Università degli Studi della Tuscia di Viterbo
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Dipartimento di
Scienze dell'Ambiente Forestale e delle sue Risorse
(DISAFRI)

Corso di Dottorato di Ricerca in
ECOLOGIA FORESTALE – XXII Ciclo

Co-dominance and Succession in Temperate Forests: a Mathematical Approach

settore scientifico disciplinare BIO/07

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Acknowledgements

The work for this thesis has been funded by the European project CIRCE: *Climate Change and Impact Research: the Mediterranean Environment* (contract num. 036961). I would like to thank my supervisor Professor Giuseppe Scarascia Mugnozza and Dr. Giorgio Matteucci for giving me the opportunity to carry out this research at the Istituto di Biologia AgroAmbientale e Forestale (IBAF) in Rome. At IBAF, I also thank my colleagues and friends for having contributed to a nice and collaborative environment. I would also like to thank Prof. Antonello Provenzale and Dr. Mara Baudena at the Institute ISAC of Torino for stimulating discussions and valuable advices. I thank Dr. Heike Lischke at WSL in Zurich for her nice hospitality and interesting discussion about forest modelling. I thank my mother, brother and friends for their support. This thesis would have been tortuous and illegible without the invaluable help and support of Dr. Ana Rey.

Roma, 7 February 2010

Abstract

Forest vegetation covers about one-third of the Earth's land surface. At the population level, forests have been widely studied through complex simulators that successfully reproduce observed patterns of long-term successions. At ecosystem level, while it is well-known that terrestrial ecosystems have potentially large effects on global climate, it is clear that uncertainties in model predictions are large as well. Such uncertainties could be reduced by incorporating in large scale models the ecological realities of biodiversity and competition for light. As vegetation simulators are too complex to run at large scale, this requires a simpler description of vegetation dynamics. Moreover, several basic mechanisms of forest dynamics, such as the co-dominance of tolerant trees competing for light, are still a matter of debate in ecological literature.

The aim of this thesis is to contribute both to an improvement of our current understanding of basic aspects of forest dynamics and to provide a simple description of their mechanisms. Investigated mechanisms include co-dominance of tolerant tree species competing for light, coexistence in a patchy habitat and the relationship between shade tolerance and successional status. For this purpose I developed a simple mechanistic model that describes competition for light in temperate forests. The model is based on a two-level stage structure. Interspecific interactions between the stage levels are key features of the model. I qualitatively compared the model with several studies of forest ecosystem in North America. These comparisons supported model predictions. Furthermore, the model provided simple interpretations for observed patterns.

List of symbols

k_i	Maximum number of adult trees of species i that can live in the habitat [m^2/m^2]
X_i	Number of adult trees of species i normalised to k_i [m^2/m^2]
x_i	Number of juvenile trees of species i normalised to k_i [m^2/m^2]
c_i	Per capita birth rate of species i [t^{-1}]
m_i	Per capita adult mortality rate of species i [t^{-1}]
g_i	Rate at which a juvenile tree of species i becomes an adult [t^{-1}]
n_i	Per capita juvenile mortality of species i in full light [t^{-1}]
α_{ij}	Interspecific effect of an adult of species j on juvenile mortality of species i [t^{-1}]
β_i	Per capita population growth rate at low densities for species i [t^{-1}]
γ_{ij}	Per capita juvenile mortality of species i under a pure canopy of species j [t^{-1}]
$1/\gamma_i$	A measure of low-light survival for species i [t]
$1/\gamma_i^*$	A measure of survival under equilibrium canopy composition for species i [t]

Contents

Chapter 1

Introduction

The present thesis deals with mathematical models of forest dynamics. This chapter is devoted to a short introduction on concepts and ideas about forest modelling for temperate forests.

1.1 An overview on vegetation models

A vegetation model is a conceptual scheme based on stated relationships between the "actors" (e.g., plant species, nutrients, physical quantities) of the system that has to be modelled. Generally, the goal of a model is either to understand observed patterns or to predict system's behaviours.

The outcomes of vegetation models range from the leaf scale (e.g., photosynthesis, gas exchange) to the planetary scale (e.g., plant distribution along climatic gradients, feedback with climate).

In all cases, the building of a model, follows the general Occam's razor principle.[1] In few words, this principle states that the simplest explanation

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[1] The principle is attributed to 14th-century English logician, theologian and Franciscan friar, William of Ockham.

or strategy tends to be the best one. A consequence of this philosophy is that, the scale of the system under study is the main driver for the level of detail required by the model. Factors that affect processes operate across different spatial and temporal scale, with different processes being more important at different scale (figure 1.1). This leads to a profound diversification of models.

<table>
<tr><th></th><th>Global</th><th>Continental</th><th>Regional</th><th>Landscape</th><th>Local</th><th>Site</th><th>Micro</th></tr>
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<tr><td>Biotic interaction</td><td></td><td></td><td></td><td></td><td colspan="3">yes</td></tr>
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Table 1.1: *Schematic example of how different factors may affect the distribution of species across varying scales. Characteristic scale domains are expressed in km (from Pearson and Dawson, 2003).*

Recent years have seen a growing interest toward large-scale vegetation models. Recognising the importance of land ecosystems in the global carbon cycle, the Kyoto Protocol to United Nations Framework Convention on Climate Change (1997) recommends the protection, enhancement and quantification of terrestrial biospheric sinks for anthropogenic CO_2 emissions (United Nations Framework Convention on Climate Change, 1997). Large-scale terrestrial ecosystems are a critical component of the global carbon cycle. Then, we require a better understanding of their decadal to century-scale carbon balance dynamics (Cramer et al., 2001, and references therein).

In turn, this requires an understanding of the relationships between plant distribution and climate. For this purpose, a number of modelling strategies have been developed. These often focus on the identification of a species' *bioclimate envelope* either through statistical techniques that correlate current species distribution with climate variables (e.g., Pearson and Dawson, 2003; Thuiller, 2003) or through an understanding of species physiological responses to climate (e.g., Woodward, 1987). Having identified a species' climate envelope, the applications of scenarios of future climate enables the potential redistribution of species' climate space to be estimated (Pearson and Dawson, 2003).

Recent studies have questioned the validity of the bioclimate envelope approach by pointing to the many factors other than climate – mainly biotic interactions such as competition – that play an important part in determining species distributions and their dynamics over time (Davis et al., 1998).

Such factors are often dealt with by another class of computer models. In the case of forests, this models are known as *gap* (or patch) *models* (see a review in Bugmann, 2001). But because these models are individual-based, they cannot describe the large-scale dynamics. This would require simulating every tree on the region under study, which would be immensely computationally demanding.

A current challenge is to understand how climate change, as well as natural disturbances, affect vegetation dynamics and ecosystem processes. One of the high priority activities of the International Geosphere-Biosphere Programme (IGBP) – the core project of the Global Change and Terrestrial Ecosystems (GCTE) – is to develop a new class of dynamic biogeography models, known as DGVMs[2] (Steffen et al., 1992, 1996). The primary framework for a DGVM was outlined by Prentice and GVDM Members (1989) over two decades ago. Based on a linkage between an equilibrium global vegetation model and smaller scale ecosystem dynamics modules, Steffen et al. (1996) proposed the structure of a first generation DGVM that simulates

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[2] Dynamic Global Vegetation Models

transient changes in vegetation distribution over a decade time scale. Potential approaches for DGVM development are summarised in figure 1.1 (Peng, 2000).

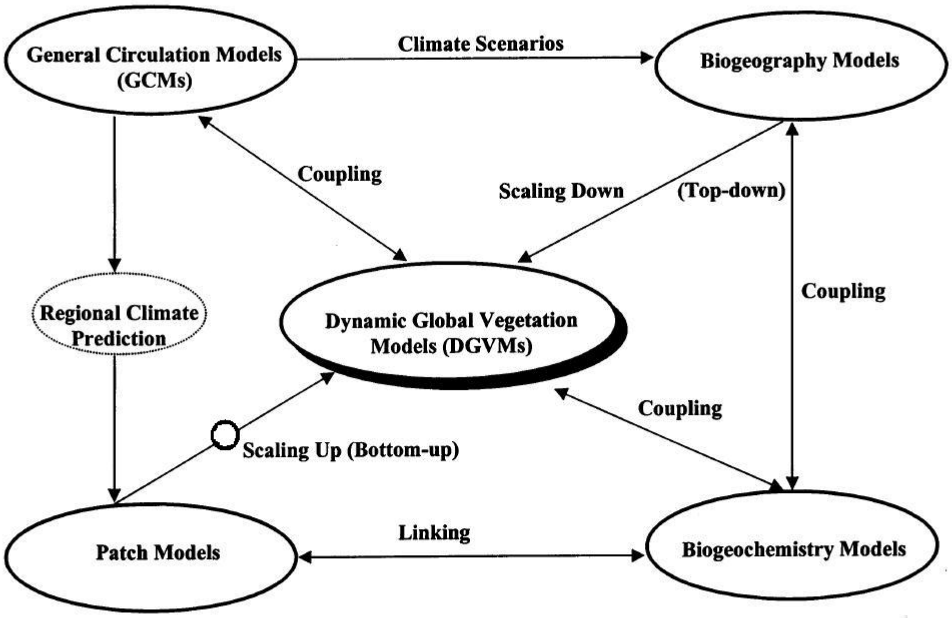


Figure 1.1: *Schematic representation of the potential approaches of the Dynamics Global Vegetation Models (DGVMs) coupling with global circulation, biogeochemistry, biogeography, and patch models (from Peng, 2000).*

However, because DGVMs were developed recently with limited information, their predictions are currently highly uncertain (figure 1.2), making vegetation dynamics one of the largest sources of uncertainty in Earth system models. Reducing this uncertainty requires work on several fronts. For example, physiological parameters need to be better constrained with data, and we need better models of disturbances, including fire and land-use change. But more fundamental improvements could be achieved by incorporating the ecological realities of biodiversity and competition for light. A recent explo-

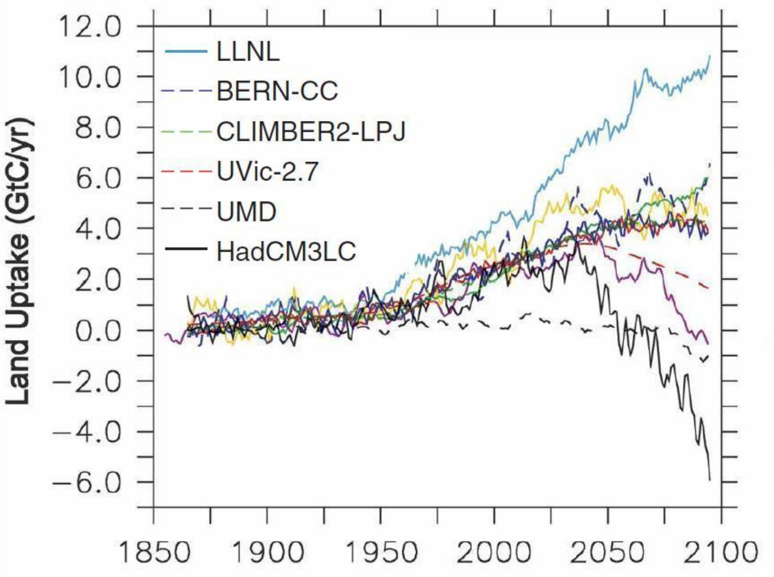


Figure 1.2: *DGVMs have shown that the terrestrial biosphere could be crucial in determining the future of Earth's climate. But this figure shows how divergent the predictions of DGVMs currently are. For comparison, current anthropogenic CO2 emissions are 7.6 pm 0.6 Gt of carbon/year. True DGVMs, with a responsive global distribution of PFTs (Plant Functional Types), are labeled. The remainder have a dynamic carbon cycle but a fixed distribution of PFTs. Some of the variation in the figure results from different climate models, but a large spread was also seen when different DGVMs were run uncoupled from global climate models under a common, fixed climate trajectory (Cramer et al., 2001). LLNL, Lawrence Livermore National Laboratory climatemodel; BERN-CC, Bern carbon-cycle climate model; CLIMBER2-LPJ, Climate-Biosphere model, coupled to the Lund-Potsdam-Jena DGVM; UVic-2.7, University of Victoria Earth system climate model, version 2.7; UMD, University of Maryland coupled carbonclimate model; HadCM3LC, Hadley Centre coupled climate-carbon cycle model (from Purves and Pacala, 2008; Friedlingstein et al., 1996).*

sion in forest inventory data might make this possible (Purves and Pacala, 2008).

DGVMs could be substantially improved by basing them on the height-structured individual-based models (IBMs) (e.g., Pacala et al., 1993). However, as I said before, IBMs are too complex to run at large scale. A more efficient approach would be to derive suitable mathematical equations to scale correctly from parameters governing individual trees to the dynamics of forested region (Kohyama et al., 2001; Hurtt et al., 1998; Moorcroft et al., 2001; Kohyama, 2005). This step in DGVMs development is depicted by the arrow marked with a circle in figure 1.1.

1.2 Models on forest dynamics

An understanding of interactions at the population level (e.g., competition) is of importance not only as a part of global vegetation models. The description, understanding and prediction of the long-term dynamics of forest ecosystems has fascinated ecologists for a long time (e.g., Watt, 1947) and nowadays, models of forest dynamics are perhaps the most widely studied class of models in the ecological literature (Pacala et al., 1993). The vast majority of forest models are derived from the computer model JABOWA (Botkin et al., 1972). They are termed gap or patch models.

The developers of JABOWA made a number of keys that allowed them to formalise tree growth, tree establishment, and tree mortality in a relatively simple fashion (figure 1.3):

1. The forest stand is abstracted as a composite of many small patches of land, where each can have a different age and successional stage. The size of the patch is chosen so that a large individual organism can

dominate the entire patch; in the case of trees, patch size thus is on the order of $100 - 1000$ m^2.

2. Patches are horizontally homogeneous, i.e., tree position within a patch is not considered. A consequence of this assumption is that all tree crowns extend horizontally across the entire patch.

3. The leaves of each tree are located in an indefinitely thin layer (disk) at the top of the stem.

4. Successional processes can be described on each of those patches separately, i.e., there are no interactions between patches, and the forest is a mosaic of independent patches.

Additional basic features of JABOWA include the following: (5) the establishment, growth, and mortality of each individual tree is considered, i.e., the entity being modelled is the individual; (6) the model considers the tree composition and size structure of the forest, but it does not deal with forest functions such as biogeochemical cycling of carbon and nitrogen, or the flows of water through the ecosystem; and (7) the competition between trees and other life forms such as shrubs, herbs, or grasses is ignored (Bugmann, 2001).

A wide variety of formulations for growth processes, establishment, and mortality factors have been developed in gap models over the past 30 years, and modern gap models include more robust parameterizations of environmental influences on tree growth and population dynamics as compared to JABOWA. In particular, in the SORTIE model (Pacala et al., 1993), which emphasises light competition as the major driver of forest succession, much larger tracts of land are considered, and within this area the position of each tree is kept track of to allow for the accurate calculation of light conditions. Whereas the SORTIE approach certainly is more realistic and accurate than

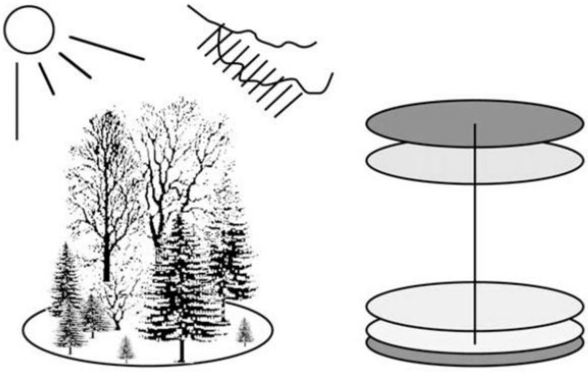


Figure 1.3: *The concept of forest gap models (from Bugmann, 2001).*

the original abstractions used in the other gap models, it comes at great cost in terms of parameterization efforts as well as computation time (Bugmann, 2001).

This kind of computer models often make use of a high number of parameters and they can provide detailed forecasts. However, an understanding of the outcomes of a computer model requires a comparison between a high number of simulations with varying parameters. The higher the number of parameters the higher the time required for a comprehensive analysis of the model.

A different approach to understand population dynamics is based on tractable mathematical models. Often, the outcome of a mathematical model is an equation which states the range of parameter values under which a phenomenon (e.g., coexistence) occurs. The analysis of such equation provides a direct explanation of the phenomenon. In order to be tractable, mathematical models need to be simple (few parameters). Then, while they are useful explanatory models (Pielou, 1977), they are often less suitable than computer models for detailed forecasts.

Mathematical models on population dynamics are the core of this thesis and they will be discussed extensively in the next chapters. They mostly deal with coexistence.

1.3 Coexistence

How large numbers of competing plant species manage to coexist is a major unresolved question in community ecology (Silvertown, 2004). Doubts about coexistence have been raised by the *competitive exclusion principle*. Roughly, it states that if two species are too similar (e.g., they feed on the same resource), they cannot coexist (Hardin, 1960). This principle is based on theory (see the third chapter) and has been tested only in laboratory experiments (e.g., Tilman and Wedin, 1991, for the case of grasses). However, ecologists are confronted with many examples of different species living together and apparently sharing the same resources. Thus, they included in their model a lot of different ideas and hypotheses to explain coexistence (reviewed in DeAngelis and Waterhouse, 1987; Chesson, 2000; Silvertown, 2004).

Hypothesised mechanisms include (among others): functional interactions between species (Vance, 1984), trade-off between strategies (Shmida and Ellner, 1984; Tilman, 1994), the effect of spatial extent (Yodzis, 1978), disturbance patterns (Huston, 1979), the effect of integrating small-scale systems into large landscapes (Levins, 1969; Taneyhill, 2000), differential responses to spatial and temporal variability of the environment (Pacala and Tilman, 1994), the effect of an open habitat with immigration (Shmida and Ellner, 1984) and facilitation (Bruno et al., 2003). According to the high complexity of this topic, it does not exist a general theory of coexistence, rather there are different approaches depending on the characteristics of the system under study (e.g. scale, the type of resources, etc...).

In particular, in the case of forest models, the effect of fluctuations in environmental conditions have been considered by Kelly and Bowler (2002) and much attention has been devoted to the role of size structure in the competition for light (Kohyama, 1992, 1993; Strigul et al., 2008; Adams et al., 2007). These size-structured models show that coexistence is possible even in the case of many tree species competing for light. But, generally, they cannot be completely solved and this complicates the analysis of mechanisms behind coexistence.

Despite the efforts outlined above, there is still debate on mechanisms behind coexistence, specially in the co-dominance of highly shade tolerant trees (e.g., Gravel et al., 2008). In many forest communities of North America external disturbances such as windstorms and fires, probably account for a small minority of tree-for-tree replacements over any long period of time. Moreover, gradients in the physical environment often can be neglected (Fox, 1977). In these cases neither external disturbances nor environmental heterogeneity should be used to explain coexistence.

A well-known example is the case of beech-maple communities (Forcier, 1975; Fox, 1977; Woods, 1979; Chyper and Boucher, 1982; Canham, 1989, 1990; Poulson and Platt, 1996; Gravel et al., 2008). From the studies that I have considered, three different hypotheses to explain coexistence emerge.

The studies of Fox (1977), Woods (1979) and Chyper and Boucher (1982) support the idea of coexistence based on reciprocal replacement. In contrast, other studies (Forcier, 1975; Canham, 1989, 1990; Poulson and Platt, 1996) support the idea of coexistence based both on a trade-off between strategies and on external fluctuations. Finally, the study of Gravel et al. (2008) points out that the high level of similarity between species in terms of their response under the relatively limited range of conditions that are typically encountered in a single stand, precludes a deterministic interpretation of coexistence, at least at a local scale (Gravel et al., 2008).

1.4 Shade tolerance and successional status

Forest dynamics cannot be understood without a clear vision of three closely related concepts: *shade tolerance*, *gap dynamics* and *successional status*. They are general concepts used in a wide range of circumstances, in this section I discuss how these concepts are considered in this thesis.

Shade tolerance is an ecological concept that refers to the capacity of a given plant to tolerate low light levels. It has been extensively studied in forests, because light competition and interspecific differences in shade tolerance are often important determinants of forest structure and dynamics (Horn, 1971; Canham et al., 1994; Gravel et al., 2008).

Gap dynamics can be described as follows: a forest is a mosaic of tree crowns. The individual trees that are the elements of this mosaic dominate the resources and block the growth of young trees. When they die and open a gap in the canopy, a number of responses are initiated in the small area below the canopy opening. These responses eventually lead to the repair of the forest canopy. The tolerance of juvenile tree species is of importance, not in allowing net growth beneath the canopy, but in allowing them to survive through long periods of suppression (e.g., Canham, 1989).

Thus, gap dynamics describes how competition works while the shade tolerance is a key feature describing the competitive ability of tree species. The result of competition determines the successional status of a tree species. However, from a quantitative point of view, shade tolerance lacks a univocally accepted definition (Valladares and Niinemets, 2008). In particular, there is not a clear difference between shade tolerance and successional status. For example, Horn (1971) wrote:

> “Foresters long ago stated the first axiom of the effects of shading on forest succession: 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.”.

However, using a more objective measure of tolerance, Horn (1971) confirmed that tolerance increases as succession proceeds.

A quantitative description of shade tolerance can be obtained in several ways. From a physiological point of view, the shade tolerance of a given plant is defined as the minimum light under which a plant can survive. A different approach to define the shade tolerance is based on the well-known trade-off between high-growth in high-light and high-growth in low-light shown in figure 1.4 (Bazzaz, 1979). Each of the two curves in figure 1.4 is defined by two parameters: growth in low-light (the slope at zero light) and growth in high-light (the maximum growth rate). These two parameters give a measure of tolerance. Foresters have published extensive tables that place tree species into categories of shade tolerance (Baker, 1949). Models derived from JABOWA (see above) used these tables in their growth submodels. They linked growth and shade tolerance on the basis of the relationship described in figure 1.4.

However, Pacala et al. (1994) and Kobe et al. (1995) showed that the

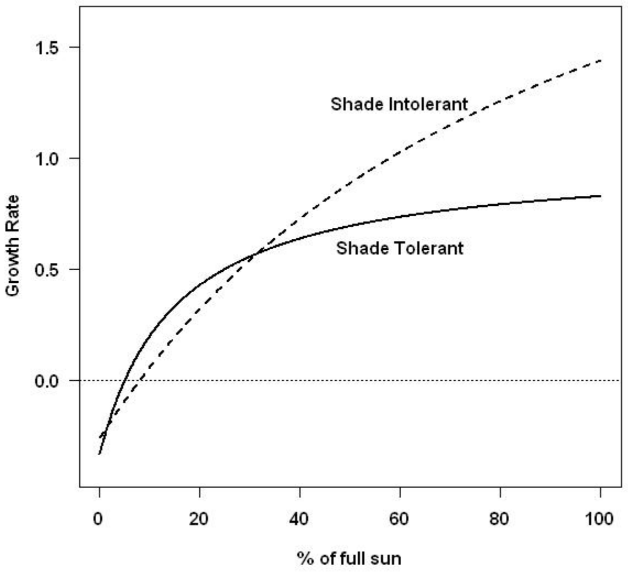
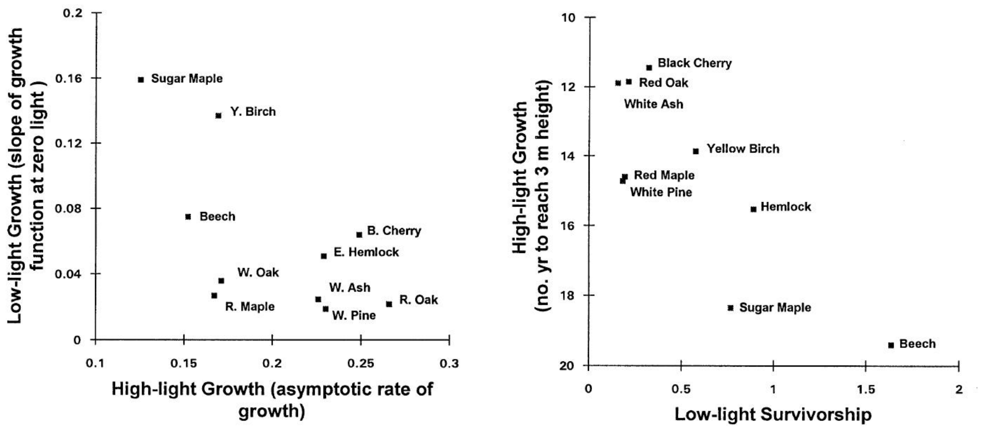


Figure 1.4: *Diameter growth rate versus light availability (from Pacala et al., 1994).*

linkage between shade tolerance and the growth abilities of figure 1.4 used in the JABOWA models is at least questionable (Pacala et al., 1993). Indeed, they estimated growth and mortality functions for nine species. Then, they plotted the nine species in a two-dimensional parameter space according to both low-light growth versus high-light growth (figure 1.5a) and high-light growth versus low-light survival (figure 1.5b). What is especially significant about the axis in figure 1.5b is that the species order according to their successional status. On the other hand, it is important to note that species do not order according to successional status when viewed in terms of low- and high- light growth abilities (figure 1.5a). Kobe et al. (1995) suggested that low-light survival rather than low-light growth should be used as a component of shade tolerance. Note that in doing so, they equated the concepts of shade tolerance and successional status.



(a) (b)

Figure 1.5: *Scatter plot of nine species according to their estimated attributes (from Kobe et al., 1995).*

In this view shade tolerance is related to species-specific parameters. In contrast, Valladares and Niinemets (2008) argued that shade tolerance is not an absolute value of, say, the minimum light availability required by a given species, but a relative concept that depends on the specific ecological context. Moreover, Horn (1971) pointed out that there is no reason to believe that the tolerance orders at a particular stage of succession (i.e., under a given canopy composition) are the same at any other stage or under other environmental conditions. In this thesis the shade tolerance is a relative concept as well: I consider the shade tolerance equivalent to survival in low-light, where survival in low-light is a function of understory light availability rather than a species-specific parameter. Then, through light transmissivity of canopy trees, the shade tolerance of a given tree species depends on canopy composition. This is of importance if different tree species have different light transmissivity through canopy. Indeed, Canham et al. (1994) found significative interspecific variation in light transmission by canopy trees. Moreover, Pacala et al. (1994) and Kobe et al. (1995) pointed out that this interspecific variation in light transmissivity has the potential to significatively affect growth rate and mortality of understory saplings even in the case of shade tolerant trees, thus playing a key role on the overall dynamics.

1.5 Aim of the thesis

The aim of this thesis is to develop and analyse a simple mathematical model that is able to account for mechanisms and behaviours discussed in the last two sections. In particular, as I am interested in explaining coexistence mechanisms as a result of the internal structure of the forest community, I focus on a homogeneous closed environment. That is, I neglect mechanisms such as: stochastic disturbances, environmental heterogeneity and immigration. These mechanisms have been studied elsewhere (e.g., Huston, 1979; Kelly and Bowler, 2002; Shmida and Ellner, 1984). This thesis deals mainly with coexistence of shade tolerant tree species, the role of interspecific variation in light transmissivity by canopy trees on the overall dynamics and the relationship between shade tolerance and successional status. These topics are of importance both from a theoretical point of view and in determining which are the important interactions that have to be considered in more complex predictive models. For example, a major result of this thesis states that, in order to describe coexistence, a critical feature is the interspecific variation in light transmissivity rather than the trade-off between abilities in low- and high-light.

Chapter 2

The model

In this chapter I will derive a simple mechanistic model to describe forest dynamics. The model is based on competition for space. Two stage levels are considered: adult and juvenile. Adult trees occupy space and cannot be dislodged by juveniles. They cast shade on juveniles but they do not shade each other. Juvenile trees have to survive in the adults shade and they grow into the canopy only when a dominating adult dies, thus releasing space.

2.1 Model derivation

In building the present model I followed the Levins's approach: I ideally divided a habitat into spatial cells; each cell can be either empty or occupied by one adult individual. The dynamics of occupancy of the habitat is then described by the following equation (Levins, 1969):

$$\frac{dx}{dt} = cx(1-x) - mx. \tag{2.1}$$

Where x is the fraction of cells occupied by a species, c is the colonisation rate and m is the mortality rate. A persistent population must satisfy the condition $c > m$. Eventually, it will approach the equilibrium density given by $\hat{x} = 1 - m/c$.

In the original interpretation (Levins, 1969), cells were occupied by a set of local populations called *metapopulation* (regional dynamic). However, the extension to the local dynamic, where each cell has the size of an adult individual, is straightforward (Klausmeir and Tilman, 2002).

I extended the Levins's model by assuming that the tree population is composed by two life history stages: *adult* and *juvenile*. Adults represent dominant trees (canopy), while juveniles comprise seeds, seedlings and saplings. It is important to note that this classification is hierarchical. Adults and juveniles represent the two main levels of a forest: *overstory* and *understory*. When a juvenile tree reaches the canopy, it becomes an adult regardless of its age and size. I assumed that only adult trees can reproduce. This assumption has been used also in other models (e.g., Adams et al., 2007).

Now, each cell has two levels: overstory and understory. On the overstory level a cell can be either empty or occupied by one adult, while on the understory level each cell can contain any number of juveniles of every species. In order to keep mathematics simple, it is assumed that the space occupied by a juvenile is negligible relative to the crown of an adult tree. I call *empty* a cell with zero adults irrespective of the number of juveniles living there. A juvenile can become an adult only in empty cells. Thus, it can either colonise new areas (transient dynamics) or grow into recently vacated cells (gap dynamics).

It is important to understand that in this scheme all adult trees are exposed to full light (i.e., they have similar height), while juveniles are suppressed if adult trees are present. That is, only juvenile mortality is affected by crowding effect.

The number of adults and juveniles is described by the state variables P_i and p_i, respectively; index i indicates the species. Then the following set of equations describes the dynamics of n species ($i = 1, \ldots, n$):

$$\frac{dP_i}{dt} = g_i'(S - \sum_{j=1}^{n} s_j P_j)p_i - m_i P_i \tag{2.2a}$$

$$\frac{dp_i}{dt} = c_i P_i - g_i'(S - \sum_{j=1}^{n} s_j P_j)p_i - (n_i + \sum_{j=1}^{n} \alpha_{ij}' P_j)p_i \tag{2.2b}$$

Here, S is the total area of the habitat and s_j is the mean[1] area occupied by an adult of species j (crown area). Then $(S - \sum s_j P_j)$ is the portion of space without adults where juveniles can grow into.

The number of adults increases by juvenile growth at the rate of g_i' (provided that empty cells are available) and decreases by mortality at the rate m_i. The number of juveniles increases by adult reproduction at the rate c_i and decreases either when juveniles grow into the adult class or by mortality.

I assumed that the juvenile mortality rate depends linearly on adult density. Then, n_i represents the base mortality (when adults are absent), while coefficients α_{ij}' represent the effect of adults j on juveniles i. Generally, I assumed that shading is the main effect of adults on juveniles. As a consequence, α_{ij}' is a compound measure of the shade projected by adults j and the tolerance level of juveniles i (see section 2.3.1). Other kind of influences will be discussed later in the text.

Let $k_i = S/s_i$ be the maximum number of adults i that can live in the habitat. It is convenient to scale the number of both, adults and juveniles,

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[1] Intuitively, in order for adult trees to fill the space, some plasticity in both crown shape and crown size is required. Thus, two adult trees of the same species could have a different crown area. However, I assumed that the mean crown area is a constant parameter (this will be discussed in more detail in the discussion section).

with respect to k_i by setting: $X_i = P_i/k_i$ and $x_i = p_i/k_i$. As k_i is a measure of the habitat area, I will refer to X_i and x_i as adult density and juvenile density, respectively (but note that they are not proper densities). X_i also indicates the fraction of space occupied by adult crowns of species i.

I set $g_i = S \cdot g'_i$ and $\alpha_{ij} = k_i \cdot \alpha'_{ij}$. Then, equation (2.2) becomes ($i = 1, \ldots, n$):

$$\frac{dX_i}{dt} = g_i(1 - \sum_{j=1}^{n} X_j)x_i - m_i X_i \tag{2.3a}$$

$$\frac{dx_i}{dt} = c_i X_i - g_i(1 - \sum_{j=1}^{n} X_j)x_i - (n_i + \sum_{j=1}^{n} \alpha_{ij} X_j)x_i. \tag{2.3b}$$

Here, the total available space is represented by the unity. X_i ranges from zero to one (equation (2.3a)) and x_i is always positive (equation (2.3b)).

Parameters c_i, m_i, g_i and n_i are positive numbers. In principle, some α_{ij} could be negative, in which case the mortality of juveniles i decreases when adults j are present. However, the juvenile mortality have to be positive for every value of X_i. The latter condition is met by imposing $\alpha_{ij} > -n_i$. Note that since adult density is bounded, so is the juvenile mortality (it is always greater than zero and smaller than $n_i + \sum_j \alpha_{ij}$).

Model (2.3) is a spatially implicit model (Klausmeir and Tilman, 2002), this means that densities are averaged over space and spatial anomalies are not considered. For example, in model (2.3) a species could be "seed-limited" but not "dispersal-limited". Thus, model (2.3) assumes that populations are well-mixed.

Parameters of model (2.3) can be usefully rearranged by setting:

$$\beta_i = g_i \left(\frac{c_i}{m_i} - 1 - \frac{n_i}{g_i} \right) \quad \text{and} \quad \gamma_{ij} = n_i + \alpha_{ij} \tag{2.4}$$

(by definition, $\gamma_{ij} > 0$). Then equations (2.3a) and (2.3b) can be combined to give $(i = 1, \ldots, n)$:

$$\frac{d}{dt}\left(\frac{c_i}{m_i}X_i + x_i\right) = [\beta_i - \sum_{j=1}^{n}(\beta_i + \gamma_{ij})X_j]x_i \tag{2.5}$$

where $\frac{c_i}{m_i}X_i + x_i$ is a measure of the overall density of species i. Equation (2.5) shows that if all densities are low (empty habitat), then a species with $\beta_i > 0$ is able to invade the habitat (see the next section for a rigorous demonstration).

Thus, β_i is the ability to invade a habitat, while γ_{ij} indicates mortality under conspecific $(i = j)$ or heterospecific $(i \neq j)$ canopies. Note that the higher the value of γ_{ij}, the higher the inhibition of adults j on juveniles i. It is also useful to define the mean mortality under canopy as: $\gamma_i = \frac{1}{n}\sum_j \gamma_{ij}$.

Summarising, we can say that β_i and $1/\gamma_i$ represent growth in high-light and survival in low-light, respectively.

System (2.3) has the trivial equilibrium P_0 (empty habitat). If $\beta_i > 0$ for some species, then P_0 is unstable (i.e. species with $\beta_i > 0$ invade an empty habitat). Generally, I will consider species with $\beta_i > 0$.

In order to find the other equilibrium points we can set $dX_i/dt = 0$ in equation (2.3a). Then, we obtain $(i = 1, \ldots, n)$:

$$x_i = \frac{m_i X_i}{g_i\left(1 - \sum_{j=1}^{n} X_j\right)}. \tag{2.6}$$

If we substitute equation (2.6) into equation (2.5), we find that the condition to have $dX_i/dt = dx_i/dt = 0$ is $(i = 1, \ldots, n)$:

$$[\beta_i - \sum_{j=1}^{n}(\beta_i + \gamma_{ij})X_j]X_i = 0. \tag{2.7}$$

Solutions of system (2.7) are the adult equilibrium densities. Then, juvenile equilibrium densities are easily found from equation (2.6).

I analysed the stability of the equilibrium points through the invasibility criterion (Chesson, 2000, and references therein). This criterion is based on the condition required for a species to be able to increase from low density in the presence of the rest of the community.

In order to find such condition, we can assume that $n-1$ species coexist in a stable equilibrium ($X_j = X_j^*$) ($j = 1, \ldots, n-1$). Then, from equation (2.5), we see that the species n increases from low density (i.e. $X_n \approx x_n \approx 0$) if $\frac{d}{dt}\left(\frac{c_n}{m_n}X_n + x_n\right) > 0$, i.e., if :

$$\beta_n - \sum_{j=1}^{n-1}(\beta_n + \gamma_{nj})X_j^* > 0. \tag{2.8}$$

The invasibility condition for the species n can be rewritten as:

$$\beta_n > \frac{\displaystyle\sum_{j=1}^{n-1}\gamma_{nj}X_j^*}{1 - \displaystyle\sum_{j=1}^{n-1}X_j^*}. \tag{2.9}$$

In other words, the species n can invade if the equilibrium point $P^* \equiv (X_j = X_j^*, X_n = 0)$ ($j = 1, \ldots, n-1$) is unstable. Indeed, if we linearise system (2.3) we find that the condition (2.8) implies the unstability of P^*.

According to the invasibility criterion, n species persist in a habitat if each species is able to increase from low density when the rest of the community is present (Chesson, 2000).

The last term on the right hand side of equation (2.3b) is the juvenile mortality. It has a critical role for coexistence. In model (2.3) the juvenile mortality rate depends linearly on adult densities. In order to show the importance of this term, I now consider a generic formulation for the juvenile mortality.

Let f_i be the juvenile mortality rate for the species i. According to the dependence of f_i on adult density, I distinguished two cases (see Nakashizuka and Kohyama, 1995):

$$f_i = f_i\left(\sum_{j=1}^{n} X_j\right) \qquad \text{additive model}$$

$$f_i = f_i(X_1, \ldots, X_n) \qquad \text{reciprocal model.}$$

For example, if f_i is a linear function, we will have $f_i = n_i + \alpha_i(\sum_j X_j)$ for the additive model and $f_i = n_i + \sum_j \alpha_{ij} X_j$ for the reciprocal model (i.e. the case of model (2.3)).

If juvenile mortality depends only on the total density of adults (i.e. additive model), then coexistence is impossible. To show this fact I replaced the juvenile mortality rate in system (2.3) by $f_i(\sum_j X_j)$, then I set $dX_i/dt = 0$, $dx_i/dt = 0$ and $x_i \neq 0$, $X_i \neq 0$. Rearranging terms, I obtained ($i = 1, \ldots, n$):

$$\frac{f_i(\sum_j X_j)}{1 - \sum_j X_j} = g_i\left(\frac{c_i}{m_i} - 1\right). \tag{2.10}$$

The system above can be rewritten simply as ($i = 1, \ldots, n$):

$$\sum_{j=1}^{n} X_j = \omega_i \tag{2.11}$$

where ω_i is a combination of parameters of species i. In general, system (2.11) has no non-trivial roots (except for some unlikely, meaningless sets of parameters). Thus, an equilibrium with more than one species does not exist, i.e. only one species can persist in the habitat. It is worth noting that the additive model prevents coexistence for any functional form of juvenile mortality.

In section 2.3.1 I will show that the additive model refers to the case where no variation in interspecific transmissivity by canopy trees is allowed.

Thus, coexistence is possible only if canopy trees of different species have different light transmissivity, i.e., the reciprocal model. Moreover, in section 2.3.1 I will show that the assumption that juvenile mortality depends linearly on adult densities is not necessary. However, I use this assumption because it allows a simple description of model behaviours. The main features of the model are illustrated in figure 2.5 (page 36).

2.2 Model predictions - one species

When only one species is present the condition to invade an empty habitat is simply $\beta_i > 0$ (equation (2.8)). The non-trivial equilibrium densities can be found through equations (2.7) and (2.6), for one species they are:

$$\hat{X}_i = \frac{\beta_i}{\beta_i + \gamma_{ii}} \quad \text{and} \quad \hat{x}_i = \frac{m_i}{g_i}\frac{\beta_i}{\gamma_{ii}} \tag{2.12}$$

(for one species the index i is redundant, however I retained it in the equations above for consistency with the case of more than one species). Throughout this work, the "hat" notation will always denote the equilibrium density of a species when alone.

Condition $\beta > 0$ indicates that the species persist. Then we expect that the equilibrium point (2.12) is stable. This can be verified by drawing the zero-growth isoclines for adults and juveniles on the (X, x) phase plane. Intersections of the isoclines give the equilibrium points, while directions in the phase plane indicate stability (see Kot, 2003). In the region $(0 < X < 1) \cap (x > 0)$, system (2.3) with $i = 1$ has two equilibria: P_0 and $\hat{P}$ (see figure 2.1).

Depending on the sign of $g - \alpha$, the juvenile zero-growth isocline has different concavity. When $\alpha < g$ (figure 2.1, left panel), it has a vertical asymptote at $X = (g + n)/(g - \alpha)$. Since we set $n > -\alpha$, then $\alpha < g$ implies

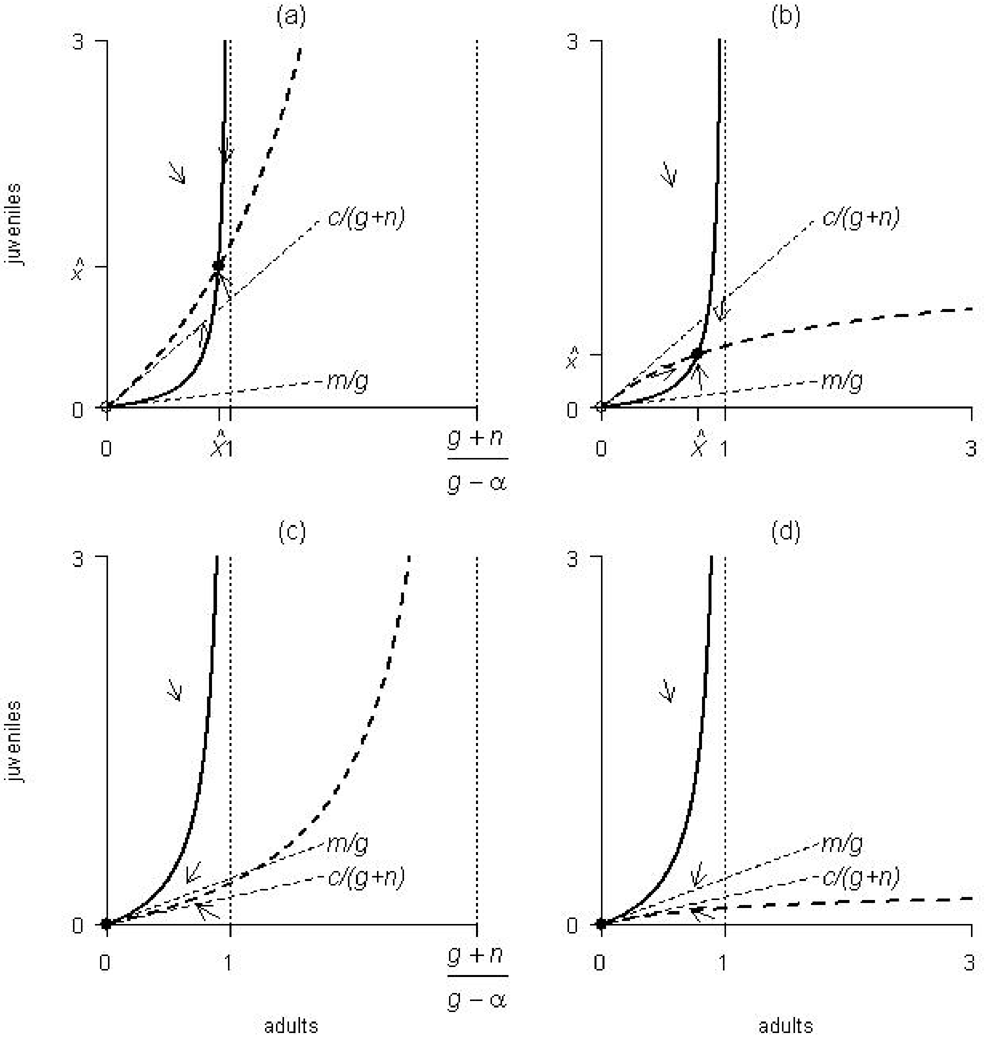

Figure 2.1: *Zero-growth isoclines for the two cases* $\alpha < g$ *(left panel) and* $\alpha > g$ *(right panel). Adult zero-growth isoclines (solid lines) have slope at origin* $= \frac{m}{g}$ *and a vertical asymptote at* $X = 1$*; juvenile zero-growth isoclines (dashed lines) have slope at the origin* $= \frac{c}{g+n}$ *and, if* $\alpha < g$*, have vertical asymptote at* $X = \frac{g+n}{g-\alpha}$ *(left panel). Arrows are directions in the phase plane. Black circles indicate stable equilibrium, white circles indicate unstable equilibrium. Coefficients were chosen for illustrative purpose only (*$c = g = 8$, $m = n = 1$ *(upper panels);* $c = 2$, $g = 8$, $m = 3$, $n = 1$ *(bottom panels);* $\alpha = 5$ *(left panel);* $\alpha = 15$ *(right panel)).*

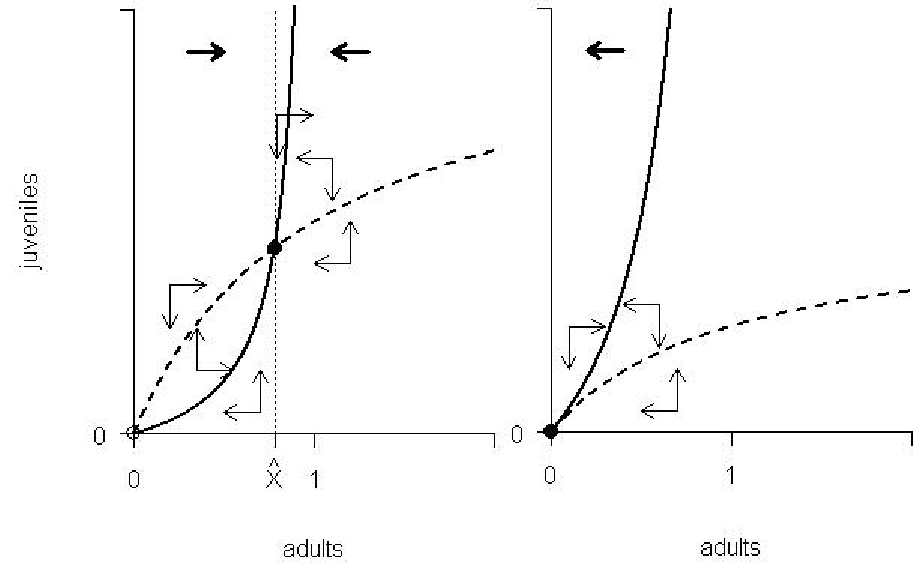

Figure 2.2: *Schematic representation of adult (solid line) and juvenile (dashed line) zero growth isoclines. See the text for the meaning of thick arrows.*

that $(g+n)/(g-\alpha) > 1$. As a consequence, through an inspection of figure 2.1, it is clear that when $c/(g+n) > m/g$ (i.e. $\beta > 0$) the species persists, and approaches the stable equilibrium $\hat{P}$. On the other hand, if $\beta < 0$ then $\hat{P}$ disappears and P_0 becomes stable.

It is worth noting that α does not affect the persistence condition, while it determines the equilibrium density. Low values of α correspond to high levels of tolerance relative to the shade of conspecific adults. Figure 2.1 (upper panels) shows two juveniles zero-growth isoclines with different values of α; it is clear that the higher the tolerance, the higher the equilibrium density or, equivalently, the denser is the canopy (see also equations (2.12)). Such a relationship is widely observed (Horn, 1971).

Equation (2.5) for one species is given by:

$$\frac{d}{dt}\left(\frac{c}{m}X + x\right) = [\beta - (\beta + \gamma)X]x. \tag{2.13}$$

It states that when $X < \hat{X}$, then $\frac{c}{m}X + x$ increases with time and vice versa. Figure 2.2 shows that the sign of $\frac{d}{dt}(\frac{c}{m}X + x)$ indicates the stability of the equilibrium points; $\frac{d}{dt}(\frac{c}{m}X + x) > 0$ is represented by a thick arrow directed towards increasing values of X and vice versa. Moreover, it shows that after some transient time interval dX/dt and dx/dt will have the same sign.

2.3 Model predictions - two species

When two species are present, system (2.7) with $i = 1, 2$ has the same form of the well-known Lotka-Volterra competition model (see for example Pielou, 1977; Kot, 2003). Four different equilibria are possible. In the (X_1, X_2) phase plane they are: $P_0 = (0, 0)$, $P_1 = (\hat{X}_1, 0)$, $P_2 = (0, \hat{X}_2)$ and $P_{12} = (X_1^{12}, X_2^{12})$ (see figure 2.3). Equilibrium points P_1 and P_2 are identical to the case of a single species (equations (2.12) with $i = 1, 2$). While coordinates for the interior equilibrium are:

$$\begin{aligned} X_1^{12} &= \frac{a}{a+b+c} & x_1^{12} &= \frac{m_1}{g_1}\frac{a}{c} \\ X_2^{12} &= \frac{b}{a+b+c} & x_2^{12} &= \frac{m_2}{g_2}\frac{b}{c}. \end{aligned} \tag{2.14}$$

Where I have defined:

$$\begin{aligned} a &= \beta_1\gamma_{22} - \beta_2\gamma_{12} \\ b &= \beta_2\gamma_{11} - \beta_1\gamma_{21} \\ c &= \gamma_{11}\gamma_{22} - \gamma_{12}\gamma_{21}. \end{aligned} \tag{2.15}$$

Here, I consider the case with both $\beta_1 > 0$ and $\beta_2 > 0$. Then, for what I said in the previous section it is clear that P_0 is unstable i.e., at least one species occupies the habitat.

Equations (2.9) states that P_i is unstable if ($i = 1, 2$, $j \neq i$):

$$\beta_j > \gamma_{ji} \frac{\hat{X}_i}{1 - \hat{X}_i}. \tag{2.16}$$

It is important to stress that the condition above means that a species j is able to invade a monoculture of species i. Using equation (2.12) it can be conveniently rewritten as:

$$\frac{\beta_j}{\gamma_{ji}} > \frac{\beta_i}{\gamma_{ii}} \tag{2.17}$$

Depending on the stability character of P_1 and P_2, four different behaviours are possible: (i) if only P_1 is stable, then species 1 wins and species 2 goes extinct (figure 2.3a); (ii) if only P_2 is stable, the opposite is true (figure 2.3b); (iii) if both P_1 and P_2 are stable, only one species wins depending on initial conditions (figure 2.3c); (iv) if both P_1 and P_2 are unstable, none species goes extinct. That is, the two species coexist (figure 2.3d).

Using equations (2.16) and (2.12), the four cases above can be summarised as follows:

$$\frac{\beta_1}{\beta_2} > \frac{\gamma_{11}}{\gamma_{21}} \text{ and } \frac{\beta_1}{\beta_2} > \frac{\gamma_{12}}{\gamma_{22}} \qquad \text{Species 1 wins} \tag{2.18a}$$

$$\frac{\beta_1}{\beta_2} < \frac{\gamma_{11}}{\gamma_{21}} \text{ and } \frac{\beta_1}{\beta_2} < \frac{\gamma_{12}}{\gamma_{22}} \qquad \text{Species 2 wins} \tag{2.18b}$$

$$\frac{\gamma_{11}}{\gamma_{21}} < \frac{\beta_1}{\beta_2} < \frac{\gamma_{12}}{\gamma_{22}} \qquad \text{Founder control} \tag{2.18c}$$

$$\frac{\gamma_{12}}{\gamma_{22}} < \frac{\beta_1}{\beta_2} < \frac{\gamma_{11}}{\gamma_{21}} \qquad \text{Coexistence.} \tag{2.18d}$$

In the third case the system approaches either the equilibrium P_1 or P_2

depending on initial conditions, that is, the equilibrium is locally[2] stable. This behaviour is commonly termed *founder control* (Yodzis, 1978). In the other three cases, the same equilibrium density is reached regardless of the initial abundances of the two species, i.e., the three equilibria are globally stable.

According to equations (2.5), the arrows in figure 2.3 represent the sign of $\frac{d}{dt}(\frac{c_i}{m_i}X_i + x_i)$: if $\frac{d}{dt}(\frac{c_i}{m_i}X_i + x_i) > 0$, then the arrow is directed towards increasing X_i and vice versa. As dX_i/dt and dx_i/dt cannot have different sign indefinitely (see figure 2.2), then such arrows indicate the stability character of the equilibrium points. Thus, conditions (2.18c) and (2.18d) imply the unstability and stability of P_{12}, respectively. This result was confirmed by numerical computation of eigenvalues for the jacobian matrix (not shown).

Condition (2.18d) implies that some degree of either intraspecific inhibition or interspecific facilitation is necessary in order to have coexistence. For example, if $\alpha_{ji} < 0$, then adults i increase the survival of juveniles j relative to an empty habitat. We know that if $\beta_j < 0$ species j cannot invade an empty habitat, but we can ask if it can invade a habitat occupied by species i when $\alpha_{ji} < 0$. To answer this question we can consider the condition for the unstability of P_i, i.e. equation (2.16). Right hand side of equation (2.16) is always positive. Then, if $\beta_j < 0$, species j can never invade a habitat, even if it is facilitated by another species. Thus, the condition to invade an empty habitat is always less restrictive than the condition to invade an occupied one. Therefore, from a successional point of view, model (2.3) agrees with the inhibition model of Connell and Slatyer (1977).

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[2] An equilibrium point is locally stable if only a set of initial densities (i.e., a region in the phase space) approaches it. Here, the term local refers to the phase space and not to the real space. In contrast, if any initial density (i.e., any point in the phase space) approaches the same equilibrium, the equilibrium point is said to be globally stable.

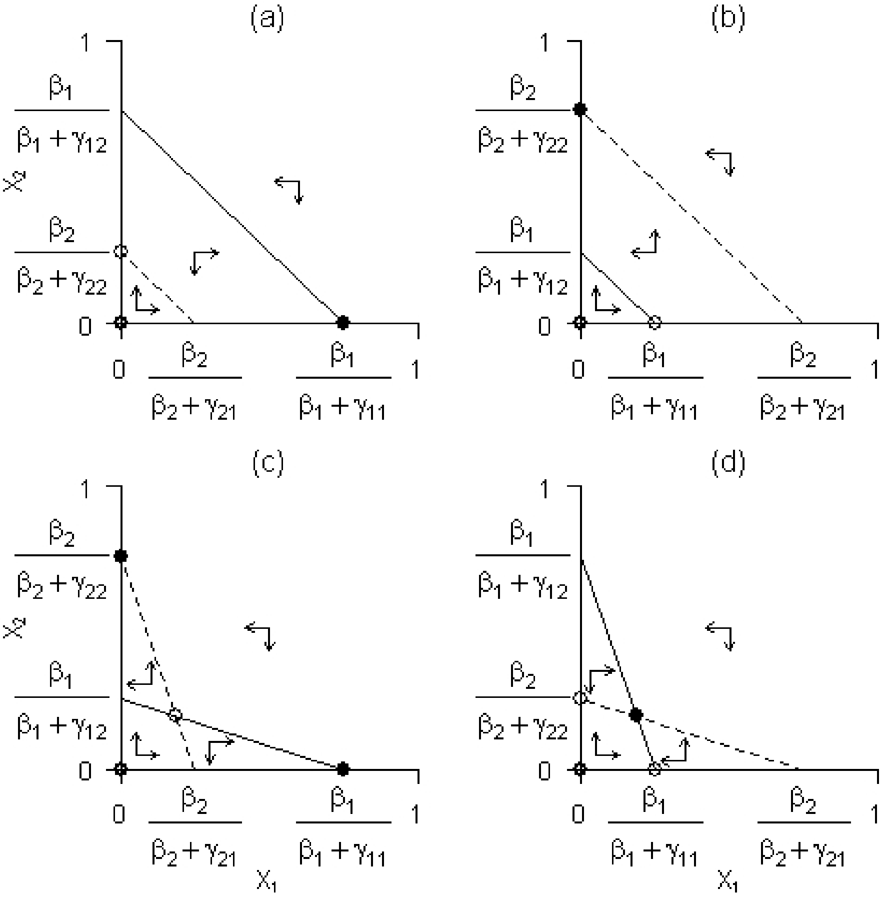

Figure 2.3: *(X_1, X_2) phase space. Black circles indicate stable equilibria, white circles indicate unstable equilibria. Lines are drawn according to system (2.7) with $X_1 \neq 0$ (solid line) and $X_2 \neq 0$ (dashed line). See the text for the meaning of arrows.*

2.3.1 Coexistence: the role of shade tolerance

Coexistence condition (2.18d) implies that at least one of the following equations is true:

$$\frac{\gamma_{12}}{\gamma_{22}} < 1 \tag{2.19a}$$

$$\frac{\gamma_{11}}{\gamma_{21}} > 1. \tag{2.19b}$$

If $\gamma_{ij} < \gamma_{jj}$, than adults j facilitate juveniles i relative to their offspring or, equivalently, they inhibit their offspring relative to juveniles i. In few words, coexistence is the result of interspecific facilitation or intraspecific inhibition, where facilitation and inhibition are relative concepts.

There are two possibilities: I termed symmetric (relative) facilitation the case when both equations (2.19) are true (species facilitate each other) and asymmetric (relative) facilitation the case where only one of the equations (2.19) is true (one species is facilitated, while the other is inhibited).

It is expected that γ_{ij} both increases with the shade cast by adults j and decreases with the level of tolerance of juveniles i. Assuming that species 1 casts the deepest shade, four patterns are possible. They are illustrated in figure 2.4: the decreasing curves represent the juvenile mortality rate versus light availability (Kobe et al., 1995), while the vertical lines indicate the light available at the ground level for a pure canopy of each species (Canham et al., 1994).

Under a pure canopy of species j (i.e., $X_j \approx 1$, and $X_i \approx 0$) the juvenile mortality of species i is approximated by $\gamma_{ij} = n_i + \alpha_{ij}$. Thus, the intersection points in figure 2.4 are an approximation of the γ_{ij} coefficients.

The shade tolerance is a complex plant feature that is hard to define. For example, Valladares and Niinemets (2008) argued that shade tolerance is not an absolute value of the minimum light availability required by a given species, but a relative concept, the meaning of which depends on the specific ecological context.

In this thesis the shade tolerance is defined as a relative concept as well: for each light level, the most tolerant species is the one with the lowest mortality rate. That is, the shade tolerance depends on the canopy composition (see also Horn, 1971).

Figure 2.4b indicates symmetric facilitation. It depicts a situation in which under a pure canopy of species 1, the juveniles of species 2 are more tolerant than those of species 1, while the reverse is true under a pure canopy of species 2. That is, the order of tolerance changes with the type of canopy. In this case both the conditions (2.19) hold. Then, according to conditions (2.18), either coexistence or competitive exclusion are possible. Note that in this case coexistence is possible both with $\beta_1/\beta_2 < 1$ and $\beta_1/\beta_2 > 1$.

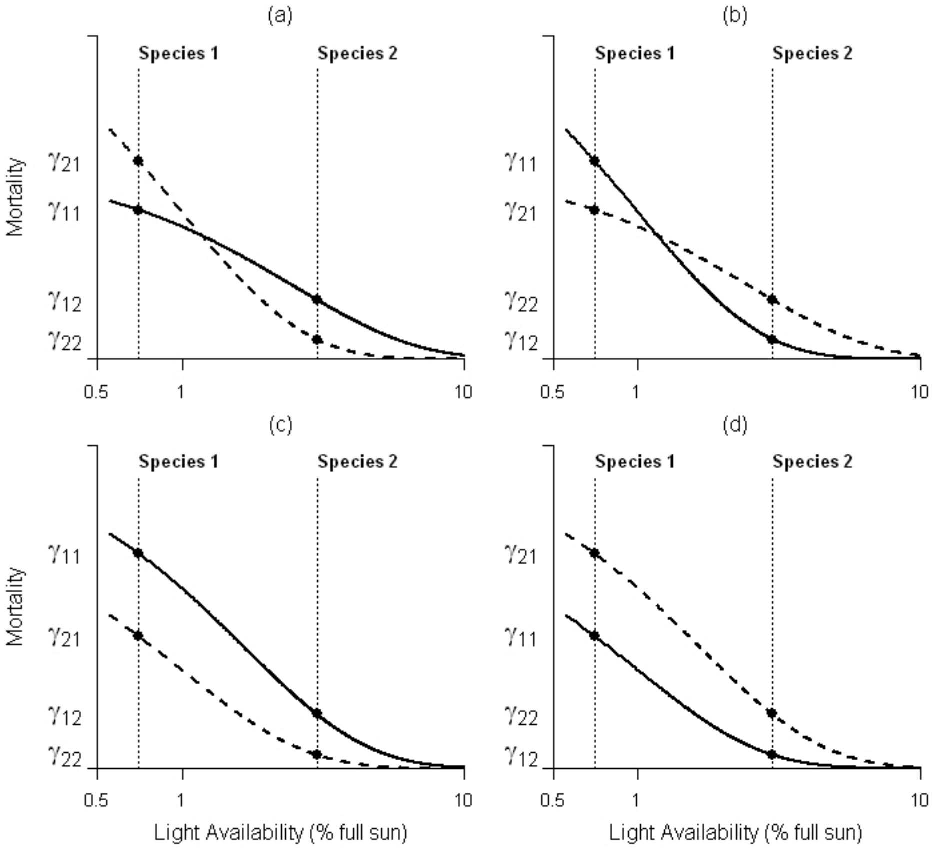

Figure 2.4: *Schematic representation of juvenile mortality of both species 1 (solid line) and species 2 (dashed line). Vertical lines represent the light available in under a pure canopy of the two species. The x axis has a logarithmic scale.*

In the case of figure 2.4a, none of the equations (2.19) is true, then globally stable coexistence is impossible. In this case there is not interspecific facilitation. Depending on values of β_1 and β_2, either founder control or competitive exclusion are possible (see conditions (2.18)).

Both figures 2.4c and 2.4d depict pattern of asymmetric facilitation. In this case, depending on values of β_1 and β_2, all the conditions (2.18) could be verified.

It is important to note that in the latter case coexistence requires a trade-off between survival in understory and growth. For example, if species 1 casts the deepest shade and has generally higher tolerance (i.e., figure 2.4d), then we have both $\gamma_{12}/\gamma_{22} < 1$ and $\gamma_{11}/\gamma_{21} < 1$. Then, condition (2.18d) implies both $1/\gamma_1 > 1/\gamma_2$ and $\beta_2 > \beta_1$. Thus, species 2 has lower survival in low-light but higher growth in high-light.[3] However, this trade-off promotes coexistence only if the effects of adults on juvenile mortality are species specific (i.e., the reciprocal model).

Note that, similarly to the Lotka-Volterra competition model, coexistence within both symmetric and asymmetric facilitation requires that interspecific facilitation is larger than intraspecific facilitation or, equivalently, that interspecific inhibition is lower than intraspecific inhibition (i.e., $\gamma_{12}\gamma_{21} < \gamma_{11}\gamma_{22}$).

Finally, note that the dependence of juvenile mortality on light availability and the crown transmissivity (i.e., the actors of figure 2.4) can be estimated (see figures 4.2 at page 69 and 4.3 at page 70). Therefore, the γ coefficients have a mechanistic interpretation and model (2.3) can be considered as a simple mechanistic model for forest dynamics.

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[3] In fact, in section 4.4, I will show that coexistence always requires a specific trade-off between growth in high-light and survival in low-light, whether in the case of asymmetric facilitation or symmetric facilitation.

The functional form of juvenile mortality in equation (2.3b) is based on the following two linear approximations:

$$\mu_i(L) = a_i - b_i L \tag{2.20}$$

and

$$L = 1 - \sigma_1 X_1 - \sigma_2 X_2. \tag{2.21}$$

Where $\mu_i(L)$ indicates the juvenile mortality of species i, L indicates light availability in the understory (here $L = 1$ means full light), a_i and b_i are parameters and $1/\sigma_i$ is a measure of canopy transmissivity by adult trees of species i. Through the two equations above, the juvenile mortality can be expressed as a function of adult densities $f_i(X_1, X_2)$:

$$f_i(X_1, X_2) = n_i + \alpha_{i1} X_1 + \alpha_{i2} X_2. \tag{2.22}$$

Where $n_i = a_i - b_i$, $\alpha_{i1} = b_i \sigma_1$ and $\alpha_{i2} = b_i \sigma_2$. From figure 4.3 at page 70 it is seen that $n_i \gtrapprox 0$. Then, $a_i \gtrapprox b_i$.

The higher the value of a_i the lower is the general tolerance of species i. Thus, a high value of b_i indicates that the species i is generally intolerant. Indeed, note that the coefficients α_{ij} are large if both the species i is intollerant (i.e., high b_i) and species j casts deep shade (i.e., high σ_j).

Compared with figure 4.3 (page 70), the approximation (2.20) is quite rough. The functional forms described by equations (2.20) and (2.21) have been chosen for the sake of simplicity. However, provided that (i=1,2):

$$\mu_i(L) > 0 \qquad \frac{d\mu_i}{dL} < 0 \tag{2.23a}$$

$$0 < L(X_1, X_2) < 1 \qquad \frac{\partial L}{\partial X_i} < 0, \tag{2.23b}$$

any choice of $L = L(X_1, X_2)$ and $\mu_i = \mu_i(L)$ produces the same pattern described by figure 2.3 (page 30). This, can be shown as follows:

I have set $f_i(X_1, X_2) = \mu_i[L(X_1, X_2)]$. Then, it follows that $(i, j = 1, 2)$:

$$\frac{\partial f_i}{\partial X_j} = \frac{d\mu_i}{dL}\frac{\partial L}{\partial X_i} > 0. \tag{2.24}$$

The zero-growth isoclines depicted in figure 2.3 can be rewritten as:

$$F_i(X_1, X_2) = g_i \tag{2.25}$$

where I have set:

$$F_i(X_1, X_2) = \frac{f_i(X_1, X_2)}{1 - X_1 - X_2}. \tag{2.26}$$

Then, it is easy to show that:

$$\frac{\partial F_i}{\partial X_i} > 0. \tag{2.27}$$

Thus, the slope of the isoclines is given by:

$$\frac{dX_2}{dX_1} = -\frac{\dfrac{\partial F_i}{\partial X_1}}{\dfrac{\partial F_i}{\partial X_2}} < 0. \tag{2.28}$$

Moreover, the isoclines can be rewritten as:

$$f_i(X_1, X_2) = g_i(1 - X_1 - X_2). \tag{2.29}$$

As $f_i(X_1, X_2) > 0$, the isoclines live in the region of the (X_1, X_2) phase plane defined by $X_1 > 0$, $X_2 > 0$ and $1 - X_1 - X_2 > 0$.

The assumptions (2.23) are reasonable and very general but they fail to exclude the possibility of multiple intersection of the isoclines. I shall henceforth cling to a third rather vague assumption that the functions $F_i(X_1, X_2)$ are sufficiently "well behaved" that multiple intersection do not occur (Vance, 1984). Figure 4.3 (page 70) suggests that this latter assumption is reasonable.

The main assumption of the model – the mean field approximation – is that both space availability and understory light availability depend on the mean densities of adult trees. Space availability affects juvenile growth into the canopy while the understory light availability affects the survival of juvenile trees. This is illustrated in figure 2.5.

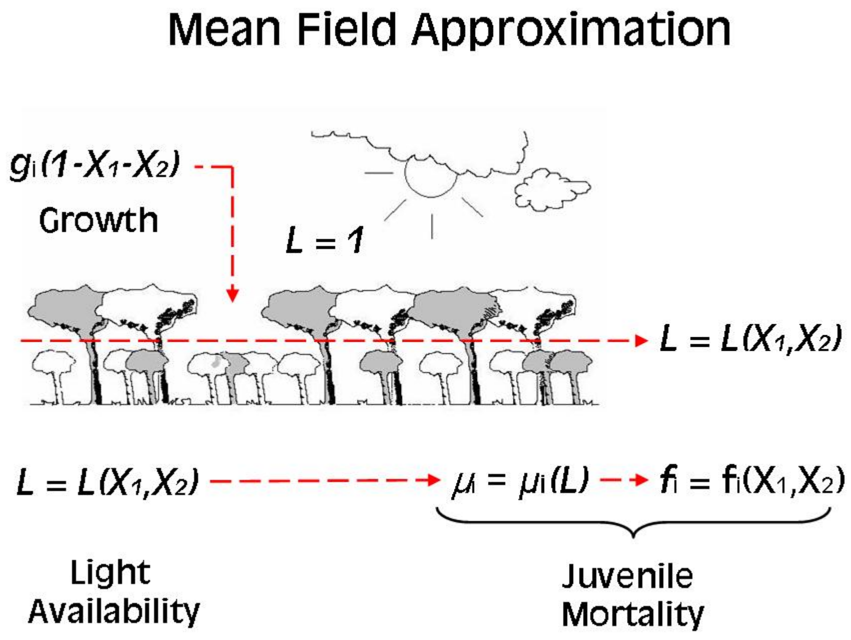

Figure 2.5: *Schematic view of the model*

2.3.2 Coexistence: relative abundances

Within the coexistence conditions, species approach the equilibrium densities given by equations (2.14). Using definitions (2.15), the ratio between adult densities can be written as:

$$\frac{X_1^*}{X_2^*} = \frac{\beta_1\gamma_{22} - \beta_2\gamma_{12}}{\beta_2\gamma_{11} - \beta_1\gamma_{21}}, \tag{2.30}$$

while the ratio between juvenile densities is:

$$\frac{x_1^*}{x_2^*} = \frac{m_1 g_2}{m_2 g_1}\frac{X_1^*}{X_2^*} \tag{2.31}$$

(to simplify notation, I redefined X_i^{ij} as X_i^* and x_i^{ij} as x_i^*). Equation (2.31) can be found directly by equations (2.6). It is simple but interesting: it states that increasing values of m_1g_2/m_2g_1 both increase x_1^*/x_2^* and decrease X_1^*/X_2^* (see equations (2.4) and (2.30)).

Fox (1977) analysed five “climax” tree communities in North America, each forest being dominated by two principal species. In most of cases he found an inversion between overstory and understory abundances. Longer-lived species were generally the more abundant in the overstory, but they had a generally lower sapling abundance. Fox pointed out that this is not obviously explained by seed year frequency, seed number or seed size (i.e., parameters c_i in model (2.3)). Equation (2.31) suggests that this fact is a consequence of the structure of the system. However, as X_1^*/X_2^* has a complex dependence on all parameters, it is difficult to find the condition which must be verified in order to have such an inversion. This obstacle can be overcome by using the following approximation ($i = 1, 2$):

$$\beta_i \gg 0 \quad \Longrightarrow \quad \beta_i \approx \frac{c_i g_i}{m_i} \quad \Longrightarrow \quad \frac{\beta_1}{\beta_2} \approx \frac{c_1 g_1 m_2}{c_2 g_2 m_1}. \tag{2.32}$$

This means that both species are good invader of an empty habitat. Now, I look for the conditions to have both $X_1^*/X_2^* > 1$ and $x_1^*/x_2^* < 1$. It is convenient to think of X_1^*/X_2^* as a function of β_1/β_2, where the range of β_1/β_2 is defined by equation (2.18d). Then equation (2.30) can be rewritten as:

$$\frac{X_1^*}{X_2^*} = \frac{\gamma_{22}}{\gamma_{21}} \frac{\dfrac{\beta_1}{\beta_2} - \dfrac{\gamma_{12}}{\gamma_{22}}}{\dfrac{\gamma_{11}}{\gamma_{21}} - \dfrac{\beta_1}{\beta_2}}. \tag{2.33}$$

X_1^*/X_2^* is an increasing function of β_1/β_2. From equation (2.30) it is easy to check that $\beta_1/\beta_2 = \gamma_1/\gamma_2$ implies $X_1^*/X_2^* = 1$. Moreover, condition (2.18d) implies that $\frac{\gamma_{12}}{\gamma_{22}} < \frac{\gamma_1}{\gamma_2} < \frac{\gamma_{11}}{\gamma_{21}}$. Thus, figure 2.6 shows that:

$$\frac{\gamma_1}{\gamma_2} < \frac{\beta_1}{\beta_2} < \frac{\gamma_{11}}{\gamma_{21}} \quad \Longrightarrow \quad \frac{X_1^*}{X_2^*} > 1. \tag{2.34}$$

If $x_1^*/x_2^* < 1$, then equation (2.31) can be rewritten as:

$$\frac{m_2 g_1}{m_1 g_2} > \frac{X_1^*}{X_2^*}. \tag{2.35}$$

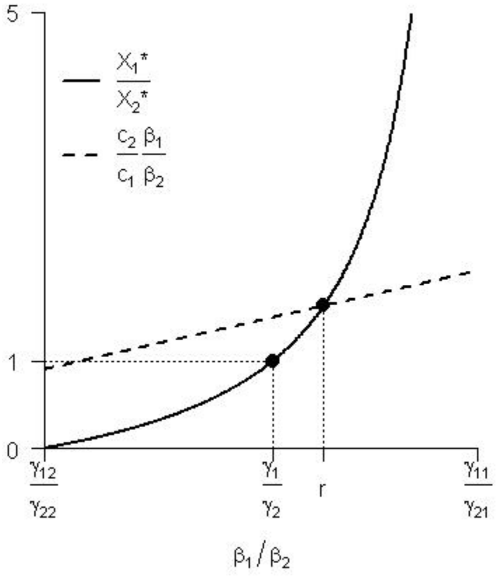

Figure 2.6: *Relative abundance X_1/X_2 as a function of β_1/β_2 in the range of coexistence (solid line). The dashed line represents the straight line passing through the origin which equation is $y = (c_2/c_1) \cdot (\beta_1/\beta_2)$.*

Finally, through the approximation (2.32) and equation (2.33), equation (2.35) becomes:

$$\frac{c_2}{c_1}\frac{\beta_1}{\beta_2} > \frac{\gamma_{22}}{\gamma_{21}} \frac{\dfrac{\beta_1}{\beta_2} - \dfrac{\gamma_{12}}{\gamma_{22}}}{\dfrac{\gamma_{11}}{\gamma_{21}} - \dfrac{\beta_1}{\beta_2}} \quad \Longrightarrow \quad \frac{x_1^*}{x_2^*} < 1. \tag{2.36}$$

Figure 2.6 shows that, provided $c_2/c_1 > \gamma_2/\gamma_1$, both conditions (2.34) and (2.36) are verified if:

$$\frac{\gamma_1}{\gamma_2} < \frac{\beta_1}{\beta_2} < r, \tag{2.37}$$

where I have defined:

$$r = \frac{\left(\frac{c_2}{c_1}\frac{\gamma_{11}}{\gamma_{21}} - \frac{\gamma_{22}}{\gamma_{21}}\right) + \sqrt{\left(\frac{c_2}{c_1}\frac{\gamma_{11}}{\gamma_{21}} - \frac{\gamma_{22}}{\gamma_{21}}\right)^2 + 4\frac{c_2}{c_1}\frac{\gamma_{12}}{\gamma_{21}}}}{2\frac{c_2}{c_1}}. \tag{2.38}$$

Thus, provided that $c_2/c_1 > \gamma_2/\gamma_1$, the condition (2.37) implies both $X_1^*/X_2^* > 1$ and $x_1^*/x_2^* < 1$.

It is important to note that in the case of symmetric facilitation ($\gamma_{12}/\gamma_{22} < 1$ and $\gamma_{11}/\gamma_{21} > 1$), it can be $\gamma_1/\gamma_2 \gtreqless 1$. Thus, we can have the inversion of abundances regardless of the relative magnitude of c_1 and c_2.

The inversion of abundances has a simple interpretation within the pattern of reciprocal replacement: individuals leave the juvenile class either by growth or death. Thus, juveniles that generally replace the shorter-lived species, are expected to have lesser abundance in the understory.

At equilibrium the number of adults that die for each species per unit of time, equals the number of juveniles of the same species that grows into the canopy (see equation (2.3a)). If juveniles of one species always replace adults of the other species (i.e., perfect reciprocal replacement), then the number of adults of each species that die in the unit of time must be equal, i.e.:

$$m_1 X_1^* = m_2 X_2^*. \tag{2.39}$$

Within model (2.3), perfect reciprocal replacement is expected if $\gamma_{12} \ll \gamma_{22}$, $\gamma_{11} \gg \gamma_{21}$, $\gamma_{11} = \gamma_{22}$, $c_1 = c_2$ and $g_1 = g_2$. The latter two conditions imply $\beta_1/\beta_2 = m_2/m_1$.[4] Indeed, in this case, equation (2.33) can be approximated by equation (2.39).

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[4] approximation (2.32) has been used.

2.3.3 Founder control

In the case of founder control (condition (2.18c)), globally stable coexistence of two species is impossible. Nonetheless, the species can still coexist in the habitat through several locally stable equilibria.

Till now, I have considered the case of well-mixed populations living in a habitat. However, "large-scale" spatial heterogeneity can be modelled by considering a habitat of disjunct patches with only weak dispersal between patches. In turn, a patch is taken to be a collection of contiguous cells capable of supporting a single adult (see figure 2.7).

In the simplest scheme, all patches have the same size. Then, model (2.3) can be applied to a generic patch rather than to the entire habitat.[5]

It is important to understand that, here, patchiness is a convenient way to describe spatial heterogeneity due to internal factors, not to environmental gradients. Thus, all model parameters have the same value in all patches of the same size. That is, all patches are potentially identical.

Intuitively, if the dynamics of the generic patch is governed either by two-species coexistence or competitive exclusion of one species by the other, then all cells coalesce into a single, homogeneous habitat-patch which will be dominated by the two species or by the stronger competitor, respectively. But, if the dynamics of the generic patch is founder controlled (i.e., condition (2.18c) holds), then the locally stable equilibria may be generated as follows. Consider first a system of isolated patches (no interpatch dispersal), each

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[5] Patches of different size have both different area and different carrying capacity (i.e., parameters S and k_i in equation (2.2), respectively). Nevertheless, if approximation (2.32) holds, then β_1/β_2 does not depend on S and if $n_i \ll \alpha_{ij}$ and $k_1 = k_2$ (i.e., the species have the same crown diameter), then γ_{ij}/γ_{jj} does not depend on k. In such circumstances, conditions (2.18) refer to all possible patches irrespective of size. Then, they refer to the entire habitat as well.

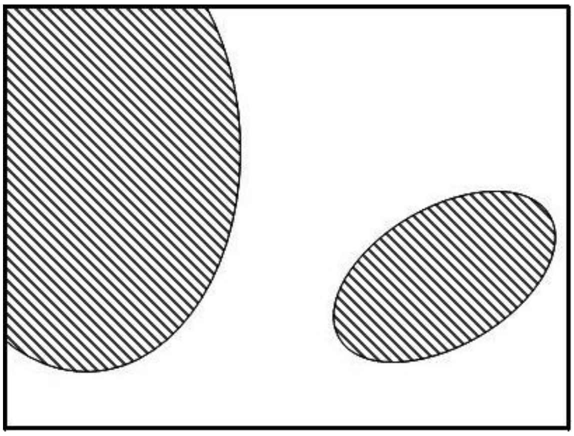

Figure 2.7: *Two species coexisting in a patchy habitat: the white part is dominated by species 1 and the filled part is dominated by species 2.*

patch containing only one species. In this case, any initial assignment of species to patches is stable. Then, even if a weak dispersal between patches is allowed, few individuals of a species cannot invade patches occupied by the other species. Intuitively, each patch should have a locally stable equilibrium with one dominating species and the other present in in small number due to interpatch dispersal (Yodzis, 1978; Shmida and Ellner, 1984). Thus, coexistence depends on the spatial patterning of suitable cells, not just the intrinsic characteristics of species and cells (Shmida and Ellner, 1984). In colonising an empty habitat, species could initially distribute in a patchy pattern because of short dispersal. Then, this pattern could persist because no species can invade a patch occupied by the other species. This requires very low inter-patch dispersal. In summary, founder control refers to patchy habitats wherein the species that numerically dominates a patch is able to resist invasion by competitors.

To illustrate this situation I have considered two patches. One is initially dominated by species 1 and the other by species two. Now, I focus on the

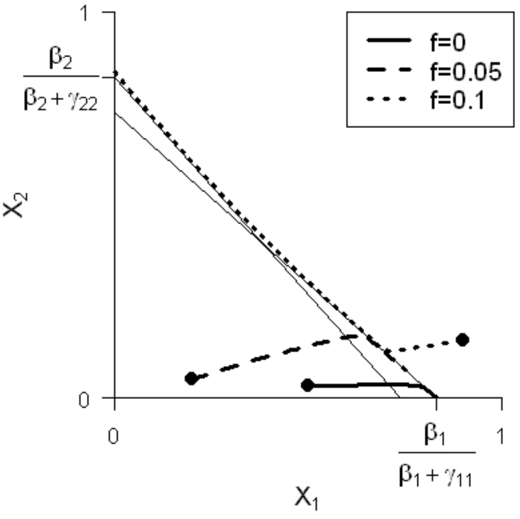

Figure 2.8: *Trajectories in the adult phase plane for three different rates of immigration:* $f = 0$ *(solid line),* $f = 0.05$ *(dashed line),* $f = 0.1$ *(dotted line); black circles indicate initial densities.*

dynamics within the first patch, where a constant immigration term for juveniles of species 2 has been added to the equation (2.3b). The magnitude of this term has been simply set to be a fraction f of the reproduction in the second patch, i.e., $fc_2X_2^*$. Figure 2.8 depicts the trajectories in the (X_1, X_2) phase plane (when condition (2.18c) holds) for three different values of f (to make the figure clearer, three different initial conditions have been chosen as well). If $f = 0$ no interpatch dispersal is allowed and species 1 approaches the equilibrium $\hat{X}_1$, if $f = 0.05$ (i.e., low dispersal) species 1 approaches an equilibrium density close to $\hat{X}_1$ and species 2 is present at low density due to dispersal, if $f = 0.1$ the dispersal is high enough to allow the invasion of species two. This shows that if interpatch dispersal is low the species that numerically dominates a patch is able to resist invasion, thus allowing the maintenance of a patchy habitat.

2.4 Model predictions - three species

A detailed analysis of dynamics with more than two species is beyond the scope of this work. However, through simple considerations about equilibrium points for two species we can find the conditions for the coexistence of three species.

When more than two species are considered several behaviours are possible. Here, I will consider only four simple examples. Results are similar to those for more classical competition models (Huisman and Weissing, 2001).

Model (2.3) with $n = 3$ has eight possible equilibria: P_0, P_i, P_{ij}, P_{ijk} $(i, j, k = 1, 2, 3;\ i \neq j \neq k)$. I consider $\beta_i > 0$, i.e. P_0 is unstable. Then, the unstability of P_i and P_{ij} means that none species goes extinct, i.e. all three species coexist.

The tools that I have used to describe the coexistence of three species are the following conditions:

$$\frac{\beta_i}{\beta_j} > \max\left(\frac{\gamma_{ii}}{\gamma_{ji}}, \frac{\gamma_{ij}}{\gamma_{jj}}\right) \qquad \text{species } i \text{ displaces species } j \tag{2.40a}$$

$$\frac{\gamma_{ij}}{\gamma_{jj}} < \frac{\beta_i}{\beta_j} < \frac{\gamma_{ii}}{\gamma_{ji}} \qquad \text{species } i \text{ and } j \text{ coexist} \tag{2.40b}$$

$$\mathrm{I}(k|i,j) > 0 \qquad \text{species } i \text{ and } j \text{ are invaded by species } k \tag{2.40c}$$

where I defined $\mathrm{I}(k|i,j) \equiv \beta_k - (\beta_k + \gamma_{ki})X_i^{ij} - (\beta_k + \gamma_{kj})X_j^{ij}$. The conditions above are the same as conditions (2.18a,b), (2.18d) and (2.8), respectively. Note that condition (2.40c) makes sense if species i and j coexist when they are alone.

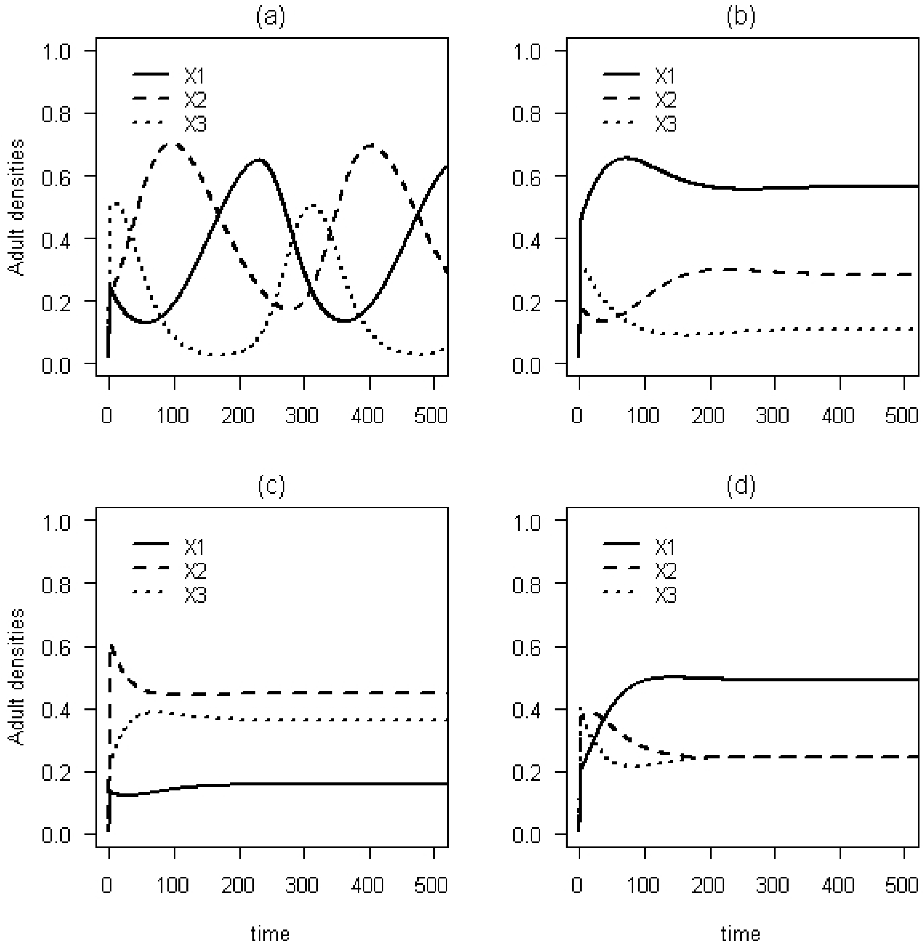

Figure 2.9: *Evolution of adult densities for a three-species system. For simplicity, in all figures have been set* $\beta_1 = \beta_2 = \beta_3$.

In the following four cases equilibria P_0 and P_i are always unstable. Then, the equilibrium points P_{ij} are critical for coexistence:

- No pair can coexist.[6] For example: species 1 displaces species 2; species 2 displaces species 3; species 3 displaces species 1. In this case equilibria P_{ij} do not exist (figure 2.9a).

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[6] Even if no pair can coexist, this case is impossible within the additive model.

- Only one pair can coexist. For example: species 1 and 2 coexist when alone, but they can be invaded by species 3; species 3 displaces species 2 while it is displaced by species 1. In this case the equilibrium P_{12} exist but it is unstable (figure 2.9b).

- Only two pairs can coexist. For example: species 1 and 2 coexist when alone, but they can be invaded by species 3; species 2 and 3 coexist when alone, but they can be invaded by species 1; species 1 displaces species 3. In this case equilibria P_{12} and P_{23} exist, but they are unstable (figure 2.9c)

- All three pairs coexist when alone but are invaded by the third species (figure 2.9d).

In the first three cases the elimination of one species could lead to a monoculture (every species for the first case and species 2 for the other two cases). This could be important for the maintenance of biodiversity.

In general, three species competition models can generate two types of oscillations (Huisman and Weissing, 2001): if such oscillations keep the species far from extinction they are said to be permanent (figure 2.9a). Otherwise, in the case of unpermanent oscillations, there is a high risk of extinction because species abundances could stay near zero for too long (not shown). A formal criterion for permanent coexistence in three-species models was derived by Hutson and Law (1985).

Provided that all the three pairs coexist separately, the three conditions

(2.40c) can be written as:

$$(\gamma_{11}\gamma_{22} - \gamma_{12}\gamma_{21})\beta_3 > \beta_1(\gamma_{22}\gamma_{31} - \gamma_{21}\gamma_{32}) + \beta_2(\gamma_{11}\gamma_{32} - \gamma_{12}\gamma_{31}) \tag{2.41a}$$

$$(\gamma_{22}\gamma_{33} - \gamma_{23}\gamma_{32})\beta_1 > \beta_2(\gamma_{33}\gamma_{12} - \gamma_{32}\gamma_{13}) + \beta_3(\gamma_{22}\gamma_{13} - \gamma_{23}\gamma_{12}) \tag{2.41b}$$

$$(\gamma_{11}\gamma_{33} - \gamma_{13}\gamma_{31})\beta_2 > \beta_1(\gamma_{33}\gamma_{21} - \gamma_{31}\gamma_{23}) + \beta_3(\gamma_{11}\gamma_{23} - \gamma_{13}\gamma_{21}). \tag{2.41c}$$

System (2.41) looks quite ugly. However, it can be instructive to consider the following special case. Assume that both species 1 and 2 are highly tolerant. Moreover, assume that species 2 facilitates species 1, while species 1 inhibits species 2 (i.e., the case of figure 2.4d). As we showed above, coexistence implies a trade-off (i.e., $\beta_2 > \beta_1$). Now, assume that species 3 is highly intolerant and that it has similar mortality under all three canopies (i.e., $\gamma_{31} \approx \gamma_{32} \approx \gamma_{33}$, with $\gamma_{33} > \gamma_{21}$). Finally, assume that species 3 casts a slight shade which does not inhibit species 2 and 3 (i.e., $\gamma_{13} \approx \gamma_{23} \approx 0$). With the last two assumptions the conditions (2.41) can be rewritten as:

$$\beta_3 > \gamma_{33}\frac{\beta_1(\gamma_{22} - \gamma_{21}) + \beta_2(\gamma_{11} - \gamma_{12})}{\gamma_{11}\gamma_{22} - \gamma_{12}\gamma_{21}} \tag{2.42a}$$

$$\frac{\beta_1}{\beta_2} > \frac{\gamma_{12}}{\gamma_{22}} \tag{2.42b}$$

$$\frac{\beta_1}{\beta_2} < \frac{\gamma_{11}}{\gamma_{21}}. \tag{2.42c}$$

Conditions (2.42b) and (2.42c) refer to the coexistence of species 1 and 2, they are equivalent to condition (2.18d). Then, condition (2.42a) fixes a threshold on β_3 for the coexistence of all three species. Condition (2.42a) can be rewritten as:

$$\frac{\beta_3}{\beta_2} > \frac{\gamma_{33}}{\gamma_{21}}\frac{\left(\dfrac{\beta_1}{\beta_2} - \dfrac{\gamma_{12}}{\gamma_{22}}\right) + \dfrac{\gamma_{21}}{\gamma_{22}}\left(\dfrac{\gamma_{11}}{\gamma_{21}} - \dfrac{\beta_1}{\beta_2}\right)}{\dfrac{\gamma_{11}}{\gamma_{21}} - \dfrac{\gamma_{12}}{\gamma_{22}}}. \tag{2.43}$$

As the two terms on right hand side are larger than one,[7] the trade-off between growth in high-light and survival in low-light is extended to the

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[7] Figure 2.4d shows that $\gamma_{21} > \gamma_{22}$.

three species system. That is, coexistence implies $1/\gamma_1 > 1/\gamma_2 > 1/\gamma_3$ and $\beta_3 > \beta_2 > \beta_1$.

Chapter 3

Comparisons with other models

An examination of differences and similarities with other approaches is a useful way to understand the meaning of a model. In this chapter I compare the model presented in this thesis with other mathematical models that try to explain coexistence in a homogeneous environment.

3.1 Classical competition

The simplest competition model was developed by Lotka (1932) and Volterra (1926). For two populations of size x_1 and x_2, it can be written as $(i = 1, 2)$:

$$\frac{dx_i}{dt} = r_i(1 - \alpha_{i1}x_1 - \alpha_{i2}x_2)x_i. \tag{3.1}$$

Coefficient r_i represents the low-density growth for species i, α_{ii} represents the inverse of the carrying capacity of species i when the other species is absent and α_{ij} $(i \neq j)$ describes the strength of the effect of species j on species i. As mechanisms of interactions are not explicit, the system above is phenomenological.

Provided that $r_i > 0$, stable coexistence is possible only if $\alpha_{11} > \alpha_{21}$ and $\alpha_{22} > \alpha_{12}$, that is, if interspecific effects are weak relative to intraspecific effects (e.g., Kot, 2003). Thus, two species coexist if there is no much interaction between them. However, if two species compete for the space they have to interact. Thus, system (3.1) have to be changed to account for the spatial interaction.

3.2 Implicit space structure

If the individuals are plants of similar size competing for the space, then interspecific and intraspecific interactions should have similar strength. Indeed, if the habitat is divided into cells where each cell has the size of an individual and x_i represents the frequency of cells occupied by individuals of species i, then equation (3.1) can be rewritten as $(i = 1, 2)$:

$$\frac{dx_i}{dt} = c_i(1 - x_1 - x_2)x_i - m_i x_i. \tag{3.2}$$

The growth rate depends on available space through the coefficient c_i, while m_i is the mortality rate. Note that the mortality does not depend on density, this means that an individual which occupy a cell cannot be dislodged unless it dies. In the model described by equation (3.2) the interspecific interaction due to competition for space is too strong. Then, the two species cannot coexist (Whittaker and Levin, 1977).

In the equations (3.2) space is implicit, this is simply a reformulation of the classical Lotka-Volterra model to highlight the role of the space as a limiting factor. However, as for the simple Lotka-Volterra model, state variables of equations (3.2) are mean densities.

Thus, in order to describe coexistence, equation (3.2) have to be changed by adding further interactions. For example, if species 1 always excludes the other locally (i.e., species 1 is the superior competitor) at a rate g, then equations (3.2) can be modified to give:

$$\frac{dx_1}{dt} = c_1(1 - x_1 - x_2)x_1 - m_1x_1 + g\,x_2x_1 \tag{3.3a}$$

$$\frac{dx_2}{dt} = c_2(1 - x_1 - x_2)x_2 - m_2x_2 - g\,x_1x_2. \tag{3.3b}$$

Provided that $c_i - m_i > 0$ $(i = 1, 2)$ coexistence is possible only if $c_1 - m_1 < c_2 - m_2$, i.e., if $\hat{x}_2 > \hat{x}_1$; where $\hat{x}_i = 1 - m_i/c_i$ is the equilibrium density of species i when the other species is absent. Thus, coexistence requires a trade-off between competitiveness and colonization ability (Klausmeir and Tilman, 2002). The special case where $g = c_1$ is interesting:

$$\frac{dx_1}{dt} = c_1(1 - x_1)x_1 - m_1x_1 \tag{3.4a}$$

$$\frac{dx_2}{dt} = c_2(1 - x_1 - x_2)x_2 - m_2x_2 - c_1x_1x_2. \tag{3.4b}$$

In this case species 1 is unaffected by species 2 and always attains the equilibrium $\hat{x}_1$, while species 2 persists only if it is able to colonise the space left empty by species 1. This can be extended to any number of species (Tilman, 1994).

In the last two cases, two species competing for space can coexist, but this require the dislodgement of adults by competing individuals (i.e., the adult mortality has to be density dependent). In the case of temperate forest, this is at odds with our scheme of gap dynamics, where juveniles cannot dislodge adults. They have to survive through long periods of suppression until an adult dies, thus releasing space.

Thus, if we want a model where both two species competing for space coexist and adults cannot be dislodged by competing individuals, we have to try something else. One example is the stage structure that I have considered in the model developed in this thesis. The adults cannot be dislodged (i.e., adult mortality is not density dependent) and the two species can coexist because of the interactions between life stages.

A second example is a model presented by Whittaker and Levin (1977). It was developed to explain patterns of interspecific facilitation in communities of sessile organisms. It can be written as:

$$\frac{dX_1}{dt} = r_{11}X_1V_1 + r_{12}X_1V_2 - m_1X_1 \tag{3.5a}$$
$$\frac{dX_2}{dt} = r_{21}X_2V_1 + r_{22}X_2V_2 - m_2X_2 \tag{3.5b}$$
$$\frac{dV_1}{dt} = m_1X_1 - r_{11}X_1V_1 - r_{21}X_2V_1 \tag{3.5c}$$
$$\frac{dV_2}{dt} = m_2X_2 - r_{12}X_1V_2 - r_{22}X_2V_2 \tag{3.5d}$$

where X_i is the fraction of cells occupied by species i and V_i is the fraction of cells vacated by species i, $X_1 + X_2 + V_1 + V_2 = 1$ (i.e., the full space), r_{ij} is the rate at which species i occupies a cell vacated by species j and m_i is the mortality rate.

Using the invasibility criterion it can be shown that provided that $r_{ii} > m_i$ $(i = 1, 2)$, stable coexistence is possible if:

$$\frac{r_{11}}{r_{21}} < \frac{m_1}{m_2} < \frac{r_{12}}{r_{22}}. \tag{3.6}$$

Thus, coexistence is possible if most of the cells vacated by species 1 are occupied by species 2 ($r_{11}/r_{21} < 1$) and vice versa ($r_{12}/r_{22} > 1$) or if species 2 occupies most of the cells vacated by both species 1 and 2 ($r_{11}/r_{21} < r_{12}/r_{22} < 1$) but species 1 has higher longevity than species 2 ($m_1/m_2 < 1$).

The system above stresses the importance of interspecific facilitation for coexistence, but, as the r_{ij} coefficients are phenomenological, it does not give any information on its mechanism. Also, as species can occupy only recently vacated cells, this system cannot describe the occupancy of an empty habitat. Finally, the juvenile dynamics is not represented. In contrast, these topics are faced by the model developed in this thesis.

An interesting modification of model (3.5) has been proposed by Kohyama (1984). There, V_i is replaced by R_i which indicates the frequency of recruitment site of type i. They can be produced by the death of both species at different rates. This stresses the importance of gap attributes (e.g., gap size) in the overall dynamics.

This is not the end of the story: there exist other models that explain coexistence for species competing for the space where adults cannot be dislodged by competing individuals. I give a third example in the next section.

3.3 Lottery models

In the model developed by Shmida and Ellner (1984), two species compete for space in a habitat divided into cells, each cell is capable of supporting a single adult. Each year, each adult produces a number of seeds. A fraction of these are dispersed uniformly over all cells. The remaining seeds are deposited in the parent's cell (non-uniform seed dispersal). All seeds germinate (i.e., become juveniles) in the year after their formation. Competition among juveniles for occupancy of a cell is by lottery. That is, among all juveniles on a vacant cell, one of them is chosen in a (possibly biassed) random draw to occupy that cell as an adult. Cells are vacated by adult mortality but adult cannot be dislodged by competing juveniles. Moreover, for mathematical tractability, the model assumes that all cells are occupied by an adult and the dynamics of juveniles is not considered (i.e., if juveniles are rejected by the lottery, they die immediately). The main result is that species can coexist if one species has the highest fecundity and the other species has the highest longevity (trade-off). However a necessary condition for coexistence is the presence of some degree of non-uniform seed dispersal. Essentially, non-uniform seed dispersal generates a clumped seedling distribution in each species, and the clumping reduces interspecific competition (see also Pacala et al., 1993).

This model is interesting because it considers the effect of dispersal. But, in contrast to the model developed in this thesis, it cannot explain coexistence by interspecific facilitation and/or intraspecific inhibition and it does not deal explicitly with the juvenile stage.

3.4 Resource competition

In section 2.1, I have stressed the importance of species-specific interactions for coexistence. That is, I showed that the reciprocal model allows coexistence, while the additive model does not. A similar result has been obtained by Vance (1984) with a simple model of two species competing for a non-accumulating resource (e.g., light). It is well-known that a single resource can support no more than one species (e.g., Kot, 2003). However, Vance showed that if two species interfere with each other for the resource acquisition, coexistence is possible. Furthermore, such interference have to be species-specific (in the same sense as for the reciprocal model). The similarity with the model presented in this thesis is clear: space acts as an intermediary to encounter the resource (e.g., light). That is, the space can be considered for itself as a non-accumulating resource. Then, two species competing for space cannot coexist (equation (3.2)) unless they interfere with the resource acquisition (e.g., through shade), but coexistence is possible only if this interference is species-specific (i.e., the reciprocal model).

Until now, all models that I have discussed in this chapter are completely solvable, but only the model presented in this thesis has all the following features: (i) species competing for space can coexist; (ii) adults cannot be dislodged by competing individuals; (iii) coexistence can be explained both by a trade-off between strategies and the effect of interspecific facilitation and/or intraspecific inhibition; (iv) model parameters have a mechanistic interpretation; (v) a stage structure is considered. In the fourth chapter I will show that all these features are important to model forest dynamics.

There exist other mathematical models that capture all the features above, but generally they have to be solved numerically, thus complicating the analysis of mechanisms behind coexistence. Some of them are discussed in the next section.

3.5 Size structure

The model presented in this thesis has the simplest stage structure: just two levels. It is possible to add more stages, for example the seed stage, but, mathematically, that complicates matters. Also, if the new stage has weak interaction with the rest of stages, it is likely that its inclusion is not relevant. For example, if all seeds have low mortality and they germinate at the same rate, then the inclusion of a seed stage should not affect the dynamics.

Essentially, the two-stage assumption means that I neglected the shade cast by a juvenile on a lower juvenile relative to the shade cast by adults and that all adults have similar height (i.e., they do not shade each other). The effect of a difference in the maximum height of adult plants in a simple two-size model has been described by Kohyama and Takada (2009).

However, there are several reasons to study the full size distribution of a forest. In this case the state variables n_i are the size distribution of the species (the index i indicates the species). They are defined as:

$$N_i(t) = \int_0^\infty n_i(t,x)\,dx. \tag{3.7}$$

Where $N_i(t)$ is the density of the total population (m^{-2}) and $n_i(t,x)$ (m^{-2} cm^{-1}) is the distribution density of trees of dbh[1] x (cm) at time t (year). The dynamics of $n_i(t,x)$ is described by the McKendrick-von Foerster equation (see Kot, 2003):

$$\frac{\partial n_i}{\partial t} = -\frac{\partial}{\partial x}(n_i G_i) - m_i n_i. \tag{3.8}$$

Where $G_i = dx/dt$ (cm year^{-1}) is the mean growth rate and m_i (year^{-1}) is the mortality rate of a species at size x and at time t. The equation above needs to be supplemented with a boundary conditions that describes the flux of newborn individuals into the smallest size class x_0: $n_i(t,x_0)G_i(t,x_0)$ (m^{-2} year^{-1}).

Size and height are assumed to be linked by some allometric equation. Then, in one-sided competition is important to know the basal area of trees larger than x: $B(t,x)$ (cm^2 m^{-2}). It is defined by:

$$B(t,x) = \sum_i B_i(t,x) = \sum_i \int_x^\infty \pi\left(\frac{y}{2}\right)^2 n_i(t,y)\,dy \tag{3.9}$$

Kohyama (1992) used this approach to model the dynamics of a rain forest. He defined:

$$G_i(t,x) = x[a_i - a_{1i}\ln x - \alpha_i B(t,x)] \tag{3.10}$$

where a_i (year^{-1}) relates to growth for small trees, $\exp(a_i/a_{1i})$ defines potential maximum dbh and α_i (m^2 cm^{-2} year^{-1}) represents the susceptibility to suppression. Also, he used a constant mortality m_i and a boundary condition defined as:

$$n_i(t,x_0)G_i(t,x_0) = d_i B_i(t,x_0)\exp[-\beta_i B(t,x_0)] \tag{3.11}$$

---

[1] stem diameter at 1.30 m height

where d_i (cm^{-2} year^{-1}) is per capita recruitment rate and β_i (m^2 cm^{-2}) is the coefficient of depression due to shading. An important advantage of this approach is that model parameters can be estimated directly through field measurements. However, it seems almost impossible to obtain an analytical solution. Thus, results have to be computed numerically.

Note that the suppression terms depend on the cumulative basal area of all trees irrespective of species. In this case (additive model), the model presented in this thesis predicts that eventually one species excludes all the competitors. In the model of Kohyama multispecies coexistence is possible, but only if the species have different maximum dbh. Coexistence is through a trade-off between maximum size and recruitment rate (Kohyama, 1993).

In a subsequent study, Nakashizuka and Kohyama (1995) addressed the dynamics of a mixed forest of evergreen coniferous and deciduous broad-leaved tree species. In this case they considered a species-specific shading effect (i.e., reciprocal model). In mathematical terms, they replaced equations (3.10) by:

$$G_i(t,x) = x[a_i - a_{1i}\ln x - \alpha_{i1}B_1(t,x) - \alpha_{i2}B_2(t,x)]. \tag{3.12}$$

Also, they reformulated the recruitment (equation (3.11)) for the additive model as:

$$n_i(t,x_0)G_i(t,x_0) = B_i(t,x_0)[d_i - \beta_i B(t,x_0)] \tag{3.13}$$

and the recruitment in the reciprocal model as:

$$n_i(t,x_0)G_i(t,x_0) = B_i(t,x_0)[d_i - \beta_{i1}B_1(t,x_0) - \beta_{i2}B_2(t,x_0)] \tag{3.14}$$

(here the coefficients β are expressed as m^2 cm^{-4} year^{-1}).

The potential maximum height for the two species was slightly different. The results of the simulations showed that coexistence is possible within both the additive and the reciprocal model, but the domain of coexistence was remarkably broader for the reciprocal model (Nakashizuka and Kohyama, 1995).

Thus, the prediction of the model presented in this thesis that coexistence is possible only within the reciprocal model seems to be verified also in a model with continuous size-structure, at least if species have the same maximum height.

Recently, Strigul et al. (2008) and Adams et al. (2007) used a similar approach. They introduced a useful concept that they termed *perfect plasticity approximation* (PPA) (Strigul et al., 2008) or *ideal tree distribution* (ITD) (Adams et al., 2007). Essentially, this concept states that canopy structure reduces to a simple form where foliage above a critical height Z^* (in turn, Z^* defines a critical size x^*) is exposed to sunlight, and other foliage is in the understory (see figure 3.1).

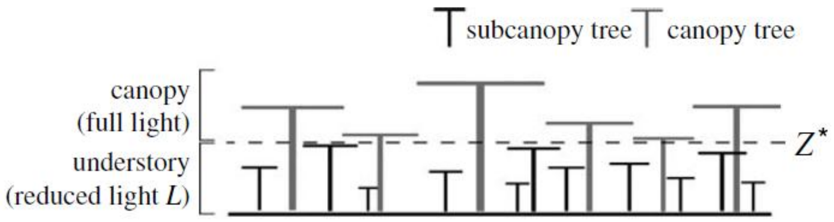

Figure 3.1: *Schematic representation of the ideal tree distribution* (from Adams et al., 2007).

As this scheme is based on the two basic levels of the size structure (i.e., understory and overstory), I expect that the model developed in this thesis is able to capture the basic features of the model developed by Strigul et al. (2008) and Adams et al. (2007). And, indeed, this is the case. In the following I will show similarities and differences between the two models.

Adams et al. (2007) defined constant growth and mortality for the two levels as follows:

$$
\begin{array}{lll}
G_i = G_{Ui} & m_i = m_{Ui} & \text{if } x < x_i^* \\
G_i = G_{Oi} & m_i = m_{Oi} & \text{if } x > x_i^*.
\end{array}
$$

This leads to a continuity condition on the flux at the boundary such that the total rate at which cohorts (i.e., trees with the same size) "arrive" at size x_i^* must equal the rate at which they "leave", as canopy trees.

They focused on the crown area of canopy trees $C_i(t, x)$ (m^2 m^{-2}) rather than on the basal area. It is defined as:

$$C(t) = \sum_i C_i(t) = \sum_i \int_{x_i^*}^{\infty} \pi(\alpha_i x)^2 n_i(t, x)\, dx \tag{3.15}$$

where α_i is the crown radius parameter (m cm^{-1}). Then, the influx of new individuals is defined by:

$$n_i(t, 0) G_{Ui} = F_i C_i(t) \tag{3.16}$$

where F_i is the fecundity parameter (m^{-2} year^{-1}).

The minimum dbh required by species i for entry into the canopy $x^*(t)$ is a dynamic state variable represented by the following integral condition:

$$C(t) = 1. \tag{3.17}$$

This reflects the assumption that, at any time t, the canopy is perfectly filled by trees with dbh$> x_i^*(t)$.

The growth and mortality rates in the understory depend on light transmitted by canopy trees (L), then $G_{Ui} = G_{Ui}(L)$ and $m_{Ui} = m_{Ui}(L)$. Hence, unless different species have the same transmissivity, this set of equations is designed for a monoculture. However, conditions for the coexistence of two species can be analysed through the invasibility criterion discussed in the second chapter.

Consider a monoculture of species i. At equilibrium, the critical size x_i^* attains the value:

$$\hat{x}_i^*(L_i) = \frac{G_{Ui}(L_i)}{m_{Ui}(L_i)} \ln \frac{2\pi\alpha_i^2 F_i G_O^2}{m_O^3} \tag{3.18}$$

(Strigul et al., 2008). Note that a juvenile of species i, survives the suppression at light level L_i if $G_{Ui}(L_i)/m_{Ui}(L_i)$ is high enough.

I set $1/\gamma'_{ii} = G_{Ui}(L_i)/m_{Ui}(L_i)$ and $\beta'_i = \ln \frac{2\pi\alpha_i^2 F_i G_O^2}{m_O^3}$. $1/\gamma'_{ii}$ is a measure of survival of understory trees of species i when they are suppressed by adult of the same species. The term $2\pi\alpha_i^2 F_i G_O^2/m_O^3$ in the equation above, is the lifetime reproductive success of a tree (Strigul et al., 2008). That is, the term c_i/m_i in the simple Levins model (Levins, 1969). Strigul et al. (2008) showed that $\beta'_i > 0$ is the condition for the persistence of a monoculture of the species i.

I chose the letters γ' and β' to highlight the relationship with the model developed in this thesis. Using γ' and β', equation (3.18) can be rewritten as:

$$\hat{x}_i^*(L_i) = \frac{\beta'_i}{\gamma'_{ii}} \tag{3.19}$$

Adams et al. (2007) showed that a species j can invade a monoculture of species i if:

$$\hat{x}_j^*(L_i) > \hat{x}_i^*(L_i) \quad \text{i.e., if} \quad \frac{\beta'_j}{\gamma'_{ji}} > \frac{\beta'_i}{\gamma'_{ii}} \tag{3.20}$$

This equation is conceptually identical to the equation (2.17). Therefore, the model developed in this thesis and the model developed by Adams et al. (2007) have identical conditions to describe all the four possible behaviours of the two-species system.

Moreover, if the two species have the same transmittivity (i.e., $L_i = L_j = L$) the model of Adams et al. (2007) predicts that eventually only the species with the highest $\hat{x}^*(L)$ dominates the habitat. Indeed, the fact that the two species have the same transmittivity is equivalent to the additive version of the model developed in this thesis (i.e., $\alpha_{i1} = \alpha_{i2} = \alpha_i$).

The approach based on the McKendrick-von Foerster equation has been extended to describe horizontal heterogeneity (Kohyama, 1993; Kohyama et al., 2001; Hurtt et al., 1998; Moorcroft et al., 2001). In this case $n(t, x)$ is replaced by $n(t, a, x)$ where a indicates the age of a gap since its formation. This model approximates the shifting-patch mosaic of forest landscapes according to the age distribution of patches with different tree-size structures, wherein the creation of tree-fall gaps corresponds to the "death" of a patch of particular age and the simultaneous "birth" of a gap, resetting the patch age to zero. Tree-size structure is developed with patch ageing, and the demography of trees in each patch is regulated by patch-scale tree-size structure. The application of this type of model simulated coexistence based on a trade-off between growth and tolerance even if the species have the same potential maximum dbh (Kohyama, 1993).

Models based on the von-Foerster equation have a high potential to simulate real forests. Indeed, model parameters, such as growth and mortality, are directly linked to individual tree attributes. However, this kind of models are too complex to be solved analytically. The model developed in this thesis is a simplified version of the von-Foersters models. Model parameters are still linked to individual tree attributes, but the linkage is less clear than for the von-Foerster models. For example the g parameters in equations (2.3) are not simply the diameter growth rates. However, the model developed in this thesis can be solved analytically. For example, this leads to an analytical expression of the equilibrium densities of two coexisting species. This could be useful in analysing the model (see next chapter).

Chapter 4

Model applications

4.1 Introduction

In this thesis I did not attempt to evaluate model parameters with data. However, to support the validity of the ideas contained in the present model, in this chapter I will qualitatively compare the three basic model behaviours – coexistence, founder control and competitive exclusion – with a number of studies based on observations of temperate forest in northern U.S. The case studies were chosen according to the general structure of the model. Essentially, I looked for an homogeneous environment (habitat) and a system governed by competition for space (gap dynamics).

The goal of this chapter is twofold. On one hand, I tested the ability of the model to predict real observations. On the other hand, I used the model to give a simple explanation of observed behaviours.

To analyse coexistence, I focused on the well-known beech-maple communities (Forcier, 1975; Fox, 1977; Woods, 1979; Chyper and Boucher, 1982; Canham, 1989, 1990; Poulson and Platt, 1996; Gravel et al., 2008). From the studies that I have considered, three different ideas emerge.

The studies of Fox (1977), Woods (1979) and Chyper and Boucher (1982) support the idea of coexistence based on reciprocal replacement. In contrast, other studies (Forcier, 1975; Canham, 1989, 1990; Poulson and Platt, 1996) support the idea of coexistence based on a trade-off between strategies. Finally, the study of Gravel et al. (2008) points out that the high level of similarity between species in terms of their response under the relatively limited range of conditions that are typically encountered in a single stand, precludes a deterministic interpretation of coexistence, at least at a local scale (Gravel et al., 2008).

The model presented in this thesis provides a simple, qualitative interpretation for all three observations. To analyse the effect of founder control and competitive exclusion, I used part of the studies carried out by Pacala and colleagues to define the individual based forest simulator SORTIE (Pacala et al., 1993). These studies focus on individual tree attributes such as growth (Pacala et al., 1994), juvenile mortality (Kobe et al., 1995) and light transmissivity (Canham et al., 1994).

In the case of founder control I simply identified a pair of species whose attributes agree with the founder control regime. As expected (see section 2.3.3), these two species (beech and hemlock) typically coexist in a patchy pattern.

Finally, I used the equations that govern the competitive exclusion regime, to analyse the link between shade tolerance and successional status.

4.2 Beech-maple communities

The dynamics of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) communities is a simple and well-studied system that can be useful in improving our understanding of coexistence in highly shade-tolerant species. (e.g. Horn, 1971; Forcier, 1975; Woods, 1979; Poulson and Platt, 1996; Gravel et al., 2008).

Generally the most tolerant tree species are those that shed the deepest shade (e.g., Canham et al., 1994). Horn (1971) proposed that beech and maple could be an exception to this rule: maple being the more tolerant and beech the one that casts the deepest shade. If this tolerance order reverses passing from the beech canopy to the maple canopy (figure 2.4b), then species tend to replace each other in a pattern of symmetric facilitation. In this case coexistence has a clear explanation (Whittaker and Levin, 1977; Fox, 1977; Woods, 1979). Several cases of reciprocal replacement in beech-maple communities have been documented (Fox, 1977; Woods, 1979; Chyper and Boucher, 1982). In this case coexistence is based on species-specific biology such as tolerance, growth rate etc. (autogenic coexistence).

In contrast, Poulson and Platt (1996) did not find statistical evidence of reciprocal replacement. They explained coexistence by means of the combined effects of environmental variation and a trade-off between strategies (allogenic coexistence).

Coexistence based on reciprocal replacement is not surprising (Whittaker and Levin, 1977) and it is easily predicted by the model developed in this thesis. On the other hand, coexistence based on trade-off between strategies is less evident specially for highly tolerant species.

For this reason it is interesting to perform a qualitative fit between model (2.3) and the observations of Poulson and Platt. They studied an old-growth forest at Warren Woods, Michigan co-dominated by beech and maple (hereafter, species 1 and 2, respectively). Roughly, the main observations of Poulson and Platt are:

1. Beech has generally higher survival in shade (low-light) and maple has generally higher growth in canopy openings (high-light). This trade-off has been observed also in other beech-maple communities (Forcier, 1975; Canham, 1989, 1990). Moreover, it is well-known that beech casts the deepest shade (Canham et al., 1994).

2. In the forest as a whole, from 1933 to 1980, sugar maple remained dominant in the understory and beech in the overstory (i.e., $X_1^* > X_2^*$ and $x_1^* < x_2^*$). Many workers have been impressed by the dominance of sugar maple in understory and so have predicted that maple might increase in the canopy. However, the size distribution of the two species appears approximately constant.

3. After 1975, a sudden increase in tree-fall gaps due to external factors (increasing windstorms) occurred. As maple grows better in gaps, this effect was concomitant with an increase in maple relative abundance. For this reason they defined the coexistence as allogenic.

I now look for a range in the model parameters such that model (2.3) qualitatively reproduces all the reported behaviours. First of all coexistence requires condition (2.18d). Then, the first point is met by setting $\gamma_{12}/\gamma_{22} < \gamma_{11}/\gamma_{21} < 1$ (see figure 2.4d) and $g_2 > g_1$. In this case species coexist under asymmetric facilitation. As discussed in section 2.3.1, this implies the trade-off between survival at low-light and growth at high-light (i.e., $1/\gamma_1 > 1/\gamma_2$ and $\beta_2 > \beta_1$).

The second point requires $c_2/c_1 > \gamma_2/\gamma_1 > 1$ (see section 2.3.2), which is reasonable as maple has more efficient dispersal mechanisms (U.S. Department of Agriculture, 1974). Then, the ratio m_2/m_1 is constrained by condition (2.37). Note that, given $g_2 > g_1$ and $X_1^* > X_2^*$, equation (2.35) implies $m_2 > m_1$ which means that beech is more longeve than maple (Fox, 1977).

Figure 2.6 has been drawn assuming that $\gamma_{12}/\gamma_{22} = 0.4$, $\gamma_{11}/\gamma_{21} = 0.9$, $g_2/g_1 = 1.1$, $c_2/c_1 = 2.26$ and, for simplicity, $\gamma_{11} = \gamma_{22}$. The ratio m_2/m_1 was then constrained by condition (2.37): $1.65 < m_2/m_1 < 1.8$.

By choosing $m_2/m_1 = 1.7$, a numerical simulation of model (2.3) shows either that beech and maple coexist and that there is an inversion between understory and overstory abundance (figure 4.1a).

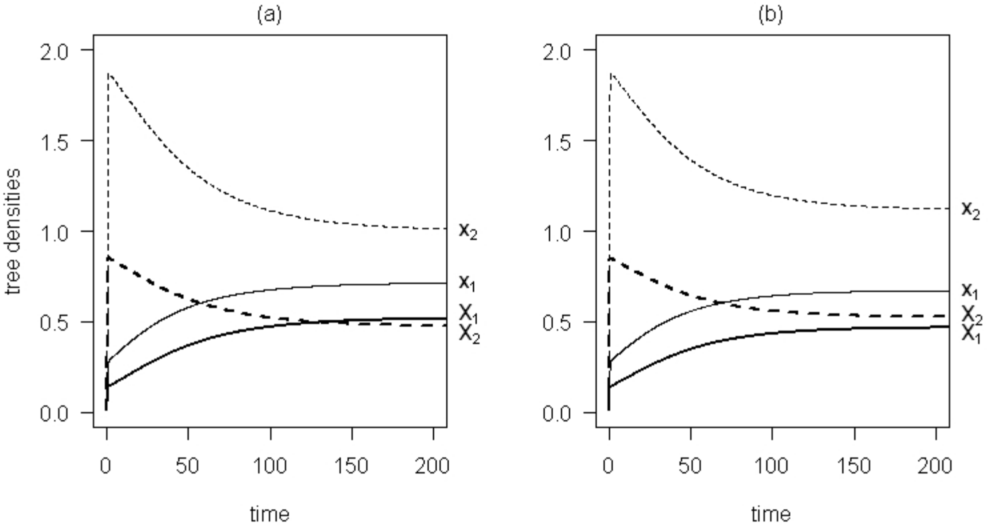

Figure 4.1: *Evolution of system* (2.3) *from low densities. Species are: adult beech* (X_1)*; juvenile beech* (x_1)*; adult maple* (X_2)*; juvenile maple* (x_2)*. Panel a):* $c_1 = 10$, $c_2 = 22.6$, $g_1 = 10$, $g_2 = 11$, $m_1 = 0.1$, $m_2 = 0.17$, $n_1 = n_2 = 0.1$, $\alpha_{11} = 10$, $\alpha_{12} = 4$, $\alpha_{21} = 11$, $\alpha_{22} = 10$. *Panel b): the same as a) except for* $m_1 = 0.11$ *and* $m_2 = 0.18$.

I recall that this fit is qualitative (units of measure are not specified) and it is simply based on ratios between parameters of the two species. Any choice of parameters in agreement with the ratios above, gives a similar qualitative pattern.

Finally, the simple condition $m_2 > m_1$ is sufficient to reproduce the third observation. I assumed that a windstorm kills a number of individuals of each species in proportion to its relative abundance. Thus, I modelled the windstorms by assuming that adult mortality of both species increase of an amount δ (i.e., $m_i \rightarrow m_i + \delta$). Then, it is easy to show that:

$$\left| \frac{d}{d\delta}\left(\frac{\beta_1}{\beta_2}\right) \right|_{\delta=0} \gtreqless 0 \quad \text{if} \quad \frac{\beta_1}{\beta_2} \gtrless \frac{c_1 g_1 m_2}{c_2 g_2 m_1} \frac{m_2}{m_1}. \tag{4.1}$$

If the approximation (2.32) holds, equation (4.1) can be rewritten as:

$$\left| \frac{d}{d\delta}\left(\frac{\beta_1}{\beta_2}\right) \right|_{\delta=0} \gtreqless 0 \quad \text{if} \quad \frac{m_2}{m_1} \lesseqgtr 1. \tag{4.2}$$

This means that if species 1 has the highest longevity (i.e., $m_2/m_1 > 1$), then raising the adult mortality of both species of an amount δ implies a decrease of the ratio β_1/β_2, which in turn implies a decrease of the ratio X_1^*/X_2^* (see figure 2.6).

Thus, model (2.3) predicts that an increase in tree-fall gaps, as a result of an increase in windstorms, is followed by an increase of maple relative abundance in the overstory. This is shown by the comparison between figure 4.1a ($\delta = 0$) and figure 4.1b ($\delta = 0.01$). From this point of view, coexistence is the result of the internal structure of the system, while external variations affect the equilibrium densities.

Forcier (1975) studied the dynamics of a beech-maple-birch community. Beech and maple showed the same trade-off between strategies as in Poulson and Platt (1996) and the yellow birch, that is too intolerant to establish advanced reproduction in its own shade, persists because of its ability to occupy recent openings (Forcier, 1975). This pattern can be interpreted through equation (2.43) where yellow birch represents the third species, while beech and maple are the species 1 and 2, respectively.

Recall that the model works if dispersal is not a critical factor. I have no information for the site of Poulson and Platt (1996), however there are examples of beech-maple communities that are not dispersal-limited (e.g., Gravel et al., 2008).

4.3 Patchiness

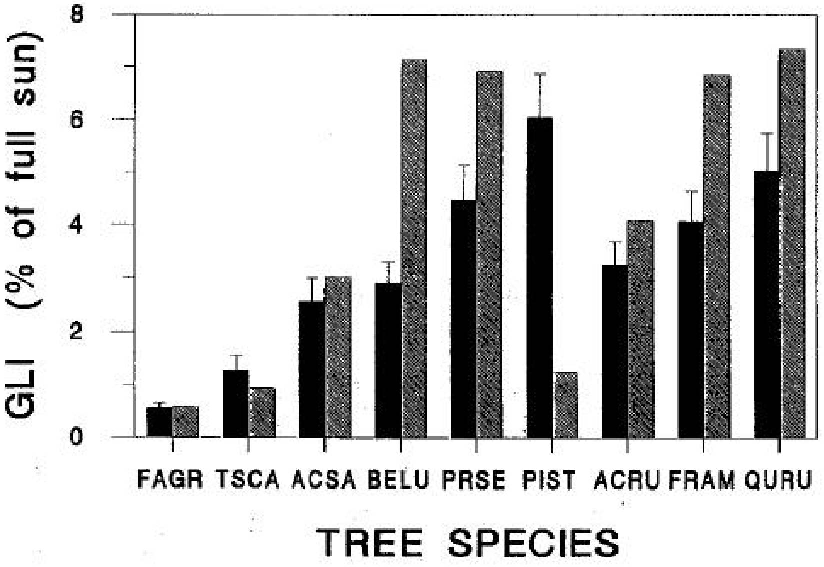

Figure 4.2: *Solid bars: Average gap light index (GLI) at 1 m height beneath mixed canopy where each species is the single dominant (FAGR=Beech; TSCA=Hemlock; ACSA=Sugar Maple; BELU=Yellow birch; PRSE=Black Cherry; PIST=White Pine; ACRU=Red Maple; FRAM=White Ash; QURU=Red Oak). Cross-hatched bars: GLI at ground level for a pure canopy of each species (from Canham et al., 1994).*

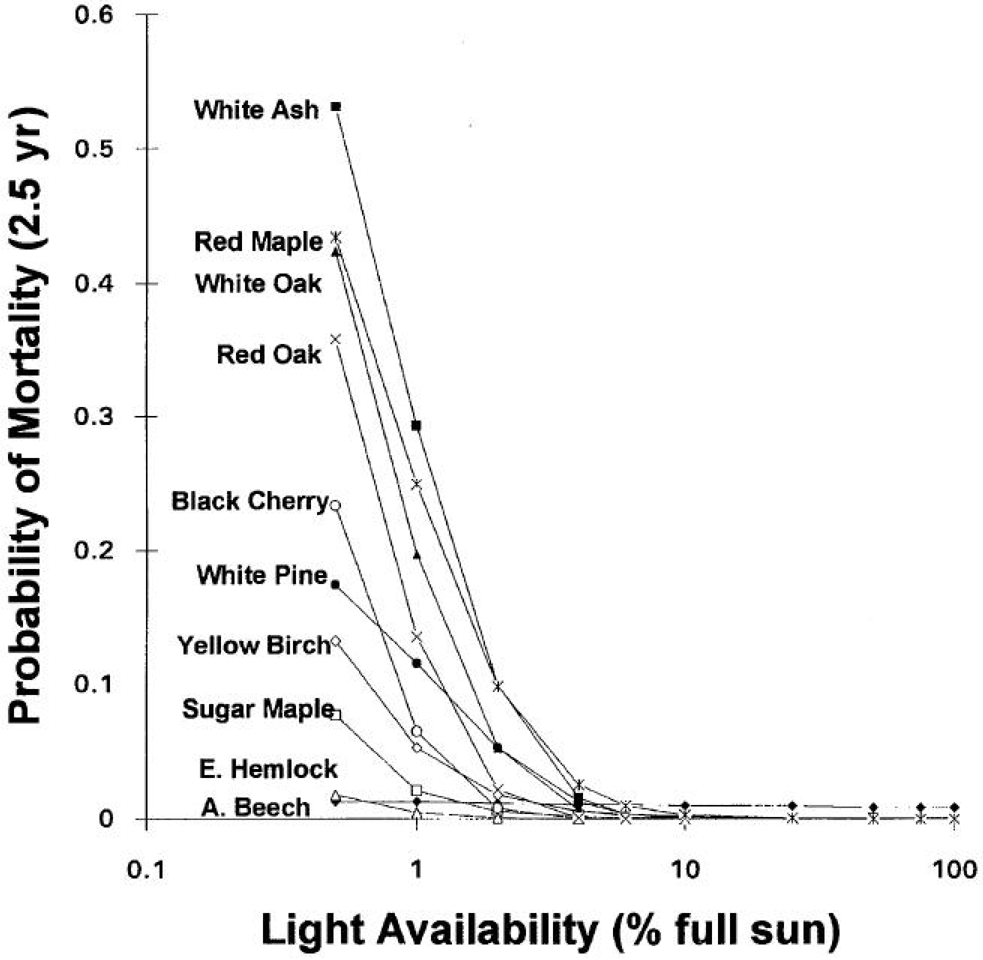

Figure 4.3: *Juvenile mortality as a function of light intensity (GLI) (from Kobe et al., 1995).*

Canham et al. (1994) and Kobe et al. (1995) studied canopy transmissivity (figure 4.2)[1] and juvenile mortality (figure 4.3) for a forest community which is numerically dominated by beech and hemlock. The two species coexist in monospecific patches that cannot be invaded by the other species. Then, competition between species becomes localised at the boundaries between

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[1] GLI is an index for light levels in the understory (Canham, 1988).

patches, resulting in a relatively slow dynamics (not discussed in this thesis).

Both beech and hemlock have both high tolerance and short dispersal (Pacala et al., 1993). The short dispersal promotes coexistence because, by reducing the number of between-species contacts, it reduces the level of interspecific competition. Pacala et al. (1993) argued that this mechanism is an essential reason for the beech-hemlock coexistence.

In section 2.3.3 I showed that both short dispersal and the founder control regime are necessary for the maintenance of patchiness. If we consider species with similar colonisation ability (i.e., $\beta_1/\beta_2 \approx 1$), then founder control is possible only if the pattern of canopy transmissivity and juvenile mortality is similar to the one depicted in figure 2.4a.

A comparison between figures 4.2 and 4.3 shows that if we indicate beech as species 1 and hemlock as species 2, then beech and hemlock fall within the case depicted by figure 2.4a, page 32. Thus, they are good candidates for coexistence in a patchy habitat.

However, this is true for almost all species when paired with beech (figures 4.2 and 4.3). This is because the beech mortality curve is an horizontal line which crosses the mortality curves of all other species (figure 4.3). That is, beech mortality does not depend on light, perhaps because, at the site investigated by Kobe et al., saplings are predominantly root sprout and could be receiving carbon subsidies from parent trees (Kobe et al., 1995).

This suggests that the ability to resprout promotes patchiness, which is reasonable. However, as in this case the other species have very low density, it is likely that the high tolerant hemlock is able to exclude all species other than beech and yellow birch. Indeed, yellow birch, which is the third most abundant species in hemlock-beech old growth stands, is able to persist in patches numerically dominated by hemlock (see also next section).

4.4 Forest succession

Connell and Slatyer considered three conceptual models to describe succession. One of them, the inhibition model, is suitable for temperate forest. It assumes that any arriving species, including those which usually appear later, may be able to colonise. However, once earlier colonists secure the space and/or other resources, they inhibit the invasion of subsequent colonists or suppress the growth of those already present. The latter invade or grow only when the dominating residents are damaged or killed, thus releasing resources. *The greater tolerance of late-succession species is of importance, not in allowing net growth beneath earlier species, but in allowing the late species to survive through long periods of suppression* (Connell and Slatyer, 1977).

The model presented in this thesis (equations (2.3)) fully agrees with such model. Indeed, the condition for a later species to invade an occupied habitat is always more restrictive than the condition to invade an empty habitat (see equation (2.8)). Moreover, later species can grow only when earlier species release space (see equation (2.3a)), but they cannot displace earlier occupants before they die (adult mortality does not depend on juvenile densities).

In order to highlight basic mechanisms behind succession, I now focus on the additive version of model (2.3) (i.e., $\gamma_i = \gamma_{ij} = \gamma_{ik}$ for every value of j and k). In this case, a species always displaces the others (i.e., competitive exclusion). Then, species i displaces species j if $\beta_i/\gamma_i > \beta_j/\gamma_j$ (see condition (2.17)). For each species it is convenient to define the competitive ability (or competitiveness) k_i as:

$$\frac{\beta_i}{\gamma_i} = k_i. \tag{4.3}$$

Then the higher the value of k_i, the higher the competitive ability of species i. In the unlikely case that more species have the same value of k_i, those

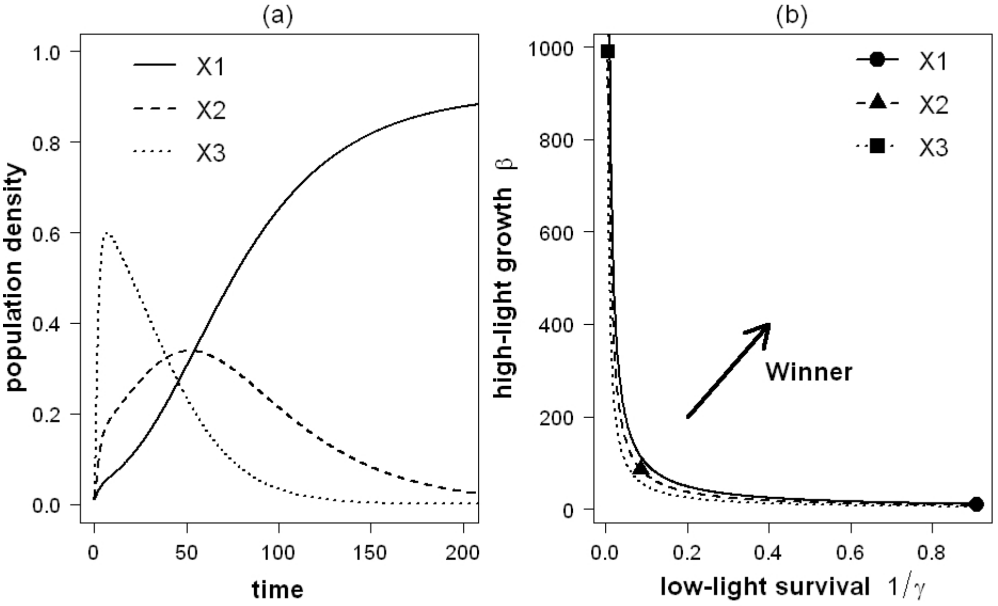

Figure 4.4: *Schematic representation of a succession. Three species are initially present as juveniles at very low density. Species 3 (dotted lines, square point) has the highest growth in high-light (GHL), the lowest survival in low-light (SLL) and the lowest overall competitive ability (OCA). Species 2 (dashed line, triangular point) has intermediate GHL, SLL, and OCA. Species 1 (solid line, circle point) has the lowest GHL, and both the highest SLL and OCA. The numerical dominance of the habitat is first achieved by species 3, then by species 2 and, eventually, species 1 exclude the others. Succession proceeds towards decreasing GHL, increasing SLL and increasing OCA.*

species are distributed on an hyperbola in the $(1/\gamma, \beta)$ plane. In this case there is no tendency for any displacement. But, if species belong to different hyperbolae, the one on the "innest" hyperbola (i.e., highest k_i) will displace the others (figure 4.4b).

It is hypothesised that species allocating a large fraction of photosynthate to internal storage would have higher survival but would preclude carbohydrate allocation to rapid growth (Kobe, 1997). Thus, the competitive ability of species is generally split into two strategies: opportunism (i.e., high growth in high-light, i.e., high β_i) and tolerance (i.e., high survival in low-light, i.e., high $1/\gamma_i$).

Note that model (2.3) predicts that the "climax" species is that with the highest value of k_i irrespective of its strategy. If it is an opportunist species, then we will not observe any succession.[2] A succession occurs only when the "climax" species is not the fastest invading species. That is, succession proceeds towards increasing competitive ability, increasing tolerance level and decreasing opportunism (figure 4.4). As we in fact observe successions, it could be argued that the tolerance strategy is more effective than the opportunist strategy in colonising a closed habitat.

Based on studies used for the parametrization of the forest simulator SORTIE (Pacala et al., 1993), Pacala and colleagues identified the tree species at their site according to both an index for high-light growth and an index for low-light survival (figure 4.5) (Pacala et al., 1994; Kobe et al., 1995). They interpreted figure 4.5 as if the species were arrayed along a one-dimensional axis according to their successional status or, equivalently, to their level of shade tolerance (successional status and shade tolerance are closely related).

Species are traditionally classified into a roughly decreasing order of shade tolerance as follows (Baker, 1949): beech, hemlock, sugar maple, red maple, yellow birch, white pine, red oak, black cherry and white ash. Figure 4.5 has

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[2] Here, I consider a situation where all possible species are present in the habitat at some initial time. The generalization to the case where some species arrive later is straightforward.

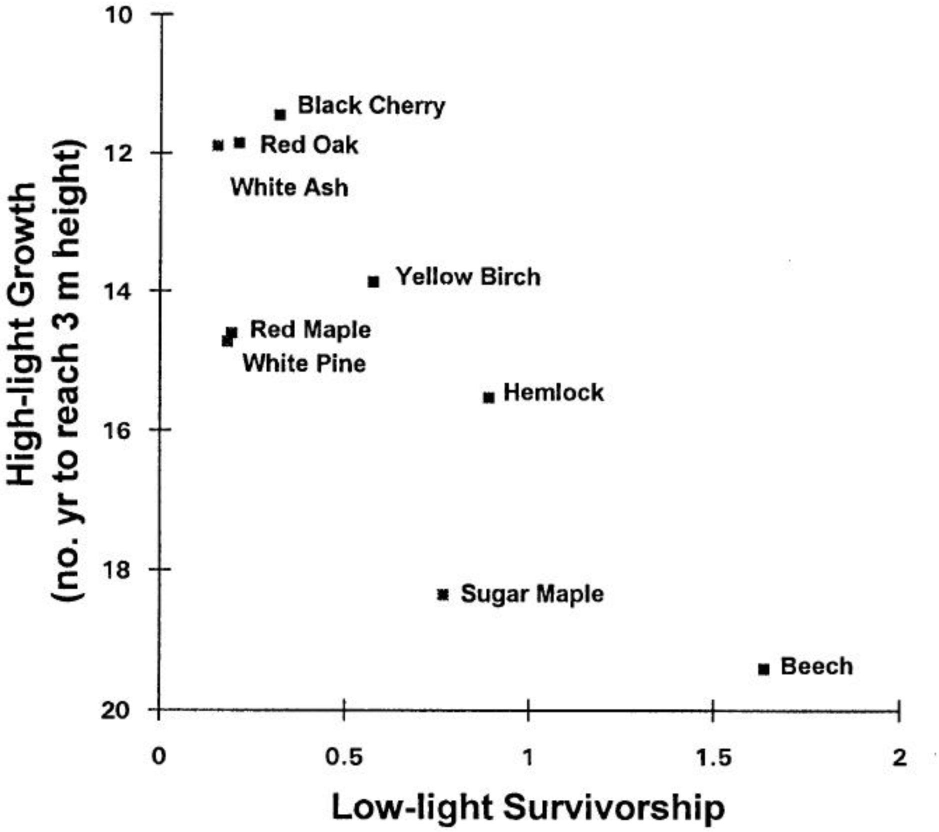

Figure 4.5: *The x axis, or low-light survival, is calculated from the decay parameter of a simple mortality predictor at low-light. The y axis represents the number of year necessary for a seedling to reach 3 m in height at full sunlight (from Pacala et al., 1994; Kobe et al., 1995)*

large error intervals (not shown) (Kobe et al., 1995). However, it seems that hemlock and sugar maple are the only discrepancy between this classification and figure 4.5.

I propose to interpret figure 4.5 in the light of figure 4.4. The hyperbolic shape in figure 4.5 is then apparent if we consider that both hemlock and yellow birch are easily found in late successional stands (Pacala et al., 1993;

Deutschman et al., 1997). That is, both hemlock and yellow birch lie on inner hyperbolae than, say, sugar maple. With this interpretation, hemlock has higher probability than sugar maple to be present in late successional stands.

These arguments can be extended to the case of the reciprocal model (i.e., $\gamma_{ij} \neq \gamma_{ik}$ with $j \neq k$). Here, the survival in understory (low-light) is not an absolute parameter but depends on canopy composition. In turn, canopy composition changes with time, then species have not a unique hyperbola as for the additive model. However, if n species coexist in the habitat, the system approaches the equilibrium given by $(X_1^*, X_2^*, \ldots, X_n^*)$. In this case it is convenient to define an *equilibrium low-light survival* as follows:

$$\frac{1}{\gamma_i^*} = \frac{1}{\gamma_{i1}X_1^* + \gamma_{i2}X_2^* + \ldots + \gamma_{in}X_n^*}. \tag{4.4}$$

Note that the additive model is the special case where $X_i^* = 1/n$ for all $i = 1, \ldots, n$. Then, through equations (2.5) it is easy to show that:

$$\frac{\beta_1}{\gamma_1^*} = \frac{\beta_2}{\gamma_2^*} = \ldots = \frac{\beta_n}{\gamma_n^*}. \tag{4.5}$$

Thus, all the coexisting species lie on the same hyperbola in the $(\beta, 1/\gamma^*)$ plane (figure 4.6). That is, coexistence is always based on a trade-off between growth in high-light and survival under the equilibrium canopy composition. Note that this is true whether in the case of asymmetric or symmetric facilitation (section 2.3.1).

Summarising, the hyperbolic shape of figure 4.5 can be interpreted in terms of succession (figure 4.4) or coexistence (figure 4.6).

Note that if two coexisting species i and j are highly tolerant (i.e., they have a high $1/\gamma^*$), then $\beta_i \approx \beta_j$. That is, species are similar in their growth strategy (see figure 4.6). This could explain the difficulty in observing the effect of the trade-off described in figure 4.6 (Gravel et al., 2008). However,

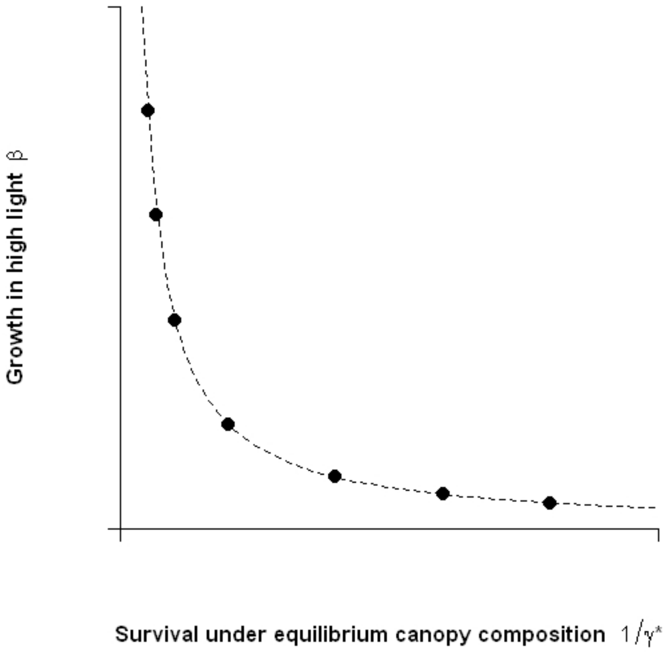

Figure 4.6: *Schematic representation of the distribution of some coexisting species along survival under equilibrium canopy composition and growth in high light. Each point represents a species.*

this hypothesis needs further study. Moreover, note that two species can coexist even when they have slightly different strategies.

Finally, note that figure 4.5 tells us that the nine species have higher variability in strategy (opportunism versus tolerance) than in competitive ability (i.e., the direction of varying k_i). This suggests that, for a tree species, an increase in competitive ability has higher cost than a shift in strategy.

Chapter 5

Concluding remarks

5.1 Model structure

Many competition models belong to the Lotka-Volterra type. Such models have been criticised because their level of abstraction makes them fundamentally disconnected from life-history parameters that can be measured in the field. A different approach is based on the von-Foerster equation (see section 3.5). In this case, model parameters are clearly linked to measurable individual tree attributes such as growth and mortality (Kohyama, 1992, 1993; Kohyama et al., 2001; Hurtt et al., 1998; Moorcroft et al., 2001; Kohyama, 2005). Generally, this second type of models has to be solved numerically, thus complicating the analysis.

The model developed in this thesis can be considered as a compromise between these two mathematical approaches: the model is completely tractable (as for the usual Lotka-Volterra equations) but it is mechanistically based on life-history parameters (as for the von Foerster type of models). The structure of the model is very simple: just two stage levels and yet it can explain many observed behaviours (see section 2.3.1). Thus, the main merit of this model is its simplicity which in turn allows an understanding of mechanisms behind forest dynamics. Note that when the von-Foerster model is simplified to a two-stage model (Adams et al., 2007), the predictions of the two approaches are similar, even if the von-Foerster model lacks an explicit description of density dependence (see section 3.5).

This simplicity was possible because I assumed that populations are well mixed. Thus, I neglected possible effects associated with explicit spatial patterns by using the simple mean field approximation (Klausmeir and Tilman, 2002). Spatial patterns can be unequivocally important (e.g., Gilad et al., 2007), also they can be studied with analytical techniques (e.g., Bolker and Pacala, 1997, 1999). However, some interesting features are predicted even in this simple case and I believe that is worth showing these results before using more sophisticated techniques.

The present model describes the dynamics of n species competing for space. The space in turn mediates for light and other resources. Competition for space follows the basic idea of gap dynamics (Watt, 1947): a forest is a mosaic of tree crowns (i.e., cells). The individual trees that are the elements of this mosaic dominate the resources and block the growth of young trees. When they die and open a gap in the canopy, a number of responses are initiated in the small area below the canopy opening. These responses eventually lead to the repair of the forest canopy. The importance of gap dynamics within the overall forest dynamics is widely recognised (e.g., Canham, 1989; McCarthy, 2001).

The real gap dynamics is often more complex than the simple description above. For example, in beech-maple communities, saplings experience several periods of suppression and release before attaining the canopy (Canham, 1990) and the gap size could be important (Poulson and Platt, 1996; Runkle, 1982; Kohyama, 1984). However, these and other mechanisms have been sacrificed for the sake of simplicity.

Once a plant attains the canopy, it does not suffer competition for resources any more. Thus, adult mortality is density independent (I implicitly considered as adult, only those trees that survive self-thinning). On the other hand, adults significatively modify the juvenile microenvironment, then juvenile mortality is density dependent. Moreover, I assumed that juvenile mortality only depends on adult density i.e., juveniles do not interfere with each other in the use of resources. This assumption both simplify the equations and is ecologically reasonable. Indeed, often light is the most limiting resource for sapling growth (Canham et al., 1994; Pacala et al., 1994) and most of shade is cast by adults. Clearly, the assumption that juveniles do not inhibit each other holds for relatively low densities of suppressed plants. This hypothesis of reduced competition has been analysed as an explanation for biodiversity in tropical forests (Wright, 2002).

Because of mortality, adult trees cannot completely fill the habitat (see equations (2.12), (2.14), (2.15)). Then, a number of gaps is always present. However, tree crowns tend to cover the full space in the limit of low adult mortality (i.e., when $\beta \to \infty$). In general, this is possible if tree crowns have plastic growth. Then, the portion of occupied space is computed through the mean crown area (s_i) times the number of adult trees (P_i) (see equations (2.2)).

I assumed that the mean crown area is a species-specific parameter even if, in principle, it could be density dependent. There is a clear link between the mean crown area of the present model and the threshold size of the model of Adams et al. (2007) discussed in section 3.5 (see also Strigul et al., 2008). In their model, the threshold size between understory and overstory is a dynamic variable. However, both models lead to conceptually identical conditions for the equilibrium behaviours of a two species system (see section 3.5). So, in order to study equilibrium dynamics, the approximation of constant mean crown area is not restrictive.

The interaction between adults and juveniles is modelled through the α coefficients. If shade is the main effect, then they represent a compound measure of shade cast by adults and shade tolerance of juveniles (see section 2.3.1). But other effects could be important e.g., root competition, allelopathy and pest facilitation (see a review in Wright, 2002). Then, the α coefficients should be considered as composed by several components:

$$\alpha_{ij} = \alpha_{ij}^{light} + \alpha_{ij}^{root} + \alpha_{ij}^{all} + \alpha_{ij}^{pest} + \dots. \tag{5.1}$$

In the model presented in this thesis, coexistence is represented as a stable equilibrium point of the system (deterministic model). A different approach is to consider a periodically perturbated system. Such perturbations (e.g., fires, windstorms) could lead to a nonequilibrium coexistence even if the unperturbed system could not (Huston, 1979). In the ecological literature there is debate on which is the better explanation for coexistence, indeed natural system are always perturbed (DeAngelis and Waterhouse, 1987). However, external perturbations promote nonequilibrium coexistence only if they have suitable magnitude and frequency. On the other hand, in a deterministic model, small perturbations often keep the system slightly away from the equilibrium. In the latter case we have a slightly perturbed equilibrium coexistence. Indeed, this is the case for the model presented in this thesis: small random perturbations can be easily added to the system. They produce some noise on curves in figure 4.1 at page 67 but the pattern is unchanged (not shown).

5.2 Model results

The basic structure of the model presented in this thesis (equations (2.3)) can be summarized in five points: (i) trees are classified in two stage levels (ii) all adult trees are exposed to full light and cannot be dislodged by juveniles; (iii) juvenile trees can grow only when adult trees die, thus releasing space; (iv) adult trees affect juvenile survival; (v) only adult trees can reproduce. Essentially, this is the "inhibition model" of succession proposed by Connell and Slatyer (1977). Moreover, it captures the essence of gap dynamics as well. All model results are consequences of these five statements. Although the model has not been validated, I have performed several qualitative comparisons with studies from literature that support the model results. Furthermore, the model provides possible explanations for the observed patterns.

When only one species is considered the most interesting prediction is that both the light transmissivity of canopy trees and the tolerance of juveniles do not affect the ability to invade a habitat. On the other hand, they affect the equilibrium density in a way that monocultures of tolerant species are denser than monoculture of intollerant species even if they have the same ability to colonise an empty habitat. This is widely observed in nature (Horn, 1971).

When two species are considered, three behaviours are possible: coexistence, founder control and competitive exclusion. Then, the simple two-stage structure allows for coexistence, but only if the one-sided effects of adult trees on juvenile trees are species-specific. This agrees with the finding of Canham et al. (1994) and Pacala et al. (1993) on the importance of species-specific traits in canopy attributes. Note that this result holds for any functional form of juvenile mortality.

Two species can coexist in two cases. First, if the juveniles of both species are more inhibited by conspecific adults than by heterospecific adults. This pattern leads to the reciprocal replacement that has been observed in many beech-maple communities (Fox, 1977; Woods, 1979; Chyper and Boucher, 1982). Secondly, coexistence could be based on a trade-off between tolerance and growth ability. This pattern has also been observed in beech-maple communities (Forcier, 1975; Canham, 1989; Poulson and Platt, 1996). In particular, Poulson and Platt (1996) hypothesised that coexistence was promoted by a change in adult mortality as a result of increased windstorms. A qualitative comparison between the model and the study of Poulson and Platt showed that coexistence could be based on the internal structure alone, while the external forcing affects the relative abundances. Moreover, in both cases mentioned above, the maintenance of the co-dominance is always based on a trade-off between growth and survival under the equilibrium canopy composition. The coexisting species are then distributed along these two strategies in a pattern similar to the one found by Kobe et al. (1995). Note that even a slight difference between these two strategies could result in coexistence, thus explaining coexistence of highly tolerant tree species.

In contrast with the simple Lotka-Volterra models, here the juvenile stage is considered explicitly. This allows us to know the abundances of both adults and juveniles. This is useful to compare equilibrium abundances of the two stages. For example, analysing several natural forests in North America which are numerically dominated by two species, Fox (1977) found that the species with highest longevity is generally more abundant in the overstory, while the other species is generally more abundant in the understory. Moreover, Fox pointed out that this is not obviously explained by seed year frequency, seed size or seed number. In particular, in the beech-maple community studied by Poulson and Platt, maple has smaller abundance in the overstory and higher abundance in the understory and this pattern seems to be a stable feature of the system (Poulson and Platt, 1996). It is possible to define a range in the model parameters that leads to this pattern irrespective of the relative magnitude of fecundity parameters for the two species. Thus, the inversion of abundances can be interpreted as an internal feature of the system: within the pattern of reciprocal replacement, individuals leave the juvenile class either by growth or death. Thus, juveniles that generally replace the shorter-lived species, are expected to have lesser abundance in the understory.

Within the model presented in this thesis, competitiveness of each species has two key components or strategies: the ability to grow when space is available (growth in high-light) and the ability to survive under a given canopy (survival in low-light). The most important feature of the model is that the low-light survival depends on the canopy composition. This is the key for the coexistence (reciprocal model). However, in the simple case where all canopy trees have the same light transmissivity, the low-light survival is an absolute species-specific parameter. In this case, the species with the highest competitiveness outcompete the others irrespective of their strategies. Moreover, if few juveniles of two species are present in a habitat at some initial time, we observe a succession only if the species with the highest competitiveness is the species with both the highest survival in low-light and the smallest growth in high-light. This suggests that we should interpret growth in high-light and survival in low-light as the two components of the successional status as well. Then, successions proceed towards increasing competitiveness, increasing survival in low-light and decreasing growth in high-light.

Successional status and shade tolerance are often considered as equivalent concepts (Horn, 1971; Kobe et al., 1995). In contrast, I considered the shade tolerance equivalent to survival in low-light. Note that this sets a subtle but profound difference between successional status and shade tolerance. For example, sugar maple could have a higher competitiveness than beech even though beech is more tolerant than maple, in this case maple could outcompete beech, thus having a higher successional status. Thus, when species are distributed along the two strategies (see Kobe et al., 1995) we have a better understanding of their successional status if both the overall competitiveness and the shade tolerance are considered as the drivers of the succession.

The model presented in this thesis is based on a mean-field approximation. This means that the model does not deal with the spatial distribution of species. However, some spatial information can be inferred. Indeed, in the case of founder control, several species could persist in a patchy habitat (Yodzis, 1978; Shmida and Ellner, 1984). A comparison of the model with the juvenile mortality curves found by Kobe et al. (1995) suggests that beech has a tendency to persist in patches. This is because beech saplings are predominantly root sprout at the site of Kobe et al.. Indeed, typically beech and hemlock coexist in a patchy habitat.

For many years competition was thought to play a predominant role in structuring plant communities. However, facilitation effects are now receiving a growing attention (Holmgren et al., 1997; Bruno et al., 2003). In the model presented in this thesis some degree of relative interspecific facilitation is a critical component for coexistence. Moreover, note that in principle, the α_{ij} coefficients could be negative indicating an absolute facilitation. Even in the latter case, species coexist in a pattern qualitatively described by figure 2.3d (page 30). Then, when the two species approach the equilibrium, one increases while the other decreases. This implies an overall competitive interaction (Pielou, 1977; Kot, 2003).

Thus, even if facilitative interactions between life stages play a critical role in structuring the community, they are always overridden by the competition for the space. This is also evident because according to the inhibition model of succession of Connell and Slatyer (1977), the condition to invade an empty habitat is always less restrictive than the condition to invade an occupied one (see equation (2.16)).

I view the present model as a step towards a comprehensive understanding of interspecific competition in forest ecosystems. Its merit is to provide a simple vision on the importance of interactions between life stages in explaining coexistence.

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