Positive interactions, discontinuous transitions and species coexistence in plant communities

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A B S T R A C T
The population and community level consequences of positive interactions between plants remain poorly explored. In this study we incorporate positive resource-mediated interactions in classic resource competition theory and investigate the main consequences for plant population dynamics and species coexistence. We focus on plant communities for which water infiltration rates exhibit positive dependency on plant biomass and where plant responses can be improved by shading, particularly under water limiting conditions. We show that the effects of these two resource-mediated positive interactions are similar and additive. We predict that positive interactions shift the transition points between different species compositions along environmental gradients and that realized niche widths will expand or shrink. Furthermore, continuous transitions between different community compositions can become discontinuous and bistability or tristability can occur. Moreover, increased infiltration rates may give rise to a new potential coexistence mechanism that we call controlled facilitation.

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1. Introduction

Facilitation and competition shape population and community structure (e.g. Schoener, 1974; Callaway, 2007). In the case of plant communities, competition has been considered as one of the main drivers of community structure and dynamics, along with tolerance to environmental conditions, disturbances and plant–animal interactions (Tilman, 1982; Smith and Huston, 1989; Pacala et al., 1996). Over the last years, however, increasing empirical evidence has built up indicating that positive interactions also play a pivotal role in shaping plant population and community structure (e.g. Holmgren et al., 1997; Callaway et al., 2002; Maestre et al., 2003; Lortie et al., 2004; Tirado and Pugnaire, 2005). The existence of interspecific positive interactions in plant communities was recognized early (Clements, 1916; Connell and Slatyer, 1977), yet, mechanistic theories of vegetation dynamics largely rely on competitive interactions (e.g. Tilman, 1982; Pacala et al., 1996). Thus, there is now a clear need to explore how positive interactions corroborate or challenge the main predictions of ecological theories (Michalet et al., 2006; Brooker et al., 2008).

Mechanistic models of plant community structure and dynamics (Tilman, 1988, 2007; Pacala and Tilman, 1994) have successfully explained a wide variety of patterns at community level based on species responses to resource variability and disturbances. According to Tilman’s resource competition theory (Tilman, 1982, 1988), resource dynamics is both a function of environmentally-driven supply and resource consumption by plants, determining the strength of the competition for resources experienced by plants. However, plant biomass can also affect resource availability by increasing resource input rates and decreasing loss rates, or modify plant performance by reducing herbivory or increasing the presence of pollinators. In such cases, the negative effects of resource depletion by neighboring plants can be outbalanced by the benefits they provide (e.g. Callaway, 2007). The potential of including positive interactions in general resource competition models, however, has been little explored (but see Gross, 2008).

The dynamics resulting from the positive effects of vegetation on the availability of a single resource, such as water or nutrients, have been previously explored (Rietkerk and van de Koppel, 1997). Positive interactions between plant biomass and resource availability result in a positive feedback whereby the presence of vegetation can maintain suitable conditions for growth even when the resource supply rates drop to low values. So, the response of the system to future changes in environmental conditions depends...
on the present biomass density. Typically, vegetation systems with feedbacks can have two steady states, high vegetation cover and bare soil, and transitions between those states occur in a discontinuous and potentially irreversible way (e.g., Rietkerk and van de Koppel, 1997; Van Nes and Scheffer, 2004). After a sudden transition the original state cannot be recovered with a simple restoration of the previous conditions, a phenomenon called hysteresis (Scheffer et al., 2001; Beisner et al., 2003). Properties of such systems, such as the implications for the system’s resilience or for the formation of regular spatial patterns, have been reported (e.g. Van de Koppel and Rietkerk, 2004; Kefi et al., 2007). However, the effects of such non-competitive interactions are not yet integrated in general mechanistic theory on plant competition and facilitation (Brooker et al., 2008).

Here, we focus on systems where plants not only compete for the same resources, but can also increase resource availability. We consider two different mechanisms of positive resource-mediated interactions (see Callaway, 1995; Stachowicz, 2001 for classifications of positive interactions) and we analyze the effects of these mechanisms on the dynamics of water-limited plant communities. In such communities both water and light can be limiting resources and their relative importance can vary along productivity gradients (e.g. associated to rainfall gradients, slope aspect, soil texture) (Zavaleta et al., 2000). In these systems we consider as positive resource-mediated effects the following: First, plant density can directly increase resource availability, and thereby indirectly increase vegetation growth rates, by improving soil properties to a point where the positive effects of increased water infiltration rates into the soil and reduced evaporation can offset the negative effects due to higher transpiration and rainfall interception (Joffre and Rambal, 1993; Rietkerk and van de Koppel, 1997). Second, higher vegetation densities positively affect plant growth because plants provide shade, preventing too much surplus radiation that can negatively affect plant growth under stressed conditions. In particular, photo-inhibition, midday stomatal closure, higher root allocation and lowered leaf area ratio may lead to reduced plant performance (i.e. relative growth rate or mortality) at high irradiance (e.g. Poorter, 1999; Quero et al., 2006), and optimum performance occurs around intermediate (25%-50%) light values (e.g. Veenendal et al., 1996; Poorter, 1999).

The consumer-resource models used in this paper (Tilman, 1982) have been fundamental in developing and structuring modern theory of exploitative resource competition (Smith and Huston, 1989; Pacala and Tilman, 1994) and despite of their simplicity provide useful insights for the development and interpretation of more complex simulation models and patterns (Tilman, 1988). Substantial details have to be sacrificed in the earlier stages of the modeling process to provide a general but also comprehensible analysis of the implication of basic mechanisms. The analysis addressed in this paper provides a full and rigorous characterization of the effects of resource-mediated facilitation in very schematic models of consumer-resource mechanisms. The results are an indispensable guide for later using these models as building blocks for more sophisticated theories that incorporate other trade-offs faced by plants, such as those between competitive ability and dispersal (Tilman, 2007).

Here, we adapt standard resource competition theory by including the described positive interactions. Then, we analyze the effect of each mechanism in isolation as well as their interaction, and we investigate how this depends on species number. By doing so, we integrate and expand two complementary models of plant community dynamics, one based on resource competition and its effect on species coexistence, and the other one centered around positive feedbacks and bistability behavior. We argue that positive interactions mediated by resources are essential to understanding when and how community transitions in species composition occur and we detail some illustrative processes for water- and light-limited systems.

2. The model

Tilman’s resource competition theory (Tilman, 1982) relies on a model consisting of differential equations for the consumption of $s$ resources by $n$ vegetation species with the following general scheme

\[
\dot{x}_i = x_i (f_i (R_1, \ldots, R_s) - m_i), \quad i = 1, \ldots, n, \tag{1}
\]

\[
\dot{R}_j = g_j (R_j) - \sum_{i=1}^{n} x_i \cdot h_{ij} \cdot f_i (R_1, \ldots, R_s), \quad j = 1, \ldots, s, \tag{2}
\]

where $x_i$ is the population density of the species $i$; $R_j$ is the availability of resource $j$; $f_i$ is the functional response of the per capita consumption and growth rate to the resources; $m_i$ is the loss rate of species $i$; $g_j$ is the function describing the supply rate of resource $j$; $h_{ij}$ is the function describing the amount of resource $j$ required to produce each new individual of species $i$.

We start with considering the case where the system is only limited by one resource ($s = 1$), water ($W$) in Eq. (2). Resource dynamics without vegetation is the result of infiltration, $I$, minus the evaporation, $E$, and deep percolation, $P$. A standard representation of these terms is (Walker et al., 1981; Porporato et al., 2001):

\[
\dot{W} = I - E - P = I - e \cdot W - r \cdot W = (e + r) \cdot \frac{I}{e + r} - W, \tag{3}
\]

where infiltration rate $I$ is constant and linked to the average precipitation $p$ and soil infiltration capacity $i$ of a given habitat, i.e. $I = p \cdot i$. Evaporation and percolation are chosen to be linearly dependent on soil water content, with rates $e$ and $r$ respectively. The equilibrium soil water density of bare soil, $W_b$, is given by the ratio of infiltration and loss rates,

\[
W_b = \frac{p \cdot i}{e + r}. \tag{4}
\]

The presence of vegetation in the system adds a consumption, or transpiration, term to Eq. (3) that, following Eq. (2), is made proportional to the plant growth rate:

\[
\dot{W} = (e + r) \left( \frac{p \cdot i}{e + r} - W \right) - \sum_{i=1}^{n} h_{ij} \cdot f_i (W) \cdot x_i. \tag{5}
\]

Because vegetation can exert effects on certain components of the soil water balance (e.g. by improving infiltration or reducing evaporation) infiltration and evaporation are made density dependent, and equilibrium soil water density might increase with plant biomass. These positive effects of biomass are given by $i = i(x_1, \ldots, x_n)$ and $e = e(x_1, \ldots, x_n)$, which are considered as increasing and decreasing functions of plants density, respectively. These effects tend to saturate as biomass increases so their net influence is more relevant for low values of plant biomass (Rietkerk and van de Koppel, 1997).

The effect of reduced evaporation and increased infiltration are qualitatively equivalent in this model. They increase water density in a similar manner, and thus all the results obtained in the paper for infiltration improvement can be directly applied to systems where only evaporation reduction is relevant or where
both infiltration and evaporation rates depend on biomass density. Thus, for mathematical convenience (e.g. see Walker et al., 1981), we will continue to model only the increase in infiltration and not the reduction of evaporation.

In systems with water deficit, equilibrium soil water density of a monospecific stand of species \( j \) can now be larger than that of bare soil, \( W_s \), due to density-dependent positive effects on resources (Eq. (6)). Under water-limited conditions, the effects of increased plant density on infiltration and/or evaporation can be large enough to compensate and outbalance the effects of transpiration. As long as the positive effect of vegetation density is able to maintain soil water above the critical value, \( W^* \), species \( j \) will survive. Such situations potentially yield systems exhibiting bistability (Rietkerk and van de Koppel, 1997; Rietkerk et al., 2004), where an unperturbed population under water-limited conditions is able to survive, although vegetation cannot colonize bare soils.

For a single species, following Walker et al. (1981), we write:

\[
i(x) = \frac{\beta_1 x_1 + b_0}{\beta_1 (x_1 + 1)},
\]

where \( b_0 \) is the infiltration rate in bare soil and \( \beta_1 \) is the inverse of the half-saturation constant. Positive interactions in the model are thus controlled by parameter \( \beta_1 \) and no facilitating effects arise when infiltration is independent of plant biomass.

For a system of \( n \) species we have

\[
i(x_1, \ldots, x_n) = \frac{\sum_{i=1}^{n} \beta_i x_i + b_0}{\sum_{i=1}^{n} \beta_i x_i + 1},
\]

where \( \beta_i \) are constants that measure species-specific positive interactions on infiltration rates, and thus higher values of \( \beta_i \) stand for species \( i \) with higher facilitating capacity.

In a water-limited system, the functional form of growth rate, \( f^W(W) \), will be described as a saturating function (Michaelis-Menten kinetics) for water availability,

\[
f^W = \frac{W - W_p}{W + k_W},
\]

where \( \sigma \) is linked to maximum relative growth rate (Hunt and Cornelissen, 1997), \( W_p \) is the wilting point and the whole plant compensation point and \( k_W \) is the half-saturation constant.

Now, we introduce a second resource, light. Its value depends on plant density values, and we use a hyperbolic form to model light decay with increasing biomass (Reynolds and Pacala, 1993):

\[
L = \frac{L_0}{1 + \sum_{i=1}^{n} \alpha_i x_i}
\]

where \( L_0 \) is maximum radiation in the open and \( \alpha_i \) is the light decay rate per unit of biomass. Eq. (9) takes into account that light consumption is instantaneous and non-absorbed light cannot accumulate in the system for later use. Mathematically, light does not require an independent variable in the model, as the resources do in Tilman’s model. Anyway the graphical analysis developed for such resources (Tilman, 1982) can also be applied for light (see Reynolds and Pacala, 1993 and Appendix A).

Plant growth in Eqs. (1) and (6) is determined by the resource which is the most limiting for plant growth (Tilman, 1982):

\[
f(W,L) = \min \left( \max \left( 0, f^W(W) \right), \max \left( 0, f^L(L) \right) \right).
\]

Here light-limited growth, \( f^L(L) \), is independent of water availability and no light-mediated facilitation is taken into account. A hyperbolic function is also used for light absorption (Reynolds and Pacala, 1993),

\[
f^L = \sigma \frac{L}{L + k_L},
\]

where \( \sigma \) is defined in Eq. (8), and \( k_L \) are the half-saturation constant.

A number of mechanisms can work in concert to hamper plant growth and survivorship at high irradiance, particularly at the seedling stage (e.g. Quero et al., 2006). As a result, growth rate responses to irradiance can be unimodal rather than hyperbolic, with higher relative growth rate or survivorship rates at intermediate rather than full irradiance (e.g. Poorter, 1999). We assume that this effect is absent with high water availability, in other words for mesic conditions plants can reach their maximal growth at full irradiance (e.g. Zavala, 2000). As water supply decreases, however, high irradiance may become harmful and maximum growth rates are reached in partially shaded habitats. We model this water-dependent decrement in plant growth through a sigmoid-type function that modifies the maximum relative growth rate,

\[
f^L(W,L) = \sigma(L,W) \frac{L}{L + k_L}.
\]

The relative maximum growth, \( \sigma(W) \) in Eq. (12), is a step function with a slope determined by \( C_2 \) and centered in \( L \). The maximum possible effects are controlled by \( C_1(W) \), meaning that a higher \( C_1 \) implies that the species experiences higher positive effects from biomass. This maximum effect is taken as a linear function of water availability

\[
C_1(W) = \max(0, \gamma \cdot (W - W_i))
\]

where is the minimum soil water density for the plant not to suffer growth inhibition at any irradiance rate and \( \gamma \) is the slope of the change of the maximum effect as soil water density decreases. Note that if \( \gamma = 0 \), i.e. \( C_1 = 0 \), the systems presents no positive effects mediated by radiation protection.

The full model, light- and water-limited, and with unimodal growth response to irradiance, for \( n \) species is given by

\[
\dot{x}_i = x_i (f_i(W,L) - m_i), \quad i = 1, \ldots, n,
\]

\[
\dot{W} = p \cdot \frac{\sum_{i=1}^{n} \beta_i x_i + b_0}{\sum_{i=1}^{n} \beta_i x_i + 1} - (e + r) \cdot W - \sum_{i=1}^{n} h_i \cdot x_i \cdot f_i(W,L),
\]

\[
L = \frac{L_0}{1 + \sum_{i=1}^{n} \alpha_i x_i}
\]

where species growth rate has the following form

\[
f_i(W,L) = \min \left( \max \left( 0, \sigma_i \cdot \frac{W - W^*_i}{W + k_{W^*_i}} \right), \max \left( 0, \sigma_i \cdot \frac{1 - \frac{\max(0, \gamma_i \cdot (W_i - W))}{1 + \exp(-C_2 \cdot (L - L_i))}}{L + k_L} \right) \right).
\]

Table 1 provides a synthetic description of the model for a two species system, including the shapes of relationships, and variables and parameters. We also show (Table 2) critical variables and parameter values.
Critical variables and parameters of the twospecies model (Eqs. (14)-(17)).

<table>
<thead>
<tr>
<th>Key variables and parameters</th>
<th>Values and parameters in the model</th>
</tr>
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<tbody>
<tr>
<td>$x_i$ Population density of species $i$</td>
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<tr>
<td>$W$ Soil water density</td>
<td></td>
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<tr>
<td>$L$ Light availability</td>
<td></td>
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<tr>
<td>$m_i$ Loss rate of species $i$</td>
<td></td>
</tr>
<tr>
<td>$p$ Average precipitation</td>
<td></td>
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<tr>
<td>$e$ Evaporation rate</td>
<td></td>
</tr>
<tr>
<td>$r$ Percolation rate</td>
<td></td>
</tr>
<tr>
<td>$h_i$ Amount of water required to produce biomass of species $i$</td>
<td></td>
</tr>
<tr>
<td>$L_0$ Maximum radiation in the open</td>
<td></td>
</tr>
<tr>
<td>$\alpha$ Light decay rate per unit of biomass</td>
<td></td>
</tr>
<tr>
<td>$\beta_i$ Species-specific positive interaction on infiltration rate</td>
<td></td>
</tr>
<tr>
<td>$W_i$ Wilting-whole plant compensation point of species $i$</td>
<td></td>
</tr>
<tr>
<td>$k_{W}$ Water consumption half saturation constant of species $i$</td>
<td></td>
</tr>
<tr>
<td>$k_{L}$ Light absorption half saturation constant of species $i$</td>
<td></td>
</tr>
<tr>
<td>$\sigma_i$ Maximum relative growth rate of species $i$</td>
<td></td>
</tr>
<tr>
<td>$\sigma_i$ Center of the growth inhibition step function</td>
<td></td>
</tr>
<tr>
<td>$\sigma_i$ Slope of the growth inhibition step function</td>
<td></td>
</tr>
<tr>
<td>$r_i$ Soil water critical value for species survival</td>
<td></td>
</tr>
<tr>
<td>$W_i$ Minimum soil water density for the plant not to suffer growth inhibition</td>
<td></td>
</tr>
</tbody>
</table>

3. Analysis of the resource consumption model

Our study is based on an extension of Tilman’s theory by including infiltration improvement and shade protection and their effects along the precipitation gradient. Graphical representations of resource consumption and supply rates for multispecies systems (Tilman, 1982) can now be adapted to explain discontinuous transitions between different communities due to positive interactions. Such behavior has been largely studied in single species systems with bistability between vegetation and bare soil due to positive feedback in water or nutrient availability (e.g., Schæffer et al., 2001; Gilad et al., 2004; Kefi et al., 2007).

In this section we remind and compare the representations associated with these two points of views. Subsequently, they are used to study the interactive effects of increased growth due to shading and increased infiltration. Our graphical analysis relies mainly on the description of the modifications of the zero-isoclines of plants and/or resources in a two-dimensional phase space when positive interactions are included. The zero-isocline of a variable is the line that joins combinations of plant and/or resources densities along which the net change of the variable is null (Noy-Meir, 1975; Rietkerk and van de Koppel, 1997). In other words, the plant zero-isocline is the frontier between those values where the change of biomass in time is positive and those where it is negative. Similarly, the water zero-isocline divides those values where soil water increases from those where it decreases. Thus, an isocline analysis along the precipitation gradient axis can be used to identify the stable states of the system, and to characterize the transitions between them. For one species we obtain under which conditions it survives. For two species, we delimit the precipitation rate ranges where the two species are both present (coexistence), where one species always outcompetes the other (species dominance) and where each species can outcompete the other depending on the initial conditions (founder effect).

3.1. One species resource consumption dynamics

Two graphical representations for light and water consumption dynamics with no positive interactions ($\beta_i = 0$ and $\gamma_i = 0$ in Eqs. (14)-(17)) of a single species are depicted for comparison (Fig. 1). The biomass isocline is a horizontal line at minimum water density for plant production, $W^*$ (full line $f^W = m$), Fig. 1A. Above a threshold value of plant density $x^*$, light becomes the limiting resource (full line $f^L = m$), Fig. 1A. This vertical branch of the biomass isocline indicates that plant growth becomes negative at the right hand side of this line. The position of the water isocline (full lines $W = 0$ in Fig. 1A) depends on rainfall. This isocline shifts down with decreasing precipitation values and the intersection of the water isocline with the $W$ axis determines the equilibrium bare soil water level, $W_0$. At mesic, or semidry, sites, if $W_{b\text{mesic}} > W^*$ or $W_{b\text{semidry}} > W^*$, the two isoclines intersect and the species density attains a stable equilibrium (dark circles, Fig. 1) ($x^W$, $W^*$), or...
Tilman, Fig. 1

Appendix B.1.2. For the derivation of the isoclines, resource consumption line and fixed soil water, $W^*$. For a mesic and a semidy habitat the isoclines intercept at the stable equilibria (dark circles) $(x_1^*, W^*)$ and $(x_2^*, W^*)$ and the intersections with the $W$ axis are the unstable bare soil equilibria (open circles), $W^*_{\text{bare}}$ and $W^*_{\text{dry}}$. For a drier habitat, the bare soil equilibrium becomes stable (dark circle, $W^*_{\text{dry}}$). The vectors indicate the direction of change of the variables $x$ and $W$ for the mesic habitat; (B) Plant isocline in the light–soil water plane and the precipitation gradient axis at full irradiance (dashed–pointed arrow). The plant isocline determines the critical values for light, $L^*$, and water, $W^*$. The intersection of the isocline and the resource consumption lines (dashed lines) in a mesic $(p^\text{mesic})$ and a semidy habitat $(p^\text{dry})$ determines the stable equilibrium $(L^*_1, W^*_1)$ and $(L^*_2, W^*_2)$ (dark circles). The arrow indicated by $x$ marks the width of the species potential niche (stable system with positive plant density) along the rainfall gradient, ending at the transition point $p^\text{dry}$ from where the arrow indicated by 0, bare soil, is the only stable equilibrium (100%, $W^*_{\text{dry}}$) (dark circle). See Appendix B.1 for the derivation of the isoclines, resource consumption line and fixed points. Parameter values: $t_{0.5} = 0.5$, $e = 0.05$, $r = 0.05$, $h = 300$, $\sigma = 0.3$, $k_i = 0.1$, $k_w = 200$, $a = 10$, $\beta = 0$, $W_f = 100$, $m = 0.13$, $C_1 = 0$, $C_2 = 0$, $I_0 = 1$, $p = 130$ (mesic), $p = 80$ (semidy) and $p = 62$ (dry).

Source: Adapted from Rietkerk and van de Koppel (1997) and Tilman (1982).

$(x_1^*, W^*)$, while at dry sites, if $W^*_{\text{dry}} < W^*$, the species goes extinct and the bare soil equilibrium $(0, W^*_{\text{dry}})$ exists.

Plant zero-isoclines can also be illustrated in the water–light plane and the effects of different resource supply rates can now be analyzed (Fig. 1B). The vertical and horizontal branches of the plant isocline indicate the minimum values of resource availability for which the plant has positive net growth (full lines, Fig. 1B).

In this representation, the resource equations (15) and (16) are used to define the resource consumption line (Tilman, 1982) (dashed lines, Fig. 1B). This line consists of all resource supply points that will lead to the same equilibrium resource values (Appendix B.1.2). In the case of no positive interactions, the resource consumption line is straight and its slope is defined by the ratio of resource consumption rates at equilibrium (Tilman, 1982). Unlike resource consumption in the original Tilman model, light absorption is non-linear with respect to biomass density (Eq. (9))! and the slope of the resource consumption line is different across different equilibrium points. The steeper the slope, the larger water consumption rate relative to light. For a given species, light absorption per capita increases as biomass at equilibrium decreases, so the slope decreases along the precipitation gradient. For different species, a steeper slope implies that a higher precipitation is required to attain the same equilibrium values of the resources. We assume full sun irradiance ($I_0 = 100\%$ in Eq. (16)) at which value we depict the precipitation gradient (dashed–dotted axis, Fig. 1B). A resource consumption line determines the equilibrium resource for each precipitation value. So, for each precipitation value, we would obtain a line, which shifts down and has a decreasing slope if rainfall decreases; for instance, at $p^\text{mesic}$ the equilibrium is $(L_1^*, W^*)$ (Fig. 1B). The minimum precipitation value for species survival $p^*$ marks the lowest value along the gradient where the resource consumption line meets the isocline (Fig. 1B compare with Fig. 1A; Appendix B.1.3). This is the transition point between bare soil and a monospecific stand and it delimits the dry end of the plant’s potential niche along the precipitation axis. This potential niche breadth is represented by the arrow labeled as $x$ (right end of Fig. 1B). At dry sites, if $P < p^*$, plants cannot survive and the only stable solution is bare soil (see arrow labeled as 0, Fig. 1B).

Suppose point $p^\text{dry}$ corresponds with the equilibrium resource values (100%, $W^*_{\text{dry}}$) (compare Fig. 1A and B).

Let us note that in the resource plane representation (Fig. 1B) each point can be dually interpreted (Tilman, 1982): (1) as the resource values of a system at a certain moment of its trajectory in the plane $L–W$; (2) as the supply point of a system in the plane $L_0–p$. In particular, we have adjusted the scale of the $p$ axis (see Fig. 1B) where $p^\text{mesic} = W^*_{\text{mesic}} (e + r) / i$ in a way that a pair of supply values defines a point in the supply plane, $(L_0, p)$, and also, in the resource plane, the state of such system when there is no initial biomass density, $(L, W) = (L_0, p \cdot i / (e + r))$.

3.2. Two species resource consumption dynamics

Here, we apply Tilman’s theory in the case of two species dynamics in water- and light-limited systems with a trade-off between drought and shade tolerances (Fig. 2; Reynolds and Pacala, 1993). Species 1 is drought intolerant and shade tolerant, and species 2 the reverse ($W^*_{\text{dry}} > W^*_{\text{mesic}}$ and $L^*_2 < L^*_1$). The plant isoclines cross and the resource consumption lines of each species passing through the intersection points between final states on the precipitation gradient (Fig. 2). For high rainfall rates, above the transition point determined by the resource consumption line of species 1 (from now on resource consumption line 1), this species depletes light below the tolerance of species 2. For low rainfall rates, below the transition point determined by the resource consumption line of species 2 (from now on resource consumption line 2), this species depletes soil water below the tolerance of species 1 (Fig. 2). In between these resource lines, rainfall allows for the presence of both species through coexistence (Fig. 2A) or founder effect (Fig. 2B). Coexistence occurs if the resource consumption line 1 has a higher slope than 2 (Fig. 2A) (see Appendix C.1). Species cannot outcompete each other because the drought intolerant species 1 consumes relatively more water while the shade tolerant species 2 consumes relatively more light.

In other words, at the isocline intersection point, species 1 being limited by water and species 2 by light, both species experience stronger competition from their congeners than from the other species (Fig. 2A). Founder effect occurs if the resource consumption
lines are switched because then the reverse is true; both species are always able to outcompete the other because interspecific competition is stronger than intraspecific competition (Fig. 3B). Such systems are bistable because each species can create monospecific stands and deplete resources to values that prevent the invasion of the other species.

4. Results for resource-mediated positive interaction effects

Here, we classify and study the effects of positive interactions in the full model (Eqs. (14)–(17)) along a precipitation gradient. We select and present graphically those cases where a positive interaction – one species improving water infiltration and/or growing better under shade – in communities of one or two species produces interesting modification of the behaviors shown in Figs. 1 or 2. The main change is that transition points can shift along the rainfall gradient. Consequently, potential niches may expand, in the case of only one species, or founder effect, and coexistence regions may contract or expand. In both cases continuous transitions can become discontinuous, leading to bistability or even tristability. For the two species dynamics, we highlight two particular cases: unlike in the purely competition model infiltration improvement can lead to stable coexistence; and radiation protection allows species coexistence under rainfall regimes outside species potential niche.

4.1. Niche modifications and bistability in one species dynamics

At low densities, benefits from positive interactions among plants, infiltration improvement or shade protection, can outbalance resource competition. At dry sites, the effect of positive effects can qualitatively change the dynamics of the system. Then, increments in growth rate, due to extra soil water density or to light reduction, determine whether the species establishes or goes extinct. For comparison with Fig. 1, Fig. 3 displays the same set of precipitation conditions: mesic (M), semidry (S) and dry (D) sites, for each of the cases of positive interactions under consideration. The main effect is that, when going down from high precipitation rates, the species, being established and improving soil water availability and/or reducing high radiation damage, expands its niche as the transition point to bare soil shifts from $p^*$ to a lower rainfall value, $p^{**}$. However, the stable state is bare soil when going up from dryer conditions, meaning there are no positive effects induced by plant biomass, and the species cannot invade. This is how bistability
arises between $p^*$ and $p^{**}$ implying that there are now two transition points depending on the direction of change in rainfall. Now, we continue with describing the changes in the graphical representations underlying bistability for the two positive interactions considered.

4.1.1. Water infiltration improvement ($\beta_1 > 0, \gamma_1 = 0$)

If biomass positively influences infiltration rates, the water isocline bends in a way that it can cross the plant isocline twice, and the system can have two stable equilibria (Fig. 3A). If plant biomass increases at low ranges, the increase in infiltration rate outbalances the increase in transpiration rate, leading to higher equilibrium soil water availability, while the reverse is true at higher ranges of biomass. In the water–light plane, resource consumption lines depend on the equilibrium points, so bistability implies that there are two resource consumption lines each one passing through one of the positive equilibrium points (only resource consumption lines associated to stable states are shown in Fig. 3B). These resource consumption lines bend due to the contribution to water dynamics of the density-dependent infiltration rate.

4.1.2. Growth inhibition at high radiation ($\beta_1 = 0, \gamma_1 > 0$)

Under conditions of low water availability and high light availability, that is, at ranges of low biomass, a damaging effect on plant performance can result in decreased growth rate. The plant isocline then bends upwards under high radiation (Fig. 3C and D), because higher water availabilities are required to sustain plant growth. This reduction in plant growth also implies a reduction in transpiration, and the water isocline also bends slightly upwards at low plant density (Fig. 3C). These non-linear shapes of both isoclines combined can again give rise to bistability (Fig. 3C and D). The damaging effect of high irradiation at low plant biomass leads to a narrowing of the species niche along the precipitation gradient, while the bistability area between $p^*$ and $p^{**}$ correspond with transition points in a similar way as for infiltration improvement (see Appendix B.3).

4.1.3. Additive effect ($\beta_1 > 0, \gamma_1 > 0$)

If both positive interactions are present a concurrent bending of isoclines and the equilibrium resource line occurs, leading to qualitatively similar behavior as in the previous case, but reinforcing the range of bistability (Fig. 3E and F). Transition point $p^{**}$ shifts to lower rainfall values as compared to the previous case, because of infiltration improvement.

4.2. Niche modifications and bistability in two species dynamics

When we consider positive interactions due to infiltration improvement from one of both species separately ($\beta_1 > 0$ or $\beta_2 > 0$) (Fig. 4), the increment in water availability due to positive interactions can bend the resource consumption lines downwards. Then, as we summarize in Fig. 4, certain transition points shift downwards as compared to the systems without infiltration improvement (Fig. 3). In Fig. 4 we compare arrows diagrams for systems with no positive interaction infiltration (Fig. 3) with infiltration increased by one of the species. Transition points are mainly determined by the resource consumption lines of each species at the isoclines intersection point, as in Fig. 3, (solid arrows). Positive interactions, however, allow bistability between species coexistence and drought tolerant species. In such case, as rainfall decreases, transition point from species coexistence to the drought tolerant species is determined by the resource consumption line of the two species coexisting (dashed lines). On large, the resource consumption lines of the benefactor species bends downwards in all cases and the resource consumption line for the coexisting species bends in (A) and in (D) (see Appendix C.2). The details of the shift and continuity of transition points depend on whether the species that improves infiltration benefits from the extra soil water density (‘selfish’ positive interaction) or not (‘altruistic’ positive interaction).

4.2.1. ‘Selfish’ water improvement

If drought intolerant species 1 increases infiltration it will attain higher biomass densities for the same rainfall supply rates. As a consequence, at lower rainfall supplies it can still deplete light below the tolerance of species 2, thereby enlarging the region where it outcompetes species 2 (Fig. 4A and C) and moving the coexistence region downwards (Fig. 4A). Now, species 1 persists in coexistence with species 2, while species 2 in isolation can deplete water below the tolerance of species 1, implying bistability behavior (Fig. 4A), and the precipitation range for which bistability occurs increases in the case of founder effect (Fig. 4C). Obviously, the transition points from species 2 towards coexistence (Fig. 4A) or towards species 1 (Fig. 4C) do not change because its capacity to deplete soil water below the tolerance of species 1 is not affected.

4.2.2. ‘Altruistic’ water improvement

If species 2 improves infiltration, its capacity to deplete soil water below the tolerance of species 1 at dry sites decreases. Thus, transition points from species 2 towards coexistence (Fig. 4B) or towards species 1 (Fig. 4D) shift down along the precipitation gradient. Species 1 depletes light below the tolerance of species 2 in the same way, thus the transitions point from species 1 towards coexistence remains unchanged (Fig. 4B).

4.3. ‘Controlled facilitation’ coexistence mechanism

Remarkably, in the case of founder effect, both species can coexist if rainfall is too low for species 1 to deplete light below the tolerance of species 2 (Fig. 4D). This is because at lower densities of species 2, increased infiltration outbalances increased transpiration, making this species less competitive for soil water. As a consequence, intraspecific competition is stronger than interspecific competition, satisfying the condition for coexistence. However, this only occurs at low densities of species 2, because at higher densities of species 2, the reverse is true and interspecific competition becomes stronger than intraspecific competition, and coexistence cannot occur. In other words, because of infiltration improvement by species 2, species 1 can profit, preventing species 2 to develop such high densities by shading, leading to coexistence. We call this new potential coexistence mechanism ‘controlled facilitation’.

4.4. Tristability in two species dynamics

When both species improve infiltration the effects of resource consumption lines bending are additive and associated transition points experience even larger shifts. When these shifts are large enough, species 1 and coexistence can even occur at rainfall rates where bare soil is also a stable solution. Then, the system can display two types of tristability: bare soil, species 2 and either species 1 or coexistence can occur depending on initial conditions (Fig. 5).

4.5. Radiation protection and facilitation

Plant morphological adaptations to tolerate shade conditions make them more susceptible to suffer from high radiation (Givnish, 1988; Poorter, 1999). Thus, we suppose that only the shade tolerant
Fig. 4. Effects of infiltration improvement of both species separately in the cases represented in Fig. 2. Upper row. From the left to the right, comparison of the arrows diagrams for a system with coexistence and: no positive interaction at extreme left (as in Fig. 2A, depicted again for convenience), infiltration only increased by species 1, $\beta_1 > 0$ (A) and infiltration only increased species 2, $\beta_2 > 0$ (B). Lower row. From the left to the right, comparison of the arrows diagrams for a system with founder effect and: no positive interaction at extreme left (as in Fig. 2B), infiltration only increased by species 1, $\beta_1 > 0$ (C) and infiltration only increased species 2, $\beta_2 > 0$ (D). The new arrows diagrams are obtained from the configuration of the isoclines and resource consumption lines in the phase spaces. Solid arrows stand for the resource consumption lines of the species at the isoclines intersection and dashed arrows stand for the resource consumption lines of the two coexisting species at the discontinuous transition towards species 2. See Appendix C.2 for the derivation of the isoclines, resource consumption lines, fixed points and transition points. Parameter values: (A) As in Fig. 2A except for $\beta_1 = 0.55$; (B) As in Fig. 2A except for $\beta_2 = 0.2$; (C) As in Fig. 2B except for $\beta_1 = 0.2$; (D) As in Fig. 2B except for $\beta_2 = 0.55$.

Fig. 5. Effects of infiltration improvement of both species simultaneously in the arrows diagrams of the cases with (A) coexistence (Fig. 2A) and (B) founder effect (Fig. 2B). Tristability among bare soil, species 2 and species 1 or coexistence appear in both cases. Parameter values: (A) As in Fig. 2A except for $\beta_1 = 0.9$. (B) As in Fig. 2B except for $\beta_2 = 0.9$.

5. Discussion

Our analysis shows how resource-mediated positive interactions can be integrated in resource competition theory. It illustrates the application of the $R^*$ criterion to study changes in community composition along environmental gradients. We show that the two proposed resource-mediated positive interactions have similar and additive effects: transition points between different species compositions can change ($Figs. 4–6$), the widths of the realized niches can reduce for facilitative species and expand for protégé species ($Figs. 2$ and $4$) and continuous transitions can become discontinuous invoking bistability and tristability ($Figs 4A, D$ and $5$). Thus, resource-mediated positive interactions can enhance community resistance against decreased precipitation but in turn transitions can occur in a sudden and irreversible way ($Figs. 2$ and $4–6$).

In traditional resource competition theory (Tilman, 1982), species coexist only if resource supplies rates are between species resource consumption lines where none of the species can grow.
enough to deplete resource availability below the tolerance of the other (Figs. 3A, 4A and B). However, we show that positive interactions can create a new potential mechanism for coexistence that we name controlled facilitation (Fig. 4D). If species 2 has a positive effect on infiltration, it’s presence in low biomass can increase the growth of species 1, in turn enhancing the capacity of species 1 to reduce the growth of species 2. Thus, the positive effect on soil water allows coexistence via a control mechanism of species 1 on the biomass of species 2, keeping this species 2 at low densities, in a range that species 1 can still profit from the presence of species 2 (Fig. 4D). As far as we know, there are no previous studies, theoretical or experimental, addressing coexistence through controlled facilitation based on a resource-mediated positive interaction.

The present approach can be extended to communities with more than two species. Resource-mediated positive interactions do not modify the main principles of R* theory and, as long as the resource consumption characteristic can be represented in the resource plane in the way presented, conclusions can be derived in a straightforward manner. In water-limited systems, the most competitive species for soil water, the one with the lowest $W^*$, outcompetes the rest regardless of its effect on infiltration rate, and for systems with $n$ limiting resources only $n$ species can coexist. This means that for two limiting resources, such as in our study, species can only coexist in pairs of two species maximum. However, the dynamics of $n$ species communities can be fundamentally altered when moving up and down environmental gradients, as we have shown for the case of one or two species. Also, it is noteworthy that the number of species along environmental gradients can be lower or equal than the number of limiting resources, depending on the species pool that is present. The appearance of bistability or tristability between communities also has consequences for diversity at a metacommunity scale (Tanehill, 2000; Mouquet et al., 2006). Disconnected communities under the same environmental conditions can have different compositions depending on their history. This means that at metapopulation scale, positive interactions allow the survival of more species than limiting resources, resulting in an increase of diversity.

Previous work has stressed that positive interactions can enhance species realized niches (Stachowicz, 2001; Bruno et al., 2003; Michalet et al., 2006). These authors mainly relied on conceptual models of plant competition (Grime, 2001), providing graphical explanations about how facilitation could modify species richness and how it could shape the relation between diversity and productivity. Relating productivity, environmental gradients and diversity would require further elaboration on the model presented here (Gross and Cardinal, 2007). Nevertheless, our work addresses the mechanisms behind niche enlargement for resource-mediated positive interactions, and shows that infiltration improvement can shift community transitions that occur along the whole environmental gradient while shade protection only affects transitions at the dry end of the rainfall gradient. Thus, relationships between positive interactions and community properties are mechanism-dependent and thus more diverse than previous studies imply.

A further analysis of interspecific facilitation due to resource-mediated positive interactions would require the study of quantitative changes of species biomass, which is not presented here. Thus, a detailed quantitative analysis of variation in species biomass due to positive interactions may be required to discern its role on facilitation processes along environmental gradients.

The results obtained here can be generalized for plant communities limited by other resources than water and light as well as ecological conditions. Positive interactions between biomass and other resources are well documented, such as soil nutrients (Rietkerk and van de Koppel, 1997) and oxygen (Callaway, 1995), and an equivalent modeling approach can be followed. We want to point out that conclusions drawn here have been just deduced for the two resource-mediated facilitation mechanisms explained. Other mechanisms, as protection from herbivores, pollination, or exchange of soil microflora communities, may have different qualitative consequences for systems dynamics (Gross, 2008). As can be deduced from our study, facilitation is a phenomenon that does not follow general rules, independent on the mechanism involved. Thus, more work is required to identify and understand the mechanisms leading to positive interactions between plants. We have shown that resource competition theory provides a versatile and general framework where those mechanisms can be incorporated and for which the graphical analysis can be also adapted, providing a handy tool to analyze the consequences of non-competitive interactions.

Finally, plant to plant interactions take place in spatially and tempo-rarily heterogeneous environments (Pacala and Tilman, 1994; Chesson et al., 2004) and future work should address the role of space and resource pulses in plant communities structured by both negative and positive resource mediated interactions. Coexistence mechanisms related to spatial trade-offs, competition-dispersion abilities, and regular spatial patterns due to the interplay between long and short interactions, are likely to affect the results presented in this paper, especially in the regions near the transition points.

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Appendix A. Light resource is a dependent variable

Light is not an independent resource of the system because it instantaneously adjusts to the values of plant densities, Eq. (9), i.e., it is not an independent state variable of the differential system in (14)–(17). Nevertheless, we can use Tilman’s diagrams to interpret light as a system’s resource. It is obvious for a single species system because biomass density, \( x \), and light, \( L \), are univocally related and Fig. 1A and B are linked by a change of variables. Tilman’s interpretation is also valid for isoclines and resource competition lines in diagrams of multispecies systems (see Reynolds and Pacala, 1993). Plant isoclines, \( \hat{x} = 0 \), given by Eq. (C.1), are functions of light and do not depend on the individual values of species densities. In mathematical terms, we can change variables from \( x_1 - x_2 = W \) to, say, \( L - x_2 = W \) and consider Figs. 2 and 4, as projections of the isoclines, that are independent of \( x_2 \), in the \( L-W \) plane. Resource competition lines are represented in the space of supply rates, i.e., \( L_0-p \) plane, and do not depend on the number of species present in the system.

Appendix B. Mathematical and graphical analysis of the single species model

B.1. No positive interactions (\( \beta_1 = 0, \gamma_1 = 0 \))

B.1.1. Soil-water and plant-biomass phase space (Fig. 1A)

Derivation of the isoclines. The equation of plant density zero-isocline, \( \hat{x} = 0 \) from Eq. (14), implies either \( x = 0 \) (bare solution) or \( f(W,L) = m \). This latter condition depends on which resource limits growth in Eq. (17): \( f^W = m \), Eq. (8), or \( f^L = m \), Eq. (11). Solving these equations, we determine the critical values for soil water and light density:

\[
W^* = \frac{W_0 + kW_0 m}{1 - \frac{m}{\sigma}}, \tag{B.1}
\]

or

\[
L^* = \frac{k^L m}{1 - \frac{m}{\sigma}}, \tag{B.2}
\]

and substituting light critical value, \( (B.2) \), in Eq. (16) and solving for \( x \) we determine the critical biomass value,

\[
\hat{x}^* = \frac{1}{\sigma} \cdot \left( \frac{L_0 (1 - \frac{m}{\sigma})}{k^L - \frac{m}{\sigma}} - 1 \right). \tag{B.3}
\]

The soil-water isocline, \( \hat{W} = 0 \) from Eq. (15), determines the soil water density as a function of plant biomass. When the growth rate is limited by water, meaning \( f(W,L) = f^W \), the isocline is a concave decreasing function (Fig. 1A) given by the positive solution of the following quadratic equation

\[
W^2 - \frac{p \cdot L_0 - (e + r) \cdot kW - h \cdot x \cdot \sigma}{e + r} W - \frac{p \cdot L_0 \cdot kW - h \cdot x \cdot \sigma \cdot W_0}{e + r} = 0. \tag{B.4}
\]

On the contrary, when the growth rate is limited by light, meaning \( f(W,L) = f^L \) (case not shown in Fig. 1A), the solution is given by

\[
W = \frac{p \cdot L_0 \cdot (L_0 + kL \cdot (1 + \alpha \cdot x)) - \sigma \cdot h \cdot x \cdot L_0}{(e + r) \cdot (L_0 + kL \cdot (1 + \alpha \cdot x))}, \tag{B.5}
\]

B.1.2. Soil-water and light phase space (Fig. 1B)

Derivation of the isocline. The plant zero-isocline, \( \hat{x} = 0 \) from Eq. (14), determines water and light critical values, respectively given by Eqs. (B.1) and (B.2).

Derivation of the resource consumption line. We look for all the supply rates that lead to the same resource values at the positive stable equilibrium, \( (L_0, W_0) \). For this, we fix \( L \) to \( L_0 \) and \( W \) to \( W_0 \) in Eqs. (15) and (16). Then, we replace \( f(W,L) \) by its value at equilibrium, \( m \), in Eq. (15) and solve Eq. (15) and (16) for the supply rates, \( p \) and \( L_0 \), obtaining the equation of the consumption resource line (Fig. 1B),

\[
p = \left( \frac{e + r}{i} \cdot W_0 - \frac{h \cdot m}{i \cdot \alpha} \right) + \frac{h \cdot m}{i \cdot \alpha \cdot L_0}. \tag{B.6}
\]

The precipitation rate, \( p \), is a linear function of \( L_0 \), with a slope that is proportional to the ratio of water, \( h \), and light, \( \alpha \), consumption rates of the plant at the positive equilibrium.

B.1.3. Fixed points

Fixed points are the intersections of the two isoclines defined in Appendix B.1.1 or the water isocline and the resource consumption line in Appendix B.1.2.

We showed in Appendix B.1.1 that \( x = 0 \) is part of the plant-isocline. It intersects the water-isocline at \( W_0 \), given in Eq. (4), and the bare soil point, \( \hat{X}_0 = (0, W_0) \), is always a fixed point of the system.

The existence of a vegetation equilibrium depends on the precipitation rate, \( p \). Vegetation exists if soil-water at bare soil, \( W_0 \) in Eq. (4), is enough for plant growth: \( W_0 > W^* \), i.e., if the precipitation rate is higher than the transition point obtained solving \( p \) in Eq. (4),

\[
p^* = \frac{W^* (e + r)}{i}. \tag{B.7}
\]

If this condition is satisfied, the fixed point for vegetation can be obtained by solving Eqs. (14)–(17). If growth at equilibrium is limited by water, the fixed point is given by:

\[
\hat{X}_0 = \left( \frac{\sigma \cdot W_0 - m \cdot kW}{\sigma - m}, \frac{p \cdot i \cdot e + r}{h \cdot m} + \frac{\sigma \cdot W_0 - m \cdot kW}{\sigma - m} \right) \tag{B.8}
\]

when light is the limiting resource at equilibrium, we obtain

\[
\hat{X}_0 = \left( \frac{1}{\alpha} \left( \frac{L_0 \cdot (\sigma - m)}{m \cdot kL} - 1 \right) \cdot \frac{p \cdot L_0}{(e + r)} + \frac{h \cdot m}{\alpha \cdot (e + r)} + \frac{h \cdot m \cdot L_0 \cdot (\sigma - m)}{\alpha \cdot m \cdot kL \cdot (e + r)} \right). \tag{B.9}
\]

B.2. Infiltration improvement (\( \beta_1 > 0, \gamma_1 = 0 \))

B.2.1. Soil-water and plant-biomass phase space (Fig. 3A)

Derivation of the isoclines. In this case, the biomass isocline, \( \hat{x} = 0 \), i.e., Eqs. (B.1)–(B.3), does not change. For the water isocline, \( \hat{W} = 0 \) from Eq. (15), we can look for the two solutions as obtained in Eqs. (B.4) and (B.5), but replacing the constant bare-soil infiltration, \( L_0 \), by its functional dependence on plant density, Eq. (7). As a consequence of \( i = i(x) \), plant zero-isocline for water limited systems at low biomass density values turns into an increasing convex function if the increment in infiltration rate is large enough to compensate competition, (Fig. 3A).
B.2.2. Soil-water and light phase space (Fig. 3B)

Derivation of the isocline. The plant isocline does not change with respect to the case in Appendix B.1.1.

Derivation of the resource consumption line. The system has now three solutions (see Appendix B.2.2). For each of the two solutions with positive biomass density, there exists a resource consumption line. In the same way as in Appendix B.2.1, each resource consumption line, is now a non-linear function. For the stable state, \((L_0, W_0)\) it has the form:

\[
p = \frac{(h \cdot m \cdot (L_0 - L_s) + (e + r) \cdot \bar{W}_s \cdot \alpha) \cdot (\beta \cdot (L_0 - L_s) + L_s \cdot \alpha)}{L_s \cdot \alpha (\beta \cdot (I_0 - L_s) + I_0 \cdot L_s \cdot \alpha)},
\]

(B.10)

which bends upwards at low biomass conditions where positive effect is higher than consumption.

B.2.3. Fixed points

When \(p > p^*\) the system has two solutions, bare soil and stable vegetation, as in the case of no positive interactions, Appendix B.1.3. When \(p\) is slightly below the transition point, there is a minimum infiltration improvement, \(\beta_{\text{min}}\), below which the system displays bistability. The mathematical condition for this is that the derivative of the resource consumption line, Eq. (B.10), at full radiation rate is zero, that is

\[
\frac{\partial p}{\partial L} \bigg|_{(W_0, L_0)} = 0,
\]

whose solution is

\[
\beta_{\text{min}} = \frac{h \cdot I_0 \cdot (\sigma - m)}{(e + r) \cdot (1 - I_0) \cdot (\sigma \cdot W_0 - m \cdot \alpha W_0)}.
\]

If \(\beta > \beta_{\text{min}}\), the bistability region expands until the transition point between vegetation cover and bare soil, \(p^{**}\). This point is given by the precipitation rate where the maximum of the resource consumption line is tangent to the plant-isocline. Thus we have first to derive the resource line and solve for the maximum, i.e. \(\frac{\partial W}{\partial L} = 0\) \(\rightarrow L_s = L_{\text{max}}\) and then substitute into resource consumption line, Eq. (B.9), and solve for the precipitation rate, obtaining the equation in Box I. If \(\beta > \beta_{\text{min}}\), in the region between transitions, \(p^{**} < p < p^*\), the system has the bare soil fixed point and two other ones with vegetation that can be calculated after substituting \(W = W^*\) in Eq. (15). The following quadratic expression is obtained,

\[
W = -\left(\frac{h \cdot m \cdot \beta}{(e + r) \cdot W^* \cdot \beta + h \cdot m - p \cdot \beta}\right) x + \frac{(e + r) \cdot W^* - p \cdot I_0}{h \cdot m \cdot \beta} = 0,
\]

(B.11)

which has two positive solutions, \(\bar{x}_U\) and \(\bar{x}_S\), if \(\beta > \beta_{\text{min}}\) and \(p^{**} < p < p^*\). \(\bar{x}_U\) (\(\bar{x}_S\)) is the unstable (stable) fixed point, open (black) circles in Figs. 1–3, that corresponds to intersection of the isolines such that the water isocline has a positive (negative) slope (see Appendix D).

B.3. Protection from high radiation. \((\beta_1 = 0, \gamma_1 > 0)\)

B.3.1. Soil-water and plant biomass phase space (Fig. 3C)

Derivation of isolines. With damaging effects of high radiation, the plant-isocline becomes a function of light availability. The shape of the plant-isocline, \(\hat{x} = 0\), differs depending on plant density, see Eq. (17). For high plant densities, the isolines are given by \(f_W = m\), i.e. Eqs. (B.1) and (B.2) still hold. For low plant densities plant isocline is given by the second term in the right hand side of Eq. (17) where growth inhibition occurs. The expression for the humped part of the plant-isocline is obtained solving \(f(L, W) = m\), which leads to

\[
W^*(x) = \frac{\bar{W} - \left(1 + \exp\left(-\gamma \cdot (L(x) - \bar{L})\right)\right)}{\gamma} \times \left(1 - \frac{m \cdot (L(x) + k_I)}{\sigma \cdot L(x)}\right),
\]

(B.12)

where \(L(x)\) is given in Eq. (16).

For the same reason, water-isocline \(\hat{W} = 0\), is modified at low biomass densities. There is no simple explicit form for the function but it can be solved numerically.

B.3.2. Soil-water and light phase space (Fig. 3D)

Derivation of isoline. We also apply here the remarks of Appendix B.3.1 about the plant-isocline, \(\hat{x} = 0\). We obtained its expression at low plant density, i.e. high radiation, as a function of plant density, \(x\), Eq. (B.12), by considering the explicit dependency on light on it, \(L(x)\), Eq. (16). But we can also directly study the plant-isocline, \(\hat{x} = 0\), as a function of \(L\) without replacing it by its expression.

Derivation of the resource consumption line. It has not changed with respect to the case with no positive interactions, case B.1.2.

B.3.3. Fixed points

If high radiation decreases the growth rate, the critical value of water increases and the transition point from bare soil to vegetation, \(p^*\), shifts up. The new value is given by substituting \(W^*(x = 0) = W^* (L = 100%)\) by its expression (B.12) in plant-isocline expression equation (B.7)

\[
p^* = e + r \cdot \frac{W_m^*}{100\%}.
\]

Bistability occurs when the slope of the plant-isocline, \(W(L)\) in Eq. (B.12), at full radiation, \(L = L_0\), is higher than the slope of the resource consumption line, Eq. (B.6), that is,

\[
\left.\frac{\partial W(L)}{\partial L}\right|_{L=100\%} > \frac{h}{i \cdot \alpha} \cdot L_0 \cdot m,
\]

(B.13)

because in this case the resource consumption line intersects the plant isocline twice. Condition (B.13) implies that efficiency to convert water into biomass needs to be high compared with light consumption, and thus the species can develop a canopy that is dense enough to protect the species from growth inhibition.

At the point where the plant starts suffering growth inhibition, \(L_i\) (i.e. when the plant isocline bends), the corresponding precipitation rate is the minimal rainfall supply for the system to display bistability. Thus, we calculate the expression of \(L_i\) solving the following equation:

\[
\left.\frac{W^* - W_p}{W^* + k_W}\right|_{L_i} = \left(1 - \frac{\gamma (\bar{W} - W^*)}{1 + \exp\left(-\gamma (L_i - \bar{L})\right)}\right) \frac{L_i}{L_i + k_I},
\]

(B.14)

where \(W^*\) is given by Eq. (B.1). By substituting \(L_i\) and \(W^*\) by their expressions from (B.14) and (B.1), respectively, in the resource consumption line passing through this point at maximum irradiance, \(L_0 = 100\%,\) Eq. (B.6), we determine the expression of \(p^{**}\):

\[
p^{**} = \left(\frac{e + r}{i} \cdot W^* - \frac{h \cdot m}{i \cdot \alpha}\right) + \frac{h \cdot m}{i \cdot \alpha} \cdot L_0.
\]

If condition (B.13) is fulfilled the system has three fixed points for the region \(p^{**} < p < p^*\) equilibrium: bare soil (stable), \(\bar{x}_U\) (unstable) and \(\bar{x}_S\) (stable).
Appendix B.1.3

Box I.

\[ p^* = \frac{(h \cdot m \cdot (L_0 - L_{\text{max}}) + (e + r) \cdot W^* \cdot L_{\text{max}} \cdot \alpha)}{L_{\text{max}} \cdot \alpha \cdot (\beta \cdot (L_0 - L_{\text{max}}) + L_0 \cdot L_{\text{max}} \cdot \alpha)}. \]

B.4. Interactive effects (\( \beta_1 > 0 \) and \( \gamma_1 > 0 \))

Calculations for this case can be performed as in the previous ones, although the formulae for the general case are too long to be displayed here.

Appendix C. Mathematical and graphical analysis of the two species model

C.1. No positive interactions (\( \beta_1 = \beta_2 = 0 \) and \( \gamma_1 = \gamma_2 = 0 \))

For clarity, we first detail the case without positive interactions although it is only an application of Tilman's analysis (Tilman, 1982).

C.1.1. Derivation of the isoclines (Fig. 2)

Eqs. (B.1) and (B.2) give the expression of the two plant isoclines, \( \hat{x}_1 = 0 \) and \( \hat{x}_2 = 0 \). The intersection point is given by:

\[
\hat{R}^* = (L_0^*, W_1^*) = \left( \frac{k_2^1 m_1^1}{1 - m_2^1}, \frac{W_1^1 + k_1^1 m_1^1}{1 - m_1^1} \right) \tag{C.1}
\]

C.1.2. Derivation of the resource consumption lines (Fig. 2)

The resource consumption lines that determine the transition points are obtained by replacing \( \hat{R}^* \) by its expression, Eq. (C.1), in the corresponding equation of the isolated species, Eq. (B.8):

Line 1: \( p = \left( \frac{e + r}{i} \cdot W_2 - \frac{h_1 \cdot m_1}{i \cdot \alpha_1} \right) + \frac{h_1 \cdot m_1}{i \cdot \alpha_1} \cdot L_0 \tag{C.2} \)

Line 2: \( p = \left( \frac{e + r}{i} \cdot W_2 - \frac{h_2 \cdot m_2}{i \cdot \alpha_2} \right) + \frac{h_2 \cdot m_2}{i \cdot \alpha_2} \cdot L_0 \tag{C.3} \)

C.1.3. Fixed points

To obtain the vegetation biomass at equilibrium, we substitute \( \hat{R}^* \) by its expression equation (C.1), and replace \( f ' (W, L) \) by their values at equilibrium, \( m_\ell \). This leads to:

\[
h_1 \cdot m_1 \cdot x_1 + h_2 \cdot m_2 \cdot x_2 - p \cdot i_0 + (e + r) \cdot W_1^* = 0, \tag{C.4}
\]

\[
\alpha_1 \cdot x_1 + \alpha_2 \cdot x_2 + 1 - \frac{L_0}{L_2} = 0, \tag{C.5}
\]

that implies that an equilibrium with positive densities for both species exists if the resource supply rates, \( p \) and \( L_0 \), are between the resource consumption lines (Fig. 2) (Tilman, 1982).

The transition points between different communities are the values of the precipitation rates obtained from Eq. (17) particularizing for the maximum irradiance, i.e. \( L_0 = 100\% \).

If a coexistence fixed point exists, Eqs. (C.1), (C.3) and (C.4), its stability is given by the sign of the determinant of the Jacobian matrix, \( |J^*| \), evaluated at this point (see Tilman, 1982 and Appendix D). If \( |J^*| > 0 \) the point is stable and species coexist while \( |J^*| < 0 \) means that species display founder effect.

The stability condition for such equilibrium point, i.e. a negative determinant of the Jacobian matrix, is

\[
\frac{\alpha_1}{h_1 \cdot m_1} < \frac{\alpha_2}{h_2 \cdot m_2} \tag{C.6}
\]

which depends on the relationship between resource consumption rates (Reynolds and Pacala, 1993) and is equivalent to the condition on the relative position on the resource consumption lines (Fig. 2) (Tilman, 1982).

C.2. Infiltration improvement (\( \beta_1 > 0 \) or \( \beta_2 > 0 \) and \( \gamma_1 = \gamma_2 = 0 \))

C.2.1. Derivation of the isolines (Fig. 4)

The plant isolines are the same as in the case with no positive interactions, Appendix C.1.1.

C.2.2. Derivation of the resource consumption lines (Fig. 4)

The resource consumption lines of either species 1 or species 2 at the coexistence point bend in the same way as in the case of isolated species, Appendix B.2.2.

C.2.3. Fixed points

The values of the plant densities at the intersection point can be determined as in the case with no positive interactions, Eqs. (C.5) and (C.6), but replacing \( L_0 \) by its functional dependence on the species density, Eq. (7). We obtain:

\[
h_1 \cdot m_1 \cdot x_1 + h_2 \cdot m_2 \cdot x_2 - p \cdot \beta_1 x_1 + \beta_2 x_2 + L_0 \tag{C.7}
\]

\[
\alpha_1 \cdot x_1 + \alpha_2 \cdot x_2 + 1 - L_0 \tag{C.8}
\]

As in that case, Appendix B.1.3, the conditions for the fixed point to have positive densities for the two species are equivalent to the graphical condition of the resource rates, \( p \) and \( L_0 \), to be in the region between the resource consumption lines (Fig. 4).

The transition points between communities can be calculated as in the case with no positive interactions, Appendix C.1.3, except for the discontinuous transitions between species coexistence and species two, Fig. 4A and D. Such a transition point is given by the minimum precipitation rate, \( p \), for which Eqs. (C.7) and (C.8) still have two solutions. It can be determined solving Eq. (C.8) for any plant density variable (for example \( x_1 \)) and substituting it in Eq. (C.7). The resulting equation is quadratic in the other variable \( (x_2) \) and solving its discriminant for \( p \) leads to the desired value.

Now, the stability condition for the coexistence point depends on the positive interactions and is given by the sign of the Jacobian matrix, which takes the following expression

\[
\frac{\alpha_1}{h_1 \cdot m_1} < \frac{\alpha_2}{h_2 \cdot m_2} \tag{C.9}
\]

Because this expression depends explicitly on plant densities, coexistence and founder effect can appear in the same system at different locations in the rainfall gradient (Fig. 4D).

Appendix D. Stability analysis

The stability analysis is given by the eigenvalues of the Jacobian matrix evaluated at the fixed points.
D.1. Single species model

The eigenvalues are negative if the trace of the two-dimensional Jacobian

$$J = \begin{pmatrix} \frac{\partial x}{\partial W} & \frac{\partial x}{\partial W} \\ \frac{\partial W}{\partial W} & \frac{\partial W}{\partial W} \end{pmatrix}$$

is negative and its determinant is positive.

Bare soil point, $\bar{X}_0$. In this case $\frac{\partial x}{\partial W}|_{\bar{X}_0} = 0$ and $\frac{\partial W}{\partial W}|_{\bar{X}_0} < 0$. Stability is determined by the sign of $\frac{\partial x}{\partial W}|_{\bar{X}_0}$. If $p > p^*$, $\frac{\partial x}{\partial W}|_{\bar{X}_0} < 0$ and the bare soil state is globally stable. If $p > p^*$, $\frac{\partial x}{\partial W}|_{\bar{X}_0} > 0$ and the bare soil solution is unstable.

Vegetated states, $\bar{X}_V$ and $\bar{X}_U$. In this case $\frac{\partial x}{\partial W}|_{\bar{X}_V} = 0$ and $\frac{\partial W}{\partial W}|_{\bar{X}_V} < 0$.

Stability is determined by the sign of $\frac{\partial x}{\partial W}|_{\bar{X}_V}$, which can be written as:

$$\frac{\partial x}{\partial W}|_{\bar{X}_V} = p - \frac{\partial x}{\partial W}|_{\bar{X}_V} - h \cdot m - h \cdot x|_{\bar{X}_V} \cdot \frac{\partial x}{\partial W}|_{\bar{X}_V} = (e + r + h \cdot x|_{\bar{X}_V} \cdot \frac{\partial x}{\partial W}|_{\bar{X}_V}) \cdot K^W|_{\bar{X}_V},$$

where $K^W|_{\bar{X}_V}$ is the slope of the water isoline at the equilibrium and the first term, inside the brackets, is always positive. Thus, if the soil-water isoline, $W = 0$, intersects the biomass isoline, $\bar{x} = 0$, with positive (negative) slope, $|J| = -\frac{\partial x}{\partial W}|_{\bar{X}_V} < 0$ (>$0$) then the corresponding steady state, $\bar{X}_U$ ($\bar{X}_V$), is unstable (stable), see Figs. 1 and 3.

D.2. Two species model

Bare soil equilibrium stability is determined by conditions of invasibility by species 2, Appendix D.2

The Jacobian matrices of the species 1 dominance, species 2 dominance and coexistence equilibrium (see Figs. 2, 4 and 6) have the following form.

$$J = \begin{pmatrix} \frac{\partial x}{\partial x} & 0 & \frac{\partial x}{\partial x} \\ \frac{\partial x}{\partial x} & \frac{\partial x}{\partial x} & \frac{\partial x}{\partial x} \\ \frac{\partial x}{\partial x} & \frac{\partial x}{\partial x} & \frac{\partial x}{\partial x} \end{pmatrix}$$

where $\frac{\partial x}{\partial x} \geq 0$ and $\frac{\partial x}{\partial x} \leq 0$. Equilibrium points are stable if the three conditions established by Routh–Hurwitz criterion hold, i.e. the eigenvalues are negative. Let us survey them for each type of equilibrium points.

Species 1 dominance. At the fixed point of species 1 dominance, $\bar{X}_1 = (x_1^*, 0, W_0^*)$, the Jacobian matrix (D.2) is such that $\frac{\partial x}{\partial x} = 0$. The stability conditions reduce to $\frac{\partial x}{\partial x} < 0$ and $\frac{\partial x}{\partial x} < 0$.

Condition $\frac{\partial x}{\partial x} < 0$ is the stability condition for single species, Appendix D.2. Inequality $\frac{\partial x}{\partial x} < 0$ is equal to $f_1^2|_{\bar{X}_1} < m_2$, that is, species 2 can not grow when species 1 reaches equilibrium. Graphically this condition is fulfilled by precipitation rates above the resource consumption line of species 1 passing through isolines intersection point (Figs. 2, 4 and 6).

Species 2 dominance. At the fixed point where species 2 is limited by light and is dominant, $\bar{X}_2 = (0, x_2^*, W_0^*)$, the Jacobian matrix (D.2) is such that $\frac{\partial x}{\partial x} = 0$, $\frac{\partial x}{\partial x} \leq 0$ and $\frac{\partial x}{\partial x} \leq 0$. The stability conditions reduce to $\frac{\partial x}{\partial x} < 0$ which is equal to $f_1^2|_{\bar{X}_1} < m_1$, that is, species 1 can not grow when species 2 reaches equilibrium. Graphically this condition is fulfilled by precipitation rates below the resource consumption line of species 2 passing through isolines intersection point (Figs. 2, 4 and 6).

Coexistence. At the coexistence equilibrium species 1 is limited by water, $\bar{X}_1 = (0, W_0^*)$, and species 2 is limited by light, $\bar{X}_2 = (0, W_0^*)$. Thus $\frac{\partial x}{\partial x} = 0$ and $\frac{\partial x}{\partial x} = 0$. In the region below the resource consumption line of species 1 and above the resource consumption line of species 2, the stability of this fixed point can be inferred from the stability of the states of species 1 and species 2 dominance. In this case coexistence is globally stable. Such region exists if the classical stability condition given by Tilman (Tilman, 1982), i.e. determinant ($J$) < 0, given by Eq. (C.6) or Eq. (C.9), is fulfilled. In systems with water infiltration amelioration below this region the determinant condition can also be fulfilled, see Fig. 4A and D. Then, two coexistence fixed solutions appear, one stable and one unstable. In the case of $\beta_1 > 0$ and $\beta_2 = 0$ it is not difficult to show that the other two Routh–Hurwitz conditions are not relevant. One is given by the trace, which is always negative. The other one can be posed as $f_1 + f_2 > 0$ or $f_1 > 0$ the determinant condition is fulfilled if the determinant is negative and $f_1 + f_2 > 0$. This latter condition is fulfilled if $f_1 > 0$ and $f_2 > 0$. Stability can be shown that $f_1 > 0$, which is obviously negative. In the case of $\beta_2 > 0$ the expressions are rather cumbersome to be handled in this appendix.

References


