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Co-dominance and succession in forest dynamics: The role of interspecific differences in crown transmissivity

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ABSTRACT

Forests that are composed of two or more tree species with similar ecological strategies appear to contradict the competitive exclusion principle. Beech–maple communities are a well-known example of such a system. On a local scale, a number of mechanisms have been proposed to explain the coexistence of these two species. These are reciprocal replacement, external factors that favour alternatively one or the other species and demographic stochasticity. This paper presents and analyses a simple mathematical model that shows that external factors are not an essential requirement for coexistence. Rather, coexistence requires interspecific differences in light transmissivity through the crowns of adult trees. However, all the three mechanisms mentioned above can be interpreted within the framework of the model. Furthermore, many models of forest dynamics make use of shade tolerance as a key feature in describing successional dynamics. Despite its importance, however, shade tolerance does not have a commonly accepted quantitative definition. Here, a simple scheme is proposed where the relationship between shade tolerance, individual traits (growth and survival) and successional status is defined. This might have important implications in understanding the overall dynamics. Theoretical results have been compared with a number of studies carried out in North American forests. In particular, coexistence in beech–maple communities and the relation between shade tolerance and successional status in a beech–hemlock–birch community have been discussed.

1. Introduction

Many temperate and boreal forests appear to be in a situation in which a few, and often only two, species with a similar strategy permanently dominate a habitat (Fox, 1977). In forest dynamics it is important to distinguish between two types of coexistence which, in this paper, I call vertically structured coexistence (adult trees of some species are commonly shaded by taller species) and coexistence of co-dominant species (all adult trees need to be exposed to full light). If, as in the study of Fox (1977), the tree species are co-dominant and adult trees cannot be dislodged by competing juveniles, the competition for space should be strong enough to prevent coexistence (Whittaker and Levin, 1977; Klausmeier and Tilman, 2002).

A typical and well-studied case is the co-dominance between American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) which is a widespread phenomenon in the north-east of the United States. Although evidence supports the coexistence of these two species (e.g. Poulson and Platt, 1996), it is not completely clear which mechanisms generate this coexistence. A number of studies support the hypothesis of an autogenic form of coexistence based on reciprocal replacement (Fox, 1977; Woods, 1979; Chyper and Boucher, 1982). Other studies suggest that this coexistence is the result of a trade-off between growth in high light and survival in low light, whereby possible external fluctuations in the frequency of formation of canopy gaps favour alternatively one or the other species (allogenic coexistence) (Canham, 1988a; Poulson and Platt, 1996). Meanwhile, other studies seem to deny the two preceding hypotheses by indicating the significant role of demographic stochasticity (Gravel et al., 2008).

Both beech and maple are highly shade tolerant species and are specialized in exploiting gaps. However, relatively recently some differences have been quantified regarding both the capacity of the two species to exploit resources (maple being more able to do so in the gaps, while beech under cover Canham, 1988a, 1990; Poulson and Platt, 1996), and the light transmissivity during the adult stage (beech being the species with the least transmissivity Canham et al., 1994). Understanding the role of these strategies in explaining coexistence of tree species is important both for the design of field experiments and the analysis of complex models.

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Many theoretical models have been developed to describe competition among tree species (Kohyama, 1992, 1993; Zavala et al., 2007; Strigul et al., 2008). However, in general they are difficult to analyse mathematically. Moreover, they do not clearly distinguish between vertically structured competition and competition between co-dominant species. This differentiation, however, is important since in the latter case competition for space is a stronger obstacle to coexistence.

Vertically structured coexistence has been considered explicitly in Kohyama and Takada (2009). The main objective of this paper is to understand if and how interspecific differences in light transmissivity of adult trees and/or in competitive ability of juveniles trees are useful for explaining coexistence of co-dominant species. For this purpose I have developed and analysed a simple mathematical model which provides an analytical basis for studying the competition of two or more co-dominant tree species. This model can be viewed as an extension of Lotka–Volterra's classic model of competition in which a two-level stage structure and an implicit spatial structure (Klausmeier and Tilman, 2002) are considered. The principal result of this analysis is that interspecific difference in light transmissivity of the adult trees rather than a trade-off between strategies is the key for the maintenance of coexistence.

A second objective of this study is to investigate the relationship between shade tolerance (the capacity of a given plant to tolerate low levels of light) and successional status (the stage of succession – early, middle or late – at which a species finds relative dominance). Despite their simplicity, the relationship between these concepts hides some subtleties. For example, a well-known axiom in forestry states that species that are progressively more shade tolerant become dominant as succession proceeds towards climax. Unfortunately, the measurement of tolerance that foresters often use includes information about the stage of succession at which the species in question is characteristically most abundant. Thus, when the axiom is examined critically, it is found to be either circular or unsupported, even though it is intuitively reasonable (Horn, 1971). Although many studies addressed the role of individual traits in driving forest succession (e.g. Huston and Smith, 1987), I am not aware of an investigation of possible differences between shade tolerance and successional status, at least from the perspective of a mathematical model. However, this differentiation might have important implications in understanding the overall stand dynamics. An analysis of the present model allowed such an investigation. The result is that shade tolerance should be considered just as a component of successional status.

In Section 2 the model is defined and analysed, then theoretical results are compared with observed patterns in Section 3.

2. The model

2.1. Assumptions and derivation

Forest dynamics is, in principle, governed by different mechanisms, the relative importance of which strongly varies according to the type of forest and the environmental context. In this article the intention is to define a model that captures some of the basic mechanisms in the dynamics of temperate forests in general. According to the concept of gap dynamics, as described by Canham (1989), and the "inhibition model" of succession, as proposed by Connell and Slatyer (1977), the model describes the dynamics of different co-dominant tree species in which adult trees occupy the space and limit the resources in the understory, thus inhibiting the growth of juvenile trees. When an adult tree dies leaving space and resources, it triggers a sort of "race" which ends when a juvenile tree reaches the canopy and closes the gap that had been created. It is important to note that in this model the tolerance of the juvenile trees indicates the capacity to withstand long periods of suppression rather than the capacity to grow with few resources (Connell and Slatyer, 1977).

The main assumptions are (i) that the abiotic environment where the tree species live is spatially and temporally homogeneous (Fox, 1977), I call this environment *patch*; (ii) that the vertical structure consists in two levels: *overstory* (adult trees that make up the canopy) and *understory* (juvenile trees of any size that live under the canopy); (iii) that the number of adult trees is limited by space availability (Yodzis, 1978) while the number of juveniles is limited by understory light availability (Pacala et al., 1994); (iv) that the light available to a given juvenile tree depends on the overall canopy composition rather than on the adult tree directly overhead (Poulson and Platt, 1996); (v) that juveniles become adults only if space (i.e. gaps) is available (Canham, 1989); (vi) that only adult trees can reproduce (Harper, 1977).

In mathematical terms the assumptions above are described by the following systems of $2n$ differential equations ($i=1,\ldots,n$):

$$\frac{dP_i}{dt} = g_i'\left(S-\sum_{j=1}^{n} s_j P_j\right)p_i - m_i P_i, \tag{1a}$$

$$\frac{dp_i}{dt} = c_i P_i - g_i'\left(S-\sum_{j=1}^{n} s_j P_j\right)p_i - f_i'(\mathbf{P})p_i, \tag{1b}$$

where the index i represents the species, P_i and p_i are the number of adult and juvenile trees, S (m^2) is the area of the patch, s_i (m^2) is the mean surface of the crown of an adult tree, g_i' ($\mathrm{t}^{-1}\ \mathrm{m}^{-2}$) is the rate at which a juvenile tree becomes an adult per unit of available space, m_i (t^{-1}) is the mortality rate for an adult tree, c_i (t^{-1}) is the reproduction rate for an adult tree supplemented by an establishment probability and $f_i'(\mathbf{P})$ (t^{-1}) is the mortality rate for a juvenile tree (I use the notation $\mathbf{P}=\{P_i\}$).

Let $k_i = S/s_i$ ($\mathrm{m}^2/\mathrm{m}^2$) be the maximum number of adult trees of species i that can live in the patch. It is useful to rescale the number of both adult and juvenile trees with regard to k_i by setting: $X_i = P_i/k_i$ and $x_i = p_i/k_i$. From here on, the quantities X_i and x_i will be called *adult relative frequency* and *juvenile relative frequency*, respectively. It is worth bearing in mind that while $X_1+X_2+\cdots+X_n=1$ indicates that adults occupy the whole patch, the juvenile relative frequencies can be greater than one. Therefore, by setting $g_i = S\cdot g_i'$ and $f_i(\mathbf{X}) = f_i'(\mathbf{P})$, system (1) can be rewritten as ($i=1,\ldots,n$):

$$\frac{dX_i}{dt} = g_i\left(1-\sum_{j=1}^{n} X_j\right)x_i - m_i X_i, \tag{2a}$$

$$\frac{dx_i}{dt} = c_i X_i - g_i\left(1-\sum_{j=1}^{n} X_j\right)x_i - f_i(\mathbf{X})x_i, \tag{2b}$$

where the parameters c_i, g_i and m_i are positive numbers. Here, the constant adult mortality reflects the fact that, as adult trees are all of similar height, they experience little interference in the acquisition of light. Conversely, juvenile mortality depends on understory light availability, therefore it is affected by adult density. For simplicity, it is assumed that the interference among juvenile trees in the acquisition of light is negligible (Wright, 2002).

A simple model for juvenile mortality can be obtained as follows: according to the assumption at point (iv), I define the understory light availability (or briefly, low light) as $L(\mathbf{X}) = 1-\sum \sigma_j X_j$ where the σ_j's are a measure crown opacity, $L=1$ means full light and $0<\sigma_j<1$. Such a mean field approximation makes sense if canopy trees are well mixed in the patch and the