



Stand dynamics and tree coexistence in an analytical structured model: The role of recruitment



Óscar Angulo^{a,*}, Rafael Bravo de la Parra^b, Juan C. López-Marcos^c, Miguel A. Zavala^d

^a Dpto. de Matemática Aplicada, ETSII, Universidad de Valladolid, Pso. Belén 15, 47011 Valladolid, Spain

^b Dpto. de Matemáticas, Universidad de Alcalá, E-28871 Alcalá de Henares (Madrid), Spain

^c Dpto. de Matemática Aplicada, Universidad de Valladolid, Spain

^d Forest Ecology and Restoration Group, Departament of Life Sciences, Science Building, Universidad de Alcalá Campus Universitario, 28871 Alcalá de Henares (Madrid), Spain

HIGHLIGHTS

- We develop an analytical model of mono and multi-species stand dynamics.
- The model study is done both analytically and by means of an ad hoc numerical method.
- A single species persistence depends on potential replacement in terms of basal area.
- Tradeoffs between shade tolerance and fecundity or growth explain species coexistence.
- The ratios of inter to intraspecific depression coefficients decide on coexistence.

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ABSTRACT

Understanding the mechanisms of coexistence and niche partitioning in plant communities is a central question in ecology. Current theories of forest dynamics range between the so-called neutral theories which assume functional equivalence among coexisting species to forest simulators that explain species assemblages as the result of tradeoffs in species individual strategies at several ontogenetic stages. Progress in these questions has been hindered by the inherent difficulties of developing analytical size-structured models of stand dynamics. This precludes examination of the relative importance of each mechanism on tree coexistence. In previous simulation and analytical studies emphasis has been given to interspecific differences at the sapling stage, and less so to interspecific variation in seedling recruitment. In this study we develop a partial differential equation model of stand dynamics in which competition takes place at the recruitment stage. Species differ in their size-dependent growth rates and constant mortality rates. Recruitment is described as proportional to the basal area of conspecifics, to account for fecundity and seed supply per unit of basal area, and is corrected with a decreasing function of species specific basal area to account for competition. We first analyze conditions for population persistence in monospecific stands and second we investigate conditions of coexistence for two species. In the monospecific case we found a stationary stand structure based on an inequality between mortality rate and seed supply. In turn, intra-specific competition does not play any role on the asymptotic extinction or population persistence. In the two-species case we found that coexistence can be attained when the reciprocal negative effect on recruitment follows a given relation with respect to intraspecific competition. Specifically a tradeoff between recruitment potential (i.e. shade tolerance or predation avoidance) and fecundity or growth rate. This is to our knowledge the first study that describes coexistence mechanisms in an analytical size-structured model in terms of competitive differences at the regeneration state.

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1. Introduction

Understanding the mechanisms of coexistence and niche partitioning in plant communities is a central question in ecology (Tilman, 1988). Current theories of forest dynamics range between the so-called neutral theories which assume functional equivalence

* Corresponding author. Tel.: +34 983 423 000x5835; fax +34 983 423 661.

E-mail addresses: oscar@mat.uva.es (Ó. Angulo),

rafael.bravo@uah.es (R. Bravo de la Parra),

lopezmar@mac.uva.es (J.C. López-Marcos), ma.zavala@uah.es (M.A. Zavala).

among coexisting species to forest simulators models that explain species assemblages as the result of tradeoffs in species strategies (Chave, 1999; Purves et al., 2008).

Tradeoffs among species strategies in relation to resource availability and disturbances determines coexistence mechanisms for a given community. Important mechanisms of coexistence however can differ throughout the developing stages of tree life history and population studies need to concentrate on specific processes to detect specific assembly rules for each forest system (Nakashizuka, 2001). To do so models of forest dynamics are critical tools that allow us to evaluate the community-level consequences of species individual strategies (e.g. Pacala et al., 1996).

Forest dynamics imply height or size structured competition (Kohyama, 1989, 1991, 1992) and spatial interactions (Pacala and Deutschman, 1995). Typically models of forest dynamics have relied on simulation approximations (e.g. individual based models) that trace the fate of each individual throughout its life cycle. Forest simulators are mechanistic in the sense that tree performance is a function of resource availability (e.g. light) which is in turn determined by stand structure. Differential competitive ability along a light gradient explains species successional niches (Shugart, 1984; Pacala et al., 1996).

The complexity associated to individual based mechanistic descriptions has hindered the development of analytical approximations, and the identification of key coexistence mechanisms is still poorly understood. Alternatively to complex forest simulators, partial differential equations provide analytical framework for describing key features of stand forest systems at a level of complexity that is tractable (e.g. Kohyama, 1989, 1991, 1992; Zavala et al., 2007). Recent work suggests convergence between forest simulators and macroscopic equations based on average densities of trees of different sizes and parameter values and that describe individual performance in the simulator (i.e. Lischke et al., 1998; Strigul et al., 2008; Adams et al., 2007; Cammarano, 2011). On the other hand, progresses in numerical methods analysis (Angulo and López-Marcos, 2004) allow us for rigorous numerical exploration of system dynamics and thus biological interpretation of key results.

Recent explanations for tree coexistence rely on interspecific differences in competitive ability at the sapling stage. In particular species-specific differences in growth and mortality determine species ability to reach the canopy and thus stand composition along successional gradients (Pacala and Deutschman, 1995; Pacala et al., 1996). Reciprocal species ability to recruit under the canopy of other species, however, is a key determinant of successional replacement (Horn, 1981; Woods, 1979). A critical question is to understand the role of recruitment in species coexistence. Specifically we aim to elucidate if recruitment alone can explain species coexistence or competitive exclusion even when there is no competition at later developmental stages.

In this study, we develop an analytical size-structured model of stand dynamics to investigate the role of competition at the seedling recruitment stage on species persistence and coexistence. We assume constant species specific mortality rates and size-dependent logistic growth. Competition takes place at the seedling stage with species differing in their fecundity and in their competitive effect on recruitment of other species. Once the seedling stage has been reached we assume that cohorts grow independently of competitive effects. Specifically we address the following issues: (i) in monospecific stands, how do species-specific rates of growth, mortality and fecundity combine to determine species persistence and stand structure?; in mixed stands can interspecific differences in recruitment rate and competition alone explain species coexistence? If so, how do species-specific competitive effects, growth, mortality and fecundity combine to determine coexistence?

In Section 2 we proceed to present the general two species model. Section 3 is devoted to state some analytical results on extinction conditions and stationary distributions, first for the mono-species model and second for the two species model, which are developed in Appendix A. These results are further studied in Section 4 by means of ad hoc numerical methods presented in Appendix B. The discussion in Section 5 and the list of references complete the paper.

2. Model description

Zavala and Bravo de la Parra (2005) propose a general analytical framework to describe stand dynamics by means of a general multi-species model of a size-structured tree population which takes into account the effects of competition for light and water. In Zavala et al. (2007) the dynamics of a mono-species stand was studied under the effect of competition for light either in the growth or the mortality rates of the population. Here our aim is studying the light competition in the recruitment of a community of two tree populations at the stand level as mechanism of coexistence.

We start presenting the model. Both independent variables size x and time t are considered continuous. The size variable x represents, following Kohyama (1991, 1992), the *d.b.h.* (diameter at breast height). Let $u_i(x, t)$, with $i=1,2$, be the population density of species i with respect to *d.b.h.* of trees in the stand per m^2 , what means that

$$\int_{x_1}^{x_2} u_i(\sigma, t) d\sigma$$

represents the number of trees of species i in the stand patch per m^2 with *d.b.h.* $x \in [x_1, x_2]$ at time t .

The light competition will be included in the model through the total basal areas of both species, defined for species i ($i=1,2$) as follows:

$$B_i(t) = \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 u_i(\sigma, t) d\sigma$$

where x_M is the maximum *d.b.h.* reached by trees and x_0 is the minimum *d.b.h.* for a tree to be considered a recruit. For technical reasons we consider the same maximum and minimum *d.b.h.* for both species.

Changes in size distribution depend on the rates of size growth, mortality and recruitment. These rates are presented in full generality in Zavala and Bravo de la Parra (2005) and Zavala et al. (2007). Here we just present the particular forms of these rates that we use in the sequel.

We assume that mortality rates, μ_i ($i=1,2$), are constant and growth rates, $g_i(x)$ ($i=1,2$), are dependent on trees individual size x but we do not take into account the effects of light competition on trees growth. We suppose that $g_i(x)$ are general regular functions, positive on $[x_0, x_M]$ and verifying $g_i(x_M) = 0$. Only to sharpen some results and in the numerical simulations we use a specific growth, logistic growth, which is a particular case of Richards law (Richards, 1959)

$$g_i(x) = r_i x \left(1 - \frac{x}{x_M} \right). \quad (1)$$

Concerning the recruitment rates, $R_i(t)$ ($i=1,2$), we suppose that they are dependent, on the one hand, on the total basal area $B_i(t)$ of the corresponding species, assuming that potential seedling supply without shading is proportional to $B_i(t)$, and, on the other hand, on a weighted sum of both total basal areas that takes into account the shading effect through a negative exponential. The particular expression for the recruitment rates ($i=1,2$) that we use

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