7]. A compact mechanistic framework can help anticipate where shade will enhance herb production by conserving water and where it will suppress production due to light limitations, and it can guide restoration and conservation efforts toward interventions that match local mechanisms. By building on the Stress Gradient Hypothesis and giving it simple, testable conditions, this framework connects a classic idea to actionable predictions for conserving dryland ecosystems in a rapidly changing world.

4 Methods

We developed a consumer-resource model (see Eq. (1)) that describes the dynamics of herbaceous biomass density (B, $kg\,m^{-2}$)[36;37], and relative soil-water content (S, dimensionless)[55].

The model makes three key assumptions: (i) Tree biomass changes on a much longer time scale than herb biomass, so tree density is treated as constant and remains in quasi steady state relative to the herbs and soil water. (ii) Herb roots occupy only the upper soil layer, whereas tree roots also reach deeper layers, allowing trees to lift water upward or to draw water away from the herb rooting zone; (iii) Herb growth is limited by light and by soil moisture, yet only water can accumulate over time and therefore is described by a balance equation. To incorporate constraints on growth beyond water and

light, we include a carrying capacity term, which is equivalent to assuming another limiting resource, such as an essential nutrient (see Supplementary Section **??**).

The dynamics of herbaceous biomass density B are governed by growth and mortality terms (Eq. (1a)). The dynamics of relative soil-water content S are dictated by a water-balance equation[55], whose input is precipitation and whose outputs are drainage to deeper soil layers and evapotranspiration, while tree-root processes can function as both inputs and outputs depending on direction of water flow.(Eq. (1b)). Herb biomass and water are averaged over the horizontal dimensions, and water is averaged over the active soil depth nz_r, following a traditional bucket-model approach[56].

The functions $f_a(d), f_k(B), f_e(d), f_r(S, d)$ are modular components of the model that can be turned on or off, either when switching between model variants or when testing the impact of different limiting factors. The features that are common to all realizations of the model are: (i): Herb biomass growth rate is linearly dependent on soil water content S (when the carrying capcity term is negligible). (ii) Herb biomass mortality rate is proportional to biomass. (iii) Evapotranspiration is down-regulated by soil moisture availability, following a linear β function of S[57;58], and is proportional to herb biomass density. (iv) Drainage is modeled by a highly nonlinear function of soil moisture[59], commonly used in ecohydrological modeling[60]. (v) The logistic growth term $f_k(B) = 1 - B/k$ was used throughout this paper and was only turned off ($f_k(B) = 1$) in Supplementary Sections **??** and **??**, where we studied the effects of removing additional limiting growth-limiting factors beyond water and light. (vi) All the model parameters (Table 1) are constant. In particular, precipitation rate p is understood as the total precipitation of the growing season divided by its duration; it is reported in $\mathrm{mm\,y^{-1}}$ instead of $\mathrm{mm\,d^{-1}}$ throughout the paper to enhance interpretability.

Our model belongs to the family of coupled soil moisture and biomass models developed for other purposes[61–63]. The key difference is that many earlier models treated biomass growth and evapotranspiration as the same function scaled by a constant conversion factor, water use efficiency, defined as water loss per unit carbon assimilation. Here, both processes depend on moisture, biomass, and tree density, but they have different functional forms, so water use efficiency varies across environments. This follows from the fact that shading can affect evapotranspiration and assimilation differently (Fig. 1a). In addition, relative biomass growth declines with size through the logistic term, whereas evapotranspiration remains proportional to biomass. These assumptions are both biologically plausible and necessary for the mechanisms we study: if water use efficiency were constant across shading levels, the trivial pattern where partial shade is beneficial but heavy shade is detrimental could not arise.

Below, we discuss in more detail the two main mechanisms employed in this paper.

Canopy mechanism

Shading affects both plant growth, by reducing light availability and thus photosynthesis, and transpiration, by lowering temperature and radiation levels, which helps retain soil moisture and improve water availability for herbs. When the shading mechanism is "on", the root mechanism is disabled by setting $f_h(S, d) = 0$, implying a complete partitioning of the soil into two distinct niches, the top available for herbs only, and deeper layers accessible to trees only.

Biomass growth is down-regulated by shading via $f_a(d)$, while evapotranspiration is down-regulated via $f_e(d)$. The shading functions are $f_j(d) = (1 - d)^{\beta_j}$, where $j = \{a, e\}$. Figure 1a shows the nonlinear decline of these functions with tree density. A necessary condition for facilitation is $\beta_e > \beta_a$; assimilation is therefore less inhibited by shade than transpiration.

Root mechanism

Trees can influence herbs access to water in two ways: they can lift water from deeper layers into the herbs rooting zone when surface soil is dry (facilitation), and they can uptake water from that zone (competition). The combined effects of hydraulic lift and tree water uptake is described by the function $f_r(S, d)$. When the root mechanism is "on", the shading mechanism is disabled by setting $f_a(d) = f_e(d) = 1$. The expression for the root function reads:

$$f_r(S, d) = d \left[\lambda_1 + \varphi \max(0, S - S_h) - \varphi \max(0, S - S_{fc}) \right], \tag{2}$$

where the slope $\varphi = (\lambda_{fc} - \lambda_h)/(S_{fc} - S_h)$. For S smaller than the hygroscopic point S_h, the upper soil is too dry for tree roots to uptake water, and hydraulic lift reaches its maximum ability to bring water from deeper soil layers to the topsoil (λ_h). For S greater than the field capacity S_{fc}, trees cease to benefit from increasing soil water content, and uptake water at a rate λ_{fc}. Between S_h and S_{fc}, the root function varies linearly between λ_h and λ_{fc}. Regardless of soil water content, the root function depends linearly on tree density d. Figure 1b shows the function f_r in the range $S_h < S < S_{fc}$, for zero tree density ($d = 0$) and maximal tree density ($d = 1$).

4.1 Numerical solutions

Numerical analyses were performed with Python 3.12, using the libraries NumPy 2.0 and SciPy 1.13. Steady-state solutions ($dB/dt = dS/dt = 0$) were obtained by finding the roots of the right-hand side of Eqs. (1) with scipy.optimize.fsolve, using random starting estimates for the roots ($0.5 < B < 1.5$ kg m^{-2} and $0.5 < S < 0.6$). A root is accepted when $B > 0.01$ kg m^{-2} and $0 < S < 1$; if these criteria are not met, a new set of random starting estimates is chosen. This procedure is repeated up to 10 times, after which the steady-state solutions are estimated by numerically integrating Eqs. (1) with scipy.integrate.solve_ivp (stiff solver, default tolerances) up to a final time of 10 thousand days, and the final configuration is taken as the steady-state solutions.

4.2 Code Availability

The code to run the model can be found in the following Zenodo repository.

4.3 Model Parameters

The model variables and parameters are summarized in Table 1. The specific parameter values (or their ranges) were chosen from typical values found in the literature.

Table 1: **Variables and parameters with typical value ranges.**

	Variables		
Symbol	**Units**	**Values**	**Description**
B	$\mathrm{g\,m^{-2}}$	0–1000	Herb biomass density
S	—	0–1	Relative soil water content
	Parameters		
a	$\mathrm{d^{-1}}$	0.05	Assimilation rate
β_a	—	1/3	Shading function exponent
β_e	—	4	Shading function exponent
k	$\mathrm{g\,m^{-2}}$	1000	Carrying capacity
m	$\mathrm{d^{-1}}$	0.01	Mortality rate
p	$\mathrm{mm\,y^{-1}}$	0–600	Precipitation rate
e_0	$\mathrm{mm\,g\,d^{-1}\,m^{-2}}$	5000	Max evapotranspiration rate per unit biomass density
q_{sat}	$\mathrm{mm\,d^{-1}}$	800	Saturated hydraulic conductivity
γ	—	10	Deep infiltration exponent
n	—	0.4	Soil porosity
z_r	mm	300	Herb rooting depth
d	—	0–1	Woody plant density
S_h	—	0.3	Hygroscopic point
S_{fc}	—	0.6	Field capacity
λ_h	$\mathrm{mm\,d^{-1}}$	−2	Max tree water provision
λ_{fc}	$\mathrm{mm\,d^{-1}}$	10	Max tree water usage

Note. Variable B range derived from Mussery et al.[64]. Variable S range and parameters q_{sat}, γ, n, z_r, S_h, S_{fc} derived from Rodriguez-Iturbe et al.[60]. Parameter a derived from James and Drenovsky[65]. The ratio between β_a and β_e is derived from Pons et al.[66]. Parameter p range derived form Huang et al.[67]. Parameter λ_{fc} is derived from Shiferaw et al.[68]. Parameter e_0 is derived from Allen et al.[69]; Garnier et al.[70].

5   Acknowledgments

6 Author Contribution

Conceptualization: O.H., Y.M., and N.D.; Analysis: O.H. and Y.M.; Funding acquisition: Y.M. and N.D.; Supervision: Y.M. and N.D.; Visualization: O.H. and Y.M.; Writing—original draft: O.H.; Writing—review and editing: Y.M. and N.D.

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