



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



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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

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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

is the following:

$$R_i(t) = \rho_i \exp(-f_{i1}B_1(t) - f_{i2}B_2(t))B_i(t), \tag{2}$$

where ρ_i is the recruitment rate without shading per basal area unit of species i and f_{ij} is the depression coefficient defining the suppression in the recruitment of species i caused by species j .

Under these assumptions the two-species stand structure model with light dependent recruitment reads as follows:

Balance law

$$(u_i)_t(x, t) + (g_i(x)u_i(x, t))_x = -\mu_i u_i(x, t), \quad (x_0 < x < x_M, t > 0), \quad (i = 1, 2), \tag{3}$$

Recruitment law

$$g_i(x_0)u_i(x_0, t) = R_i(t), \quad (t > 0), \quad (i = 1, 2), \tag{4}$$

Initial d.b.h. distribution

$$u_i(x, 0) = u_i^0(x), \quad (x_0 \leq x \leq x_M), \quad (i = 1, 2). \tag{5}$$

3. Model analysis

In Zavala et al. (2007) it treated the case of light competition in the growth and mortality rates but not in recruitment rate. Here, before developing the case of two species, we study the particularization of systems (3)–(5) to a single population, that is when intra-specific competition acts on recruitment.

3.1. Intra-competition in recruitment and mono-species stand structure

We can write systems (3)–(5), for a single population in the following form:

$$u_t(x, t) + (g(x)u(x, t))_x = -\mu u(x, t), \quad (x_0 < x < x_M, t > 0), \tag{6}$$

$$g(x_0)u(x_0, t) = R(t), \quad (t > 0), \tag{7}$$

$$u(x, 0) = u_0(x), \quad (x_0 \leq x \leq x_M), \tag{8}$$

where $R(t) = \rho \exp(-fB(t))B(t)$ and $B(t) = \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 u(\sigma, t) d\sigma$.

We begin by studying the evolution of the total population $U(t) = \int_{x_0}^{x_M} u(\sigma, t) d\sigma$, see Appendix A.

We get the following equation for $U(t)$:

$$U'(t) - \rho \exp(-fB(t))B(t) = -\mu U(t), \tag{9}$$

from which we can deduce that $U(t)$ is decreasing whenever $U(t) \geq \rho/ef\mu$ and that the total population, as well as the total basal area, are bounded for any solution of systems (6)–(8).

We also obtain sufficient conditions for extinction and non-extinction of the population. The non-extinction condition can be expressed as follows in terms of parameters μ , ρ and x_0 :

$$\mu < \left(\frac{\pi}{4}x_0^2\right)\rho \tag{10}$$

while the extinction condition is

$$\mu \geq \left(\frac{\pi}{4}x_M^2\right)\rho, \tag{11}$$

in this case we also have $U(t) \leq U(0)$.

In both conditions (10) and (11) parameter f plays no role and, though they are just sufficient conditions, this is always the case because if we call $v_1(x, t)$ and $v_2(x, t)$ the solutions of Eqs. (6) and (7) for two different values of parameter f , f_1 and f_2 , it is straightforward to prove that they verify $f_1 v_1(x, t) = f_2 v_2(x, t)$, i.e. they are related at any time by the same proportionality constant.

3.1.1. Logistic individual tree growth

Here we consider a particular growth rate, the logistic growth rate (1), $g(x) = rx(1-x/x_M)$, that allows sharpening the sufficient

conditions on extinction and non-extinction of the population. To get them we follow with the total basal area $B(t)$ the reasoning done in the previous section with $U(t)$. We can obtain, see Appendix A, the following equation for $B(t)$:

$$B'(t) - \frac{\pi}{4}x_0^2\rho \exp(-fB(t))B(t) - 2rB(t) + \frac{2r}{x_M} \int_{x_0}^{x_M} \sigma \frac{\pi}{4} \sigma^2 u(\sigma, t) d\sigma = -\mu B(t) \tag{12}$$

and then deduce the sufficient non-extinction condition that coincides with (10), $\mu < ((\pi/4)x_0^2)\rho$, and the sufficient extinction condition that, in most cases, is much sharper than (11)

$$\mu \geq \left(\frac{\pi}{4}x_0^2\right)\rho + 2r \left(1 - \frac{x_0}{x_M}\right). \tag{13}$$

3.1.2. Stand stationary distribution

In the study of systems (6)–(8) we can also look for the existence of stationary size distributions of trees as reported in Kohyama (1991). If we call $u^*(x)$ the stationary distribution, it must be a solution of the following initial value problem:

$$(g(x)u^*(x))' = -\mu u^*(x), \tag{14}$$

$$g(x_0)u^*(x_0) = R^*, \tag{15}$$

where we denote

$$B^* = \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 u^*(\sigma) d\sigma \quad \text{and} \quad R^* = \rho \exp(-fB^*)B^*. \tag{16}$$

Integrating Eq. (14) we get

$$u^*(x) = g(x_0)u^*(x_0) \frac{1}{g(x)} \exp\left(-\mu \int_{x_0}^x \frac{d\sigma}{g(\sigma)}\right),$$

and using (15) and (16) we get

$$u^*(x) = \rho \exp(-fB^*)B^* \frac{1}{g(x)} \exp\left(-\mu \int_{x_0}^x \frac{d\sigma}{g(\sigma)}\right), \tag{17}$$

Now if we multiply Eq. (17) by $(\pi/4)x^2$ and integrate on $[x_0, x_M]$ with respect to x we obtain the following equation for the total basal area B^* of the stationary solution $u^*(x)$:

$$B^* = \rho \exp(-fB^*)B^* \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 \frac{1}{g(\sigma)} \exp\left(-\mu \int_{x_0}^{\sigma} \frac{d\beta}{g(\beta)}\right) d\sigma,$$

and denoting

$$C = \rho \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 \frac{1}{g(\sigma)} \exp\left(-\mu \int_{x_0}^{\sigma} \frac{d\beta}{g(\beta)}\right) d\sigma, \tag{18}$$

we finally get

$$B^* = \exp(-fB^*)B^* C. \tag{19}$$

This equation has the 0 solution and

$$B^* = \ln C/f. \tag{20}$$

So, the necessary and sufficient condition for the existence of a positive stationary size distribution $u^*(x)$ of systems (6)–(8) is that $C > 1$, which allows $B^* = \ln C/f > 0$ to be its total basal area. In this case we have

$$u^*(x) = \frac{\rho \ln C}{fC} \frac{1}{g(x)} \exp\left(-\mu \int_{x_0}^x \frac{d\sigma}{g(\sigma)}\right). \tag{21}$$

From Eq. (14), it is easy to see that $(d/dt)u^*(x) = (-\mu - g'(x))u^*(x)/g(x)$, and so its sign depends on the sign of $-\mu - g'(x)$.

In the case of logistic growth the stationary size distribution is

$$u^*(x) = \frac{\rho \ln C}{fCr} \left(\frac{x_0 x_M}{x_M - x_0}\right)^{\mu/r} x^{-(1+\frac{\mu}{r})} \left(1 - \frac{x}{x_M}\right)^{\mu/r-1},$$

and $-\mu - g'(x) = -\mu - r + 2rx/x_M$, so it is straightforward to infer that if $\mu \geq r$ then $u^*(x)$ is decreasing in (x_0, x_M) and if $\mu < r$ then

$u^*(x)$ is decreasing in $(x_0, ((\mu + r)/2r)x_M)$ and increasing in $((\mu + r)/2r)x_M, x_M)$.

Constant C can be interpreted as the mean basal area by which a unit basal area of new recruits will be replaced by the end of their life-span without taking into account the competition part in the recruitment rate ($\exp(-fB(t))$). As we illustrate in Section 4, C can be taken as a measure deciding between extinction ($C < 1$) and non-extinction ($C > 1$) of the population. In the former case the population is not able to grow in absence of competition so it gets extinct and in the latter case there exists an equilibrium distribution whose total basal area B^* can be taken as a sort of specific stand carrying capacity.

Constant C is proportional to ρ , the potential recruitment rate per basal area unit (i.e. in absence of shading or predation). C as a function of ρ could be as large as fertility allows. Also, if we assume C as a function of μ , the mortality rate, turns to be decreasing. On the other hand, it is not so evident how C depends on the growth rate $g(x)$. Considering the logistic growth rate (1), $g(x) = rx(1 - x/x_M)$, it is obtained the following expression for C (see (A.3) in Appendix A):

$$C = \frac{\pi\rho x_0^2}{4\mu} + \frac{\pi\rho}{2\mu} \int_{x_0}^{x_M} \sigma \left(\frac{x_0(x_M - \sigma)}{\sigma(x_M - x_0)} \right)^{\mu/r} d\sigma. \tag{22}$$

The parameter r in the logistic growth represents the slope of the growth rate with respect to size or growing speed until growth slows down as size approaches the maximum diameter x_M (i.e., larger r values implies faster growth rates). Taking C as a function of r , denoted $C(r)$, we show in Appendix A that it is increasing and bounded. A faster growing rate decreases the likelihood of the species extinction as well as increases the total basal area B^* of its stationary distribution $u^*(x)$.

3.2. The two-species stand model

In the case of the two-species stand model described by systems (3)–(5) we can develop a similar analysis to that performed in the case of one species for each one of the two species. So, to study the evolution of the total i population we use Eq. (3), $(u_i)_t(x, t) + (g_i(x)u_i(x, t))_x = -\mu_i u_i(x, t)$, to obtain (see Appendix A)

$$U_i(t) - \rho_i \exp(-f_{i1}B_1(t) - f_{i2}B_2(t))B_i(t) = -\mu_i U_i(t), \tag{23}$$

which yields, as in the one species case, that $U_i(t)$ is bounded with the following upper bound

$$U_i(t) \leq \max \left\{ U_i(0), \frac{\rho_i}{ef_{ii}\mu_i} \right\}. \tag{24}$$

A straightforward consequence of Eq. (23) is inequality

$$U_i(t) < \rho_i \exp(-f_{ii}B_i(t))B_i(t) - \mu_i U_i(t),$$

which proves that a population that gets extinct alone also does when competing with another population.

To obtain conditions of extinction and non extinction analogous to those found in Section 3.1 for each one of the two species we could follow similar arguments. If i represents the index of one of the species let j represents the other one. In Appendix A are proved sufficient conditions on extinction and non extinction for any form of the growth rate $g_i(t)$. In these conditions we use the following three constants, $\bar{g}_i = \max_{x \in [x_0, x_M]} 2g_i(x)/x$, which exists due to the continuity of g_i , and \bar{b}_j and \underline{B}_j , lower and upper bounds of $B_j(t)$, $\bar{b}_j \leq B_j(t) \leq \underline{B}_j$ for every $t > 0$, which existence has already been proved.

A sufficient condition for the extinction of species i is

$$\mu_i > \bar{g}_i + \frac{\pi}{4} x_0^2 \rho_i \exp(-f_{ij}\bar{b}_j), \tag{25}$$

and a sufficient condition for the non extinction of species i reads

as follows:

$$\mu_i < \frac{\pi}{4} x_0^2 \rho_i \exp(-f_{ij}\bar{B}_j). \tag{26}$$

This last inequality give us a partial answer to the following question concerning extinction and persistence, what is the result of competition between two populations for which, in absence of competitors, the first one persists and the second one gets extinct. We already know that the second one will also get extinct under competition. From inequality (26), we can deduce that if the first population verifies the sufficient condition of persistence (10), $\mu_i < ((\pi/4)x_0^2)\rho_i$, then it also persists when competing with a population that gets extinct without competition.

We noticed in the single species case that parameter f representing intra-species competition plays no role in the asymptotic extinction or persistence of the population. To analyze this question in the two-species case we can perform a change of variables in systems (3)–(5), $v_1 = f_{11}u_1$ and $v_2 = f_{22}u_2$, that yields a new system with the same form but for the competition coefficients, f_{ij} . Now the intra-specific competition coefficients, f_{11} and f_{22} , are equal to 1 while the inter-specific ones read f_{12}/f_{22} and f_{21}/f_{11} . The values of these two ratios decide the result of competition, coexistence or exclusion.

3.2.1. Stand stationary distribution

In this section we find conditions for a positive stationary distribution to exist and compare the results with those obtained in Section 3.1.2.

We denote, as done in Section 3.1.2,

$$C_i = \rho_i \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 \frac{1}{g_i(\sigma)} \exp\left(-\mu_i \int_{x_0}^{\sigma} \frac{d\beta}{g_i(\beta)}\right) d\sigma \quad i = 1, 2,$$

and it is proved in Appendix A that, under some conditions, a positive stationary distribution of both species exists, that means coexistence with fixed densities and size structures.

The conditions to be met are of two types. First,

$$C_1 > 1 \quad \text{and} \quad C_2 > 1 \tag{27}$$

what means that each one of the two species verifies the necessary and sufficient condition for the existence of a positive stationary size distribution when growing alone without interspecific competition. To reach a coexistence equilibrium when competing both species must be able to attain an equilibrium on their own. Second,

$$\frac{f_{22} \ln C_1 - f_{12} \ln C_2}{f_{11}f_{22} - f_{12}f_{21}} > 0 \quad \text{and} \quad \frac{f_{11} \ln C_2 - f_{21} \ln C_1}{f_{11}f_{22} - f_{12}f_{21}} > 0. \tag{28}$$

These two quantities represent the total basal areas of both species at equilibrium and obviously they need to be positive.

The form of the positive stationary distribution is the following:

$$\begin{cases} u_1^*(x) = \frac{\rho_1}{C_1} \frac{f_{22} \ln C_1 - f_{12} \ln C_2}{f_{11}f_{22} - f_{12}f_{21}} \frac{1}{g_1(x)} \exp\left(-\mu_1 \int_{x_0}^x \frac{d\sigma}{g_1(\sigma)}\right) \\ u_2^*(x) = \frac{\rho_2}{C_2} \frac{f_{11} \ln C_2 - f_{21} \ln C_1}{f_{11}f_{22} - f_{12}f_{21}} \frac{1}{g_2(x)} \exp\left(-\mu_2 \int_{x_0}^x \frac{d\sigma}{g_2(\sigma)}\right) \end{cases} \tag{29}$$

The first question that we notice is that the size structure of both species does not change with competition. The difference between the expression of $u^*(x)$ in (21) and $u_i^*(x)$ in (29) is a constant. The ratio $\ln C/f$ in (21) becomes $(f_{ij} \ln C_i - f_{ij} \ln C_j)/(f_{11}f_{22} - f_{12}f_{21})$ in (29) (for $ij = 1, 2$ and $i \neq j$), the rest being identical. So, we can do similar precisions on the form of either $u_1^*(x)$ or $u_2^*(x)$ to those we did in the case of one species. Competition at the regeneration state does not affect size structure when a coexistence equilibrium is attained.

Numerical simulations show that solutions of systems (3)–(5) tend to the stationary distribution (29) when (27) and (28) hold,

existence of stationary distributions, and $f_{11}f_{22}-f_{12}f_{21} > 0$. The latter condition together with (28) is equivalent to

$$\frac{f_{12} \ln C_2}{f_{22} \ln C_1} < 1 \quad \text{and} \quad \frac{f_{21} \ln C_1}{f_{11} \ln C_2} < 1, \tag{30}$$

so that we can take as coexistence conditions (27), $C_1 > 1$ and $C_2 > 1$, and (30).

Calling $\bar{B}_1 = \ln C_1/f_{11}$ and $\bar{B}_2 = \ln C_2/f_{22}$, the stationary stand basal areas for each of the two species when living alone, inequalities (30) read as follows:

$$\frac{f_{12}}{f_{11}} \frac{\bar{B}_2}{\bar{B}_1} < 1 \quad \text{and} \quad \frac{f_{21}}{f_{22}} \frac{\bar{B}_1}{\bar{B}_2} < 1,$$

and coincide with the conditions of coexistence in the classical Lotka–Volterra competition model, see Murray (2002, pp. 9499), if considering \bar{B}_1 and \bar{B}_2 as carrying capacities of each species, and f_{12}/f_{11} and f_{21}/f_{22} as the corresponding coefficients measuring the competitive effect of the second species on the first one and of the first one on the second, respectively.

Assuming (27), conditions (30) can be used to make clear the trade-offs involved in species coexistence. Let us consider a shade intolerant species (species-1) and a shade tolerant species (species-2), what can be represented in our model by taking large depression coefficients on species-1, f_{11} and f_{12} , relative to depression coefficients on species-2, f_{21} and f_{22} . Equivalently, we can assume that both fractions f_{11}/f_{21} and f_{12}/f_{22} are large.

To describe the tradeoff between shade tolerance and fecundity let us call

$$H_i = \int_{x_0}^{x_M} \frac{\pi \sigma^2}{4} \frac{1}{g_i(\sigma)} \exp\left(-\mu_i \int_{x_0}^{\sigma} \frac{d\beta}{g_i(\beta)}\right) d\sigma \quad i = 1, 2,$$

thus we have

$$C_i = \rho_i H_i \quad i = 1, 2,$$

and conditions (30) can be expressed in the following form:

$$\frac{1}{H_1} C_2^{f_{12}/f_{22}} < \rho_1 < \frac{1}{H_1} C_2^{f_{11}/f_{21}}. \tag{31}$$

We first notice that as $f_{11}f_{22}-f_{12}f_{21} > 0$ implies that $f_{12}/f_{22} < f_{11}/f_{21}$ and $C_2 > 1$ there always exist values of ρ_1 ensuring coexistence. In particular, however large fraction f_{12}/f_{22} be there are high enough values of ρ_1 yielding coexistence.

To analyze the tradeoff between shade tolerance and growing speed we can express conditions (30) as follows:

$$C_2^{f_{12}/f_{22}} < C_1 < C_2^{f_{11}/f_{21}},$$

and consider logistic growing, $g(x) = rx(1-x/x_M)$, so that C_1 can be taken as a function of parameter r representing the growing speed.

In Appendix A it is shown that $C_1(r)$ is an increasing function such that, (A.4),

$$\lim_{r \rightarrow \infty} C_1(r) = \frac{\pi \rho_1 x_M^2}{4\mu_1},$$

what implies that growing speed can compensate shade intolerance to give rise to coexistence provided that

$$C_2^{f_{12}/f_{22}} < \frac{\pi \rho_1 x_M^2}{4\mu_1},$$

because in that case there exist large enough values of r ensuring

$$C_2^{f_{12}/f_{22}} < C_1(r). \tag{32}$$

4. Numerical simulations

Systems (3)–(5) cannot, in general, be solved analytically and the same happens to systems (6)–(8) associated to the mono-specific model. In Section 3.1 we have obtained, for this latter system, some sufficient conditions for the extinction, (11) and (13), and non-extinction, (10), of the population, as well as a necessary and sufficient condition for the existence of a stand stationary distribution, in terms of constant C defined in (18), $C > 1$.

We next use the efficient numerical method introduced in Appendix B to study the asymptotic behavior of systems (6)–(8) with logistic individual tree growth, Section 3.1.1, where we set the following parameters values: $x_0 = 1$, $x_M = 51$, $r = 0.1$ and $\rho = 0.5$.

In a first experiment, setting $f = 10^{-8}$, we look for the threshold between extinction and non-extinction making parameter μ to vary. Condition (13) tells us that a sufficient extinction condition is $\mu \geq \pi/8 + 10/51 \approx 0.588775$ which turns out to be fairly accurate because as we see in Fig. 1 for $\mu = 0.5875$ there is extinction. To illustrate that constant C can be taken as a measure deciding between extinction ($C < 1$) and non-extinction ($C > 1$) of the population we calculate it in terms of μ in (18)

$$\begin{aligned} C(\mu) &= 0.5 \int_1^{51} \frac{\pi x^2}{0.4x(1-x/51)} \exp\left(-\mu \int_1^x \frac{1}{0.1\sigma(1-\sigma/51)} d\sigma\right) dx \\ &= 51\pi 2^{-10\mu-2} 5^{1-20\mu} \int_1^{51} (51/x-1)^{10\mu-1} dx \end{aligned}$$

and solving equation $C(\mu) = 1$ we obtain the value $\mu^* \approx 0.5874989$ which seems to be much more accurate than the one we get out of condition (13).

In a second experiment we try to study further the long-term behavior of the population. In Fig. 2 we see the evolution of the total basal area of the population for different values of μ ($f = 0.01$)

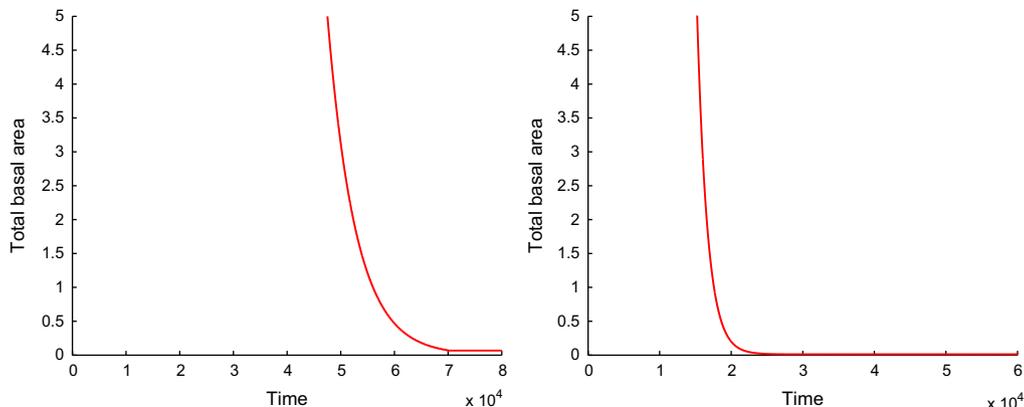


Fig. 1. Evolution of the total basal area of the population in systems (6)–(8) with logistic growth rate: $x_0 = 1$, $x_M = 51$, $r = 0.1$, $\rho = 0.5$ and $f = 10^{-8}$. Left side, $\mu = 0.5870$, non-extinction; right side, $\mu = 0.5875$, extinction.

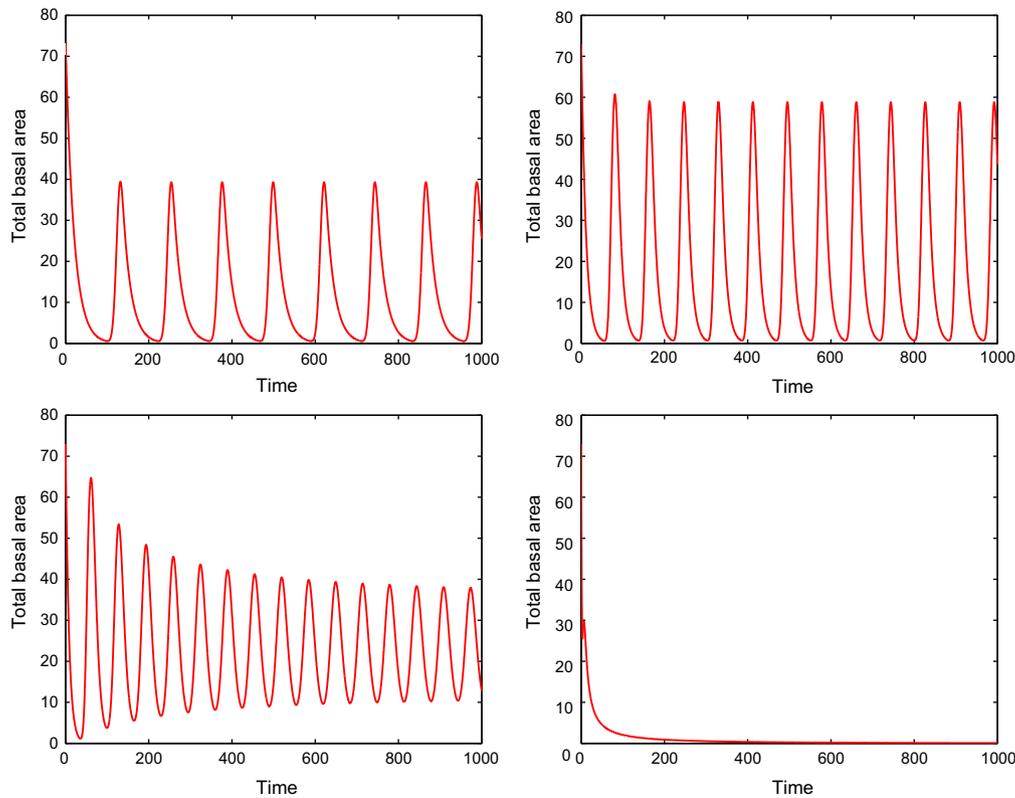


Fig. 2. Evolution of the total basal area of the population in systems (6)–(8) with logistic growth rate: $x_0 = 1$, $x_M = 51$, $r = 0.1$, $\rho = 0.5$ and $f = 0.01$. Different values of μ , left–right and up–down: $\mu = 0.05$ and $\mu = 0.09$ undamped oscillations; $\mu = 0.125$, damped oscillations; $\mu = 0.59$ monotonically decreasing to extinction.

and we notice that the non-extinction cases ($\mu = 0.05, 0.09, 0.125$) give oscillatory behavior which tend to be damping as the mortality rate increases while in the extinction case ($\mu = 0.59$) the trivial equilibrium is attained monotonically.

The good stability properties of the numerical method we use, Appendix B, allow us to study in more detail for which values of μ the stand stationary distribution, whose existence is proved in Section 3.1.2 for $\mu < \mu^* \approx 0.5874989$, is stable. In Fig. 3 we extend the represented interval of time and we see that for $\mu = 0.12$ the total basal area tends to stationary oscillations while for $\mu = 0.13$ the oscillations are damped and the total basal area of the stand stationary distribution is attained.

The last experiment illustrates the issue of coexistence in the two-species stand model. In Section 3.2.1 are found conditions, (30), for the existence of a coexistence stand stationary distribution which can be translated into those ones ensuring coexistence in the classical Lotka–Volterra competition model. We show that the stationary distribution is attained in most of the cases that it exists.

Let us consider in systems (3)–(5) two populations with logistic individual tree growth and with the same parameters values: $x_0 = 1$, $x_M = 51$, $r = 0.1$, $\mu = 0.2$ and $\rho = 0.5$. The fact that $\mu = 0.2$ implies that both populations if living alone would tend to a stationary stand distribution. We distinguish between the two species through the depression coefficients f_{ij} where recruitment competition is reflected. We set $f_{11} = 0.01$ and $f_{22} = 0.02$, what means that population 1 would double the size of population 2 considering both living alone. Coexistence conditions (30) reduce in this case to $f_{12} < 0.02$ and $f_{21} < 0.01$, so we explore the long-term behavior of the system on the parameters values range $f_{12} \in (0, 0.02)$ and $f_{21} \in (0, 0.01)$. The results in Section 3.2.1 say that there exists the coexistence stand stationary distribution and that population 1 attains a larger size than population 2 if $f_{21} > f_{12} - 0.01$ and the contrary happens if $f_{21} < f_{12} - 0.01$.

Fig. 4 shows that in the parameters range $f_{12} \in (0, 0.02)$ and $f_{21} \in (0, 0.01)$ where the coexistence stand stationary distribution is attained, in the dark (red) domain population 1 is larger than population 2 while in the light (blue) domain population 2 is the largest one. In the rest of the parameters range, the white domain where either f_{12} is very close to 0.02 or f_{21} to 0.01, it seems that the proven existence of the coexistence stand stationary distribution does not entail its stability at least globally.

5. Discussion

Understanding the mechanisms underlying tree species coexistence is a central topic in current ecology. The development of simple analytically tractable models of forest dynamics is critical for understanding the role of a specific mechanism in generating a given pattern. In this study we introduce an analytical size-structured forest dynamics model in which species interactions take place at the regeneration stage and are the result of multiple interacting processes; chiefly competition but also differential seed predation, fecundity, etc. Species differ in their growth and mortality rates but, in contrast to regeneration, they are not differentially influenced by competition. We show that species specific differences and competitive interactions at the regeneration stage can explain stand species coexistence even in the absence of competition at later stages. Also tradeoffs among potential recruitment rate and speed of growth rate allow for coexistence.

In our model the condition for the non-extinction of an isolated species can be summarized in constant C that reflects the mean basal area by which a unit basal area of new recruits will be replaced by the end of their life-span in the absence of competition at the recruitment stage, i.e. potential replacement in terms of basal area. If $C < 1$ the species gets extinct when growing in

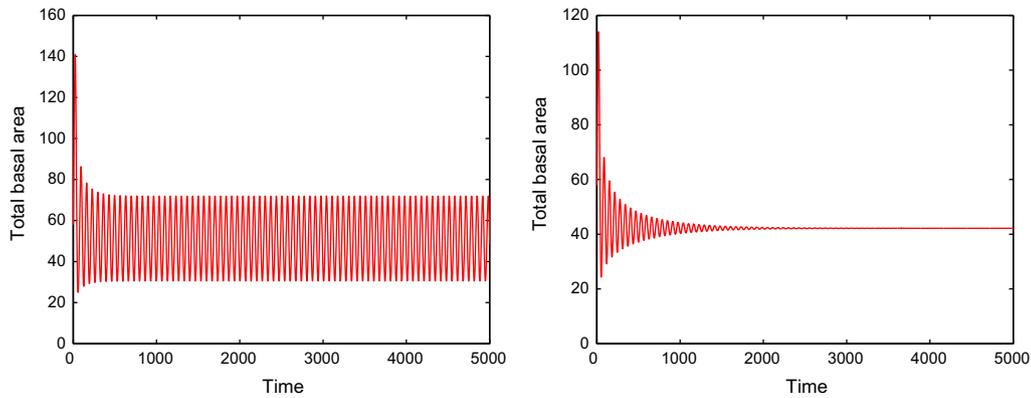


Fig. 3. Evolution of the total basal area of the population in systems (6)–(8) with logistic growth rate: $x_0 = 1$, $x_M = 51$, $r = 0.1$, $\rho = 0.5$ and $f = 0.1$. Left side, $\mu = 0.12$, undamped oscillations; $\mu = 0.13$, stable stand stationary distribution.

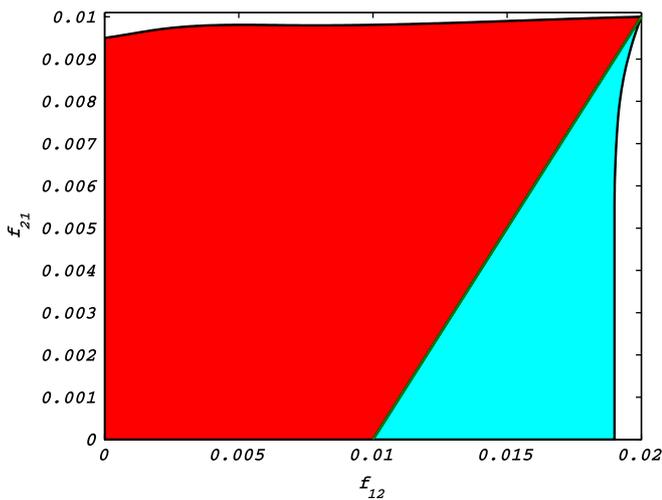


Fig. 4. Values range of parameters f_{12} and f_{21} for stable coexistence equilibrium in systems (3)–(5). Both species with logistic growth rate: $x_0 = 1$, $x_M = 51$, $r = 0.1$, $\mu = 0.2$ and $\rho = 0.5$. Depression coefficients: $f_{11} = 0.01$, $f_{22} = 0.02$, $f_{12} \in (0, 0.02)$ and $f_{21} \in (0, 0.01)$. Colored range corresponds to stable coexistence equilibrium, in the dark (red) part population 1 attains a larger size than population 2 and the contrary happens in the light (blue) part. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

isolation, and consequently also when sharing the overstory with other species. On the other hand, a species with $C > 1$ will survive alone and reach a steady stand distribution. The coexistence of two species with $C_1 > 1$ and $C_2 > 1$ depends on the comparison of some given ratios of intra- vs interspecific competition. These ratios are defined through the depression coefficients f_{ij} and constants C_i , $i, j = 1, 2$ (30).

An interesting result is that coexistence is possible in the absence of one-sided competition and suggests that differences alone in the recruitment processes can induce coexistence. These differences can be due to a number of factors not necessarily associated with resource competition and shade tolerance but also to other stages influencing the recruitment process such as seed predation, germination, seedling establishment and seedling mortality. Coexisting species have been shown to differ in these rates in temperate forests (e.g. Pérez-Ramos et al., 2008) and tropical forests (e.g. Janzen–Connell effects, see Wright, 2002) so this mechanism alone can explain coexistence even in the absence of spatial heterogeneity or an storage effect. Species with lower recruitment (e.g. shade intolerant or one that suffers relatively higher predation rates or herbivory levels) can compensate this disadvantage with a higher fecundity or with higher growth rates (independently of its shade tolerance as a sapling). This mechanism of coexistence is

plausible in oak dominated temperate forests in which interspecific differences in seed size can underlie differential recruitment strategies (e.g. Pérez-Ramos et al., 2012).

Previous analytical models of tree coexistence generally fall between two broad categories; those in which species coexistence results from the fluctuation-mediated, non-equilibrium processes, the so-called lottery models (Warner and Chesson, 1985) and models implying tradeoffs at different ontogenetic stages (see review in Nakashizuka, 2001). The former approximation emphasizes coexistence due to dispersal limitation resulting from competition colonization tradeoffs (Hurtt and Pacala, 1995). In the first case dominant species limited recruitment allows inferior competitors to win some sites by forfeit. Recruitment limitation lessens the effect of competitive asymmetries and slows population and community dynamics. This effect is expected to be more pronounced in highly diverse communities because of the rarity of many species, thus these authors suggest that there is no conflict between the hypothesis that species-rich plant communities are more influenced by chance and history than regulated by competition. The latter type of models typically introduces a rather different view of species coexistence from the fluctuation-mediated, non-equilibrium coexistence, and locally involve one-sided competition (Kohyama, 1992); chiefly tradeoffs between the ability to grow or to die at low light versus maximal growth rate (Purves et al., 2008; Cammarano, 2011) or a tradeoff between potential maximum size and potential recruitment rate (Kohyama, 1992).

Both the autogenic effect of spatial architecture and the stochastic effect of recruitment fluctuation can contribute to coexistence (e.g. the shifting mosaic Kohyama, 1993) and extend further the possibility of coexistence through species differentiation on the basis of stand age. Fast-growing, less-tolerant species and slow-growing, more-tolerant species can coexist stably even without differentiation in maximum size and recruitment rate. Both the stochastic view and the forest architecture hypothesis (sensu Kohyama, 1992) can be reconciled as spatial architecture provides the ‘storage effect’ in lottery models.

More recently, emphasis has been given to the convergence among stochastic individual based models and size-structured models (Strigul et al., 2008). These studies suggest that under the premise of a perfectly plastic allometry (i.e. individual canopies fill out the open space), “perfect plasticity approximation” (PPA) or ideal tree distribution (ITD) (Adams et al., 2007), the tree population can be structured in two classes, suppresses and dominant (see also Cammarano, 2011). Under this premise the PPA approximation results in predictions which are consistent with the predictions with long-term successional dynamics in different soil types data, and predictions from a data defined IBM of forest succession (SORTIE) (Purves et al., 2008).

Species coexistence in cool temperate and tropical forests (Nakashizuka, 2001) has been widely explained by colonization strategies and by sapling performance, yet the mechanisms underlying coexistence in other forest types in which light competition is not the primary driving force remains largely unexplored. In water limited forests with sparse canopies and in which species filtering takes place mostly at the regeneration stage, inter-specific differences in recruitment are of paramount importance for explaining niche diversification and coexistence (Clark et al., 2003). Differential species establishment during stand recovery following disturbances or during colonization events may be driven by differential responses to seed predation (Pérez-Ramos et al., 2008, 2012), germination, establishment and survivorship during the dry season (Pérez-Ramos et al., 2012).

Our results suggest that stand diversity can be explained by recruitment inter-specific differences, providing a given set of conditions in species reciprocal influences on recruitment. Previous studies have reported specific cases that fit within this general result. For example a particular case in which the proposed coexistence conditions are met is reported in Woods (1979) where beech-maple co-dominance is explained by reciprocal replacement. This mechanism translates in our model by considering very small values for the depression coefficients f_{12} and f_{21} which entail that coexistence conditions (30) hold. These results are very similar to what is expected from classical competition theory which states that two species can coexist if none of them at its carrying capacity can prevent the other from growing (Murray, 2002). Our result however stems from a size-structured non-aggregated model that considers explicitly size heterogeneities within the population and time scales more realistic in terms of stand dynamics.

Acknowledgments

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Appendix A. Proofs

(Section 3.1): Integrating on $[x_0, x_M]$ with respect to x in Eq. (6):

$$\int_{x_0}^{x_M} u_t(\sigma, t) d\sigma + \int_{x_0}^{x_M} (g(\sigma)u(\sigma, t))_{,\sigma} d\sigma = -\mu \int_{x_0}^{x_M} u(\sigma, t) d\sigma$$

$$U'(t) - g(x_0)u(x_0, t) = -\mu U(t)$$

If we now use Eq. (7) we obtain Eq. (9): $U'(t) - \rho \exp(-fB(t))B(t) = -\mu U(t)$. This last equation, having in mind that, for $\beta > 0$, $x \exp(-\beta x) \leq 1/(e\beta)$, yields the following inequality:

$$U'(t) + \mu U(t) \leq \frac{\rho}{ef}$$

which implies that $U(t)$ is decreasing whenever $U(t) \geq \rho/ef\mu$. If we write the inequality in the form $d/dt(e^{\mu t}U(t)) \leq (\rho/ef)e^{\mu t}$ and integrate on $[0, t]$ we deduce that

$$U(t) \leq \frac{\rho}{ef\mu} + \left(U(0) - \frac{\rho}{ef\mu} \right) e^{-\mu t}, \quad t \geq 0.$$

This inequality assures the boundedness of the solutions for any

form of the growth rate $g(x)$, provided that $g(x_M) = 0$, and any values of the parameters μ , ρ and f . In particular we have the following upper bound for the total population $U(t) \leq \max\{U(0), \rho/ef\mu\}$ and the asymptotic bound $\lim_{t \rightarrow \infty} U(t) \leq \rho/ef\mu$.

To obtain conditions of extinction (11) and non-extinction (10) of the population we look for upper and lower bounds of $U'(t)$. First we notice that $(\pi/4)x_0^2 U(t) \leq B(t) \leq (\pi/4)x_M^2 U(t)$ and thus

$$\exp\left(-f \frac{\pi}{4} x_M^2 U(t)\right) \frac{\pi}{4} x_0^2 U(t) \leq \exp(-fB(t))B(t) \leq \exp\left(-f \frac{\pi}{4} x_0^2 U(t)\right) \frac{\pi}{4} x_M^2 U(t),$$

that substituted into Eq. (9) give the next two inequalities

$$U'(t) \geq -\mu U(t) + \left(\rho \frac{\pi}{4} x_0^2\right) U(t) \exp\left(-\left(f \frac{\pi}{4} x_M^2\right) U(t)\right),$$

$$U'(t) \leq -\mu U(t) + \left(\rho \frac{\pi}{4} x_M^2\right) U(t) \exp\left(-\left(f \frac{\pi}{4} x_0^2\right) U(t)\right).$$

Some consequences of the asymptotic behavior of $U(t)$ can be inferred from these two inequalities with the help of the straightforward qualitative analysis of the scalar autonomous equation $y' = -ay + by \exp(-cy)$ where a, b and c are positive parameters: if $a < b$ then for $y(0) > 0$ the corresponding solution $y(t)$ verifies $\lim_{t \rightarrow \infty} y(t) = (\ln b - \ln a)/c$, while if $a \geq b$ we have $\lim_{t \rightarrow \infty} y(t) = 0$.

Now the first inequality yields the non-extinction condition (10), $\mu < ((\pi/4)x_0^2)\rho$, which implies that

$$U(t) \geq \min\left\{U(0), \frac{\ln\left(\left(\frac{\pi}{4}x_0^2\right)\rho\right) - \ln \mu}{\left(\frac{\pi}{4}x_M^2\right)f}\right\} \quad \text{for every } t \geq 0,$$

$$\text{and } \lim_{t \rightarrow \infty} U(t) \geq \frac{\ln\left(\left(\frac{\pi}{4}x_0^2\right)\rho\right) - \ln \mu}{\left(\frac{\pi}{4}x_M^2\right)f}.$$

And the second inequality in turn leads to the extinction condition (11), $\mu \geq ((\pi/4)x_M^2)\rho$, implying that $U(t) \leq U(0)$, for every $t \geq 0$, and $\lim_{t \rightarrow \infty} U(t) = 0$.

(Section 3.1.1): To obtain Eq. (12) for $B(t)$ we multiply Eq. (6) by $(\pi/4)x^2$ and integrate on $[x_0, x_M]$ with respect to x

$$\int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 u_t(\sigma, t) d\sigma + \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 (g(\sigma)u(\sigma, t))_{,\sigma} d\sigma = -\mu \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 u(\sigma, t) d\sigma,$$

$$B'(t) - \frac{\pi}{4} x_0^2 g(x_0)u(x_0, t) - \int_{x_0}^{x_M} \frac{\pi}{2} \sigma g(\sigma)u(\sigma, t) d\sigma = -\mu B(t).$$

Now using Eq. (7) we obtain

$$B'(t) - \frac{\pi}{4} x_0^2 \rho \exp(-fB(t))B(t) - \int_{x_0}^{x_M} \frac{\pi}{2} \sigma r \sigma \left(1 - \frac{\sigma}{x_M}\right) u(\sigma, t) d\sigma = -\mu B(t),$$

which yields Eq. (12)

$$B'(t) - \frac{\pi}{4} x_0^2 \rho \exp(-fB(t))B(t) - 2rB(t) + \frac{2r}{x_M} \int_{x_0}^{x_M} \sigma \frac{\pi}{4} \sigma^2 u(\sigma, t) d\sigma = -\mu B(t).$$

The next two inequalities follow

$$B'(t) \leq -\left(\mu - 2r + 2r \frac{x_0}{x_M}\right) B(t) + \frac{\pi}{4} x_0^2 \rho \exp(-fB(t))B(t), \tag{A.1}$$

$$B'(t) \geq -\mu B(t) + \frac{\pi}{4} x_0^2 \rho \exp(-fB(t))B(t), \tag{A.2}$$

and reasoning with them as done in the case of $U(t)$ we get the non-extinction condition (10), $\mu < ((\pi/4)x_0^2)\rho$, which also implies that $\lim_{t \rightarrow \infty} B(t) \geq (\ln((\pi/4)x_0^2\rho) - \ln(\mu))/f$, and the extinction condition (13), $\mu \geq ((\pi/4)x_0^2)\rho + 2r(1 - x_0/x_M)$.

To study the dependence of C on $g(x)$ we first take its definition (18)

$$C = \rho \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 \frac{1}{g(\sigma)} \exp\left(-\mu \int_{x_0}^{\sigma} \frac{d\beta}{g(\beta)}\right) d\sigma,$$

and integrating by parts we obtain

$$C = \frac{\pi\rho x_0^2}{4\mu} - \frac{\pi\rho x_M^2}{4\mu} \lim_{\sigma \rightarrow x_M} \exp\left(-\mu \int_{x_0}^{\sigma} \frac{d\beta}{g(\beta)}\right) + \frac{\pi\rho}{2\mu} \int_{x_0}^{x_M} \sigma \exp\left(-\mu \int_{x_0}^{\sigma} \frac{d\beta}{g(\beta)}\right) d\sigma,$$

Now, using the logistic growth rate $g(x) = rx(1-x/x_M)$, the expression for C takes the following form:

$$C = \frac{\pi\rho x_0^2}{4\mu} + \frac{\pi\rho}{2\mu} \int_{x_0}^{x_M} \sigma \left(\frac{x_0(x_M-\sigma)}{\sigma(x_M-x_0)}\right)^{\mu/r} d\sigma, \tag{A.3}$$

It is straightforward to see that

$$h(\sigma) = \frac{x_0(x_M-\sigma)}{\sigma(x_M-x_0)}$$

is a decreasing function with $h(x_0) = 1$ and $h(x_M) = 0$. This yields that for

$$0 < r_1 < r_2$$

we have

$$h(\sigma)^{\mu/r_1} < h(\sigma)^{\mu/r_2}, \text{ for every } \sigma \in (x_0, x_M)$$

and so that C as a function, $C(r)$, of parameter r is increasing. Moreover, it can be proved that $C(r)$ is bounded for $r > 0$. In fact

$$\begin{aligned} \lim_{r \rightarrow \infty} C(r) &= \lim_{r \rightarrow \infty} \left(\frac{\pi\rho x_0^2}{4\mu} + \frac{\pi\rho}{2\mu} \int_{x_0}^{x_M} \sigma \left(\frac{x_0(x_M-\sigma)}{\sigma(x_M-x_0)}\right)^{\mu/r} d\sigma \right) \\ &= \frac{\pi\rho x_0^2}{4\mu} + \frac{\pi\rho}{2\mu} \int_{x_0}^{x_M} \sigma d\sigma = \frac{\pi\rho x_M^2}{4\mu} = C_{\infty} \end{aligned} \tag{A.4}$$

(Section 3.2): To obtain the conditions of extinction (25) and non extinction (26) for each one of the two populations we begin writing the equation for $B_i(t)$ analogous to Eq. (12) in the case of one species but keeping a general growth rate $g_i(t)$. From Eq. (3) we get

$$B'_i(t) - \frac{\pi}{4} x_0^2 \rho_i \exp(-f_{i1} B_1(t) - f_{i2} B_2(t)) B_i(t) - \int_{x_0}^{x_M} \frac{2g_i(\sigma)}{\sigma} \frac{\pi}{4} \sigma^2 u_i(\sigma, t) d\sigma = -\mu_i B_i(t), \tag{A.5}$$

and denoting $\bar{g}_i = \max_{x \in [x_0, x_M]} 2g_i(x)/x$ we deduce the next two inequalities

$$B'_i(t) - \frac{\pi}{4} x_0^2 \rho_i \exp(-f_{i1} B_1(t) - f_{i2} B_2(t)) B_i(t) - \bar{g}_i B_i(t) \leq -\mu_i B_i(t)$$

and

$$B'_i(t) - \frac{\pi}{4} x_0^2 \rho_i \exp(-f_{i1} B_1(t) - f_{i2} B_2(t)) B_i(t) \geq -\mu_i B_i(t),$$

which assuming, for $j \neq i$, that $\bar{b}_j \leq B_j(t) \leq \bar{B}_j$ for every $t > 0$, yield, on the one hand,

$$B'_i(t) \leq -(\mu_i - \bar{g}_i) B_i(t) + \frac{\pi}{4} x_0^2 \rho_i \exp(-f_{ij} \bar{b}_j) \exp(-f_{ii} B_i(t)) B_i(t),$$

which gives the extinction condition (25): $\mu_i > \bar{g}_i + (\pi/4)x_0^2 \rho_i \exp(-f_{ij} \bar{b}_j)$, and, on the other hand

$$B'_i(t) \geq -\mu_i B_i(t) + \frac{\pi}{4} x_0^2 \rho_i \exp(-f_{ij} \bar{B}_j) \exp(-f_{ii} B_i(t)) B_i(t),$$

which gives the non extinction condition (26): $\mu_i < \frac{\pi}{4} x_0^2 \rho_i \exp(-f_{ij} \bar{B}_j)$.

(Section 3.2.1): To study the existence of stationary size distributions of systems (3)–(5), $(u_1^*(x), u_2^*(x))$, we must solve the

following initial value problem:

$$\begin{cases} (g_1(x)u_1^*(x))' = -\mu_1 u_1^*(x) & g_1(x_0)u_1^*(x_0) = R_1^* = \rho_1 \exp(-f_{11}B_1^* - f_{12}B_2^*)B_1^* \\ (g_2(x)u_2^*(x))' = -\mu_2 u_2^*(x) & g_2(x_0)u_2^*(x_0) = R_2^* = \rho_2 \exp(-f_{21}B_1^* - f_{22}B_2^*)B_2^* \end{cases}$$

where $B_i^* = \int_{x_0}^{x_M} (\pi/4)\sigma^2 u_i^*(\sigma) d\sigma$ ($i=1,2$). Integrating the system we obtain

$$\begin{cases} u_1^*(x) = \rho_1 \exp(-f_{11}B_1^* - f_{12}B_2^*) B_1^* \frac{1}{g_1(x)} \exp\left(-\mu_1 \int_{x_0}^x \frac{d\sigma}{g_1(\sigma)}\right) \\ u_2^*(x) = \rho_2 \exp(-f_{21}B_1^* - f_{22}B_2^*) B_2^* \frac{1}{g_2(x)} \exp\left(-\mu_2 \int_{x_0}^x \frac{d\sigma}{g_2(\sigma)}\right) \end{cases}$$

and multiplying both equations by $(\pi/4)x^2$ and integrating on $[x_0, x_M]$ with respect to x we get the following system for the total basal areas (B_1^*, B_2^*) of the stationary solution $(u_1^*(x), u_2^*(x))$:

$$\begin{cases} B_1^* = \rho_1 \exp(-f_{11}B_1^* - f_{12}B_2^*) B_1^* \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 \frac{1}{g_1(\sigma)} \exp\left(-\mu_1 \int_{x_0}^{\sigma} \frac{d\beta}{g_1(\beta)}\right) d\sigma \\ B_2^* = \rho_2 \exp(-f_{21}B_1^* - f_{22}B_2^*) B_2^* \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 \frac{1}{g_2(\sigma)} \exp\left(-\mu_2 \int_{x_0}^{\sigma} \frac{d\beta}{g_2(\beta)}\right) d\sigma \end{cases}$$

which denoting

$$C_i = \rho_i \int_{x_0}^{x_M} \frac{\pi}{4} \sigma^2 \frac{1}{g_i(\sigma)} \exp\left(-\mu_i \int_{x_0}^{\sigma} \frac{d\beta}{g_i(\beta)}\right) d\sigma \quad i = 1, 2, \tag{A.6}$$

gives a simple system to be hold by (B_1^*, B_2^*)

$$\begin{cases} B_1^* = \exp(-f_{11}B_1^* - f_{12}B_2^*) C_1 \\ B_2^* = \exp(-f_{21}B_1^* - f_{22}B_2^*) C_2 \end{cases}$$

This system has the solution $(0, 0)$, if $C_1 > 1$ the non-negative solution $(\ln C_1 / f_{11}, 0)$, if $C_2 > 1$ the non-negative solution $(0, \ln C_2 / f_{22})$, and a possible positive solution (B_1^*, B_2^*) verifying

$$\begin{cases} f_{11}B_1^* + f_{12}B_2^* = \ln C_1 \\ f_{21}B_1^* + f_{22}B_2^* = \ln C_2 \end{cases}$$

so that necessary and sufficient conditions for the existence of a positive stationary size distribution $(u_1^*(x), u_2^*(x))$ of systems (3)–(5) are $C_1 > 1$ and $C_2 > 1$ together with

$$\begin{cases} B_1^* = \frac{f_{22} \ln C_1 - f_{12} \ln C_2}{f_{11}f_{22} - f_{12}f_{21}} > 0 \\ B_2^* = \frac{f_{11} \ln C_2 - f_{21} \ln C_1}{f_{11}f_{22} - f_{12}f_{21}} > 0 \end{cases}$$

and the positive stationary size distribution (29) reads as follows

$$\begin{cases} u_1^*(x) = \frac{\rho_1}{C_1} \frac{f_{22} \ln C_1 - f_{12} \ln C_2}{f_{11}f_{22} - f_{12}f_{21}} \frac{1}{g_1(x)} \exp\left(-\mu_1 \int_{x_0}^x \frac{d\sigma}{g_1(\sigma)}\right) \\ u_2^*(x) = \frac{\rho_2}{C_2} \frac{f_{11} \ln C_2 - f_{21} \ln C_1}{f_{11}f_{22} - f_{12}f_{21}} \frac{1}{g_2(x)} \exp\left(-\mu_2 \int_{x_0}^x \frac{d\sigma}{g_2(\sigma)}\right) \end{cases}$$

Appendix B. Numerical method

The increase in biological realism in size-structured population models is achieved at the expense of a loss in mathematical tractability. We should point out here that, without other restrictive assumptions, these kinds of models cannot be solved analytically. Moreover, when such models include nonlinearities and environmental dependence on the different physiological rates, the use of efficient methods which provide a numerical approach is the most suitable mathematical tool for studying the problem and, indeed, it is often the only available one. It also allows us to make a complete study of its asymptotic behavior. Nevertheless, the numerical approach to these equations has important drawbacks because they are usually nonlinear equations and the nonlinearities of the PDE and the nonlocal boundary condition are caused by nonlocal terms. During the last decades different

numerical schemes have been proposed for solving size-structured models, we refer to Abia et al. (2004) and the references there in for a review and a description of numerical methods applied to solve this kind of models. Besides, numerical methods has been successfully applied to structured models to replicate available field and/or laboratory data for a variety of different systems (e.g. recently references Abia et al., 2010a, 2010b; Angulo et al., 2012, 2011a, 2011b, 2013a, 2013b).

In order to describe the schemes we present here, we begin rewriting the partial integro-differential equations in a more suitable form for their numerical treatment. So we define

$$\mu_i^*(x, t) = \mu_i(x, t) + (g_i)_x(x, t), \quad i = 1, 2,$$

thus (3) has the form

$$(u_i)_t(x, t) + g_i(x, t)(u_i)_x(x, t) = -\mu_i^*(x, t) u_i(x, t), \quad i = 1, 2, \quad (B.1)$$

$x_0 < x < x_M$, $t > 0$. Next, we denote by $x_i(t; t^*, x^*)$, $i=1,2$, the characteristic curve of equations given by (B.1) that take the value x^* at time t^* . This is the solution of the next initial value problem

$$\begin{cases} x'_i(t; t^*, x^*) = g_i(x_i(t; t^*, x^*), t), & t \geq t^*, \\ x_i(t^*; t^*, x^*) = x^*, \end{cases} \quad (B.2)$$

$i=1,2$. Note that $x_i(t; 0, x_M) = x_M$, $t \geq 0$, $i=1,2$; because we are assuming that $g_i(x_M, t) = 0$, $t > 0$, $i=1,2$. Then, we define the function

$$w_i(t; t^*, x^*) = u_i(x_i(t; t^*, x^*), t), \quad t \geq t^*, \quad i = 1, 2, \quad (B.3)$$

that satisfies the next initial value problem

$$\begin{cases} \frac{d}{dt} w_i(t; t^*, x^*) = -\mu_i^*(x_i(t; t^*, x^*), t) w_i(t; t^*, x^*), & t \geq t^*, \\ w_i(t^*; t^*, x^*) = u_i(x^*, t^*), \end{cases} \quad (B.4)$$

$i=1,2$; and therefore, it can be represented with the next formula

$$w_i(t; t^*, x^*) = u_i(x^*, t^*) \exp \left\{ - \int_{t^*}^t \mu_i^*(x_i(\tau; t^*, x^*), \tau) d\tau \right\}, \quad i = 1, 2. \quad (B.5)$$

We suppose that $u_i(x_M, 0) = 0$ and then $u_i(x_M, t) = 0$, $t \geq 0$, $i=1,2$. We shall use this property in our numerical methods, however, they can be easily modified to cover other cases.

Now, we present the numerical scheme we employ for the solution of the two species model. Note that it includes the difficulty of considering two different grids which are computed independently of each other. Therefore, in each level of time we will have to calculate two different grids. The numerical method integrates the model along the characteristic curves, it uses an open composite quadrature rule to approximate the nonlocal term and keeps constant the number of nodes, in both grids, by means of a selection of them at each time level.

Let J and N be positive integers, we define the spatial and time discretization parameters as $h = x_M - x_0 / J$ and $k = T / N$, respectively. The discrete time levels are $t_n = n k$, $0 \leq n \leq N$, and the initial grid nodes are ${}^i X_j^0 = j h$, $0 \leq j \leq J$, $i=1,2$. We suppose that the approximations to the theoretical solution in such nodes are known, ${}^i U_j^0$, $0 \leq j \leq J$, $i=1,2$. Thus, we denote

$${}^i \mathbf{X}^0 = \{ \{ {}^i X_0^0 = x_0, {}^i X_1^0, \dots, {}^i X_{J-1}^0, {}^i X_J^0 = x_M \} \},$$

$${}^i \mathbf{U}^0 = \{ \{ {}^i U_0^0, {}^i U_1^0, \dots, {}^i U_{J-1}^0, {}^i U_J^0 = 0 \} \},$$

$i=1,2$. Note that with ${}^i U_J^n$, we consider a numerical approximation to $u({}^i X_J^n, t_n)$, and ${}^i X_j^n$ is the grid corresponding to the species i , $0 \leq j \leq J$, $0 \leq n \leq N$, $i=1,2$.

First, we define the grid nodes at the time level t_1 , by the numerical integration of (B.2) as follows:

$${}^i X_0^1 = x_0; \quad {}^i X_{j+1}^1 = {}^i X_j^0 + k g_i \left({}^i X_{j+1}^{1/2}, t_0 + \frac{k}{2} \right),$$

$$0 \leq j \leq J-1; \quad {}^i X_{j+1}^1 = x_M; \quad i = 1, 2, \quad (B.6)$$

where

$${}^i X_0^{1/2} = x_0; \quad {}^i X_{j+1}^{1/2} = {}^i X_j^0 + \frac{k}{2} g_i({}^i X_j^0, t_0),$$

$$0 \leq j \leq J-1; \quad {}^i X_{j+1}^{1/2} = x_M; \quad i = 1, 2.$$

Now, we calculate the corresponding approximations to the theoretical solution by means of the following discretization of (B.5)

$${}^i U_{j+1}^1 = {}^i U_j^0 \exp \left(-k \mu_i^* \left({}^i X_{j+1}^{1/2}, t_0 + \frac{k}{2} \right) \right),$$

$$0 \leq j \leq J-1; \quad {}^i U_{j+1}^1 = 0; \quad i = 1, 2, \quad (B.7)$$

where

$${}^i U_{ij+1}^{1/2} = {}^i U_j^0 \exp \left(-\frac{k}{2} \mu_i^* \left({}^i X_j^0, t_0 \right) \right),$$

$$0 \leq j \leq J-1; \quad {}^i U_{j+1}^{1/2} = 0; \quad i = 1, 2.$$

In addition, we derive the approximation ${}^i U_0^1$ to $u_i(x_0, t_1)$, $i=1,2$, from a discrete version of the boundary condition (5)

$$\frac{{}^i U_0^1 = R(t_1) + Q({}^i \mathbf{X}^1, {}^i \alpha({}^i \mathbf{X}^1, {}^i \mathbf{U}^1) {}^i \mathbf{U}^1)}{g_i(x_0, t_1)}, \quad (B.8)$$

where ${}^i \alpha_j({}^i \mathbf{X}^1, {}^i \mathbf{U}^1) = \alpha_i({}^i X_j^1, Q({}^i \mathbf{X}^1, \gamma({}^i \mathbf{X}^1) {}^i \mathbf{U}^1))$, $0 \leq j \leq J+1$, $i=1,2$,

$$Q(\mathbf{Y}, \mathbf{V}) = (Y_1 - Y_0) V_1 + \sum_{j=1}^J \frac{Y_{j+1} - Y_j}{2} (V_j + V_{j+1}), \quad \mathbf{Y}, \mathbf{V} \in \mathbb{R}^{J+2}, \quad (B.9)$$

and $\gamma_j({}^i \mathbf{X}^1) = \pi/4({}^i X_j^1)^2$, $0 \leq j \leq J+1$, $i=1,2$. In (B.8) and henceforth, we denote the componentwise product of the pair of vectors $\alpha({}^i \mathbf{X}^1, {}^i \mathbf{U}^1)$ and ${}^i \mathbf{U}^1$ and $\gamma({}^i \mathbf{X}^1)$ and ${}^i \mathbf{U}^1$ by $\alpha({}^i \mathbf{X}^1, {}^i \mathbf{U}^1) {}^i \mathbf{U}^1$ and $\gamma({}^i \mathbf{X}^1) {}^i \mathbf{U}^1$, respectively, $i=1,2$.

Now, we have $J+2$ nodes at the time level t_1 and we want to keep constant the number of nodes, therefore we select one characteristic curve and we do not compute the approximations at such curve. Then, we eliminate the first grid node ${}^i X_0^1$ that satisfies

$$|{}^i X_{l+1}^1 - {}^i X_{l-1}^1| = \min_{1 \leq j \leq J} |{}^i X_{j+1}^1 - {}^i X_{j-1}^1|, \quad i = 1, 2. \quad (B.10)$$

Note that these values could be different because the growth rate functions of both populations are different, this reason is enough for considering different grids, one for each population. We point out that all the equations in our scheme are completely explicit.

Next, we describe the general time step t_{n+1} , $0 \leq n \leq N-1$. Now, we suppose that the numerical approximations at the previous time level t_n are known

$$\{ {}^i X_0^n = x_0, {}^i X_1^n, \dots, {}^i X_{J-1}^n, {}^i X_J^n = x_M \}, \quad \{ {}^i U_0^n, {}^i U_1^n, \dots, {}^i U_{J-1}^n, {}^i U_J^n = 0 \},$$

$i=1,2$. We recall that ${}^i X_j^n$ and ${}^i X_{j+1}^{n+1}$, $0 \leq j \leq J-1$, $i=1,2$, are (numerically) in the same characteristic curve. First, we compute the grid values at the time level t_{n+1} by means of the numerical integration of (B.2)

$${}^i X_0^{n+1} = x_0; \quad {}^i X_{j+1}^{n+1} = {}^i X_j^n + k g_i \left({}^i X_{j+1}^{n+1/2}, t_n + \frac{k}{2} \right), \quad 0 \leq j \leq J-1; \quad {}^i X_{j+1}^{n+1} = x_M; \quad (B.11)$$

$i=1,2$, and the approximations to the theoretical solution in these nodes at such time level using the discretization of (B.5)

$${}^i U_{j+1}^{n+1} = {}^i U_j^n \exp \left(-k \mu_i^* \left({}^i X_{j+1}^{n+1/2}, t_n + \frac{k}{2} \right) \right),$$

$$0 \leq j \leq J-1; \quad {}^i U_{j+1}^{n+1} = 0; \quad i = 1, 2. \quad (B.12)$$

We complete the equations at the time level t_{n+1} with the approximation ${}^iU_0^{n+1}$ to $u_i(x_0, t_{n+1})$, $i=1,2$, using a discretization of the boundary condition (4)

$$\frac{{}^iU_0^{n+1} = R(t_{n+1}) + Q({}^i\mathbf{X}^{n+1}, {}^i\alpha({}^i\mathbf{X}^{n+1}, {}^iU^{n+1}))}{{}^iU_0^{n+1} = R(t_{n+1}) + Q({}^i\mathbf{X}^{n+1}, {}^i\alpha({}^i\mathbf{X}^{n+1}, {}^iU^{n+1}))} \quad (B.13)$$

where

$$\begin{aligned} {}^iX_0^{n+1/2} &= x_0; \quad {}^iX_{j+1}^{n+1/2} = {}^iX_j^n \\ &+ \frac{k}{2} g_i({}^iX_j^n, t_n), \quad 0 \leq j \leq J-1; \quad {}^iX_{J+1}^{n+1/2} = x_M; \\ {}^iU_{j+1}^{n+1/2} &= {}^iU_j^n \exp\left(-\frac{k}{2} \mu_i^*({}^iX_j^n, t_n)\right), \quad 0 \leq j \leq J-1; \quad {}^iU_{J+1}^{n+1/2} = 0; \end{aligned}$$

$i=1,2$, where ${}^i\alpha_j({}^i\mathbf{X}^{n+1}, {}^iU^{n+1}) = \alpha_i({}^iX_j^{n+1}, Q({}^i\mathbf{X}^{n+1}, \gamma({}^i\mathbf{X}^{n+1}) {}^iU^{n+1}))$, $0 \leq j \leq J+1$, $i=1,2$, Q is defined in (B.9), and $\gamma_j({}^i\mathbf{X}^{n+1}) = \frac{\pi}{4} ({}^iX_j^{n+1})^2$, $0 \leq j \leq J+1$, $i=1,2$.

Now, we have $J+2$ nodes at the time level t_{n+1} and we want to keep constant the number of nodes therefore we select one characteristic curve and we do not compute the approximations at such curve. Then, we eliminate the first grid node ${}^iX_{l_i}^{n+1}$ that satisfies

$$|{}^iX_{l_i+1}^{n+1} - {}^iX_{l_i-1}^{n+1}| = \min_{1 \leq j \leq J} |{}^iX_{j+1}^{n+1} - {}^iX_{j-1}^{n+1}|, \quad (B.14)$$

and the corresponding value in the vector ${}^iU^{n+1}$, $i=1,2$. We again point out that our scheme is completely explicit. We also have to note that, in this case, the problems (B.2) and B.5) are not coupled as in Angulo and López-Marcos (2004); Zavala et al. (2007) and the grid could be performed first and defined at every time step by means of Eqs. (B.6) and B.11) and the selection procedures (B.(10) and B.14). However, when we compute the approximations to the solution with (B.7), B.8), (B.12) and (B.13), we need to know the nodes to employ and, therefore, to manage a necessary control of the eliminated nodes.

The numerical experiments presented in Section 4 have been developed with small enough parameter values ($h=0.03125$ and $k=0.15625$) and for initial conditions with compact support in the interval defined by $[x_0, x_M]$, what ensures the compatibility between initial and boundary conditions. This is done to preserve the good behavior of the numerical scheme.

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