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Positive interactions, discontinuous transitions and species coexistence in plant communities

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ABSTRACT

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.

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

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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) (Zavala 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

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

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

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):

$$\begin{aligned}\dot{W} &= I - E - P = I - e \cdot W - r \cdot W \\ &= (e + r) \cdot \left(\frac{I}{e + r} - W\right),\end{aligned} \tag{3}$$

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:

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

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,

$$\begin{aligned}\dot{W} &= \left(e\left(x_1,\ldots,x_n\right) + r\right)\left(\frac{p \cdot i\left(x_1,\ldots,x_n\right)}{e\left(x_1,\ldots,x_n\right) + r} - W\right) \\ &\quad - \sum_{i=1}^{n} h_i \cdot f_i(W) \cdot x_i,\end{aligned} \tag{6}$$

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