

Spatial structure and the survival of an inferior competitor: a theoretical model of neighbourhood competition in plants

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Abstract

Recent changes in forestry practices raise new scientific issues concerning the dynamics of mixed forests, and especially the coexistence of different species. The spatial structure of such forest stands is known to play a key role in their dynamics, but classical forest models are not adapted to study this phenomenon. Foresters have therefore begun to build distance-dependent individual-based forest models. As far as theoretical models are concerned, the relation between competition and the coexistence of various plant species in a mixed community has been studied extensively in theoretical ecology, but few of the corresponding models explicitly take the spatial structure of the community into account. The aim of this paper is to present a simple individual-based mechanistic model of neighbourhood competition that allows to study the relation between the spatial structure of mixed stands and the survival of an inferior competitor. We have build this model as an extension of former theoretical models of competition for a soil resource, by adding explicit spatial interactions. We have studied it both analytically and through simulations, using generalised Gibbs processes to simulate stands of various spatial structures. At the individual scale, we have obtained an explicit relation between the survival of a tree, the specific composition of its neighbourhood, and soil fertility. At the stand scale, we have linked the number of surviving trees to the spatial structure, and shown how interspecific repulsion and aggregated patterns improve the survival of inferior competitors. We have also illustrated how the competition process modifies the spatial structure of the stand. Such a neighbourhood competition model is thus a useful tool to study the relation between the spatial structure of a community and its dynamics. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Species coexistence; Mechanistic model; Individual-based model; Soil nutrient; Forest dynamics; Ripley function

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1. Introduction

In order to take into account the recent social concern for biodiversity conservation, landscape improvement and sustainable development (EEC, 1997), European foresters have had to adapt their

practices and to manage more complex, especially mixed, forest stands (Crave and Otto, 1990; Spellmann, 1992; Barthod, 1994; Otto, 1997; Carey et al., 1999; Otto, 2000). However, the management of mixed tree communities can be difficult in temperate forest, and often results in the exclusion of some less competitive species (Assmann, 1970; Duchiron, 1994; Otto, 1998; Brokaw and Busing, 2000). For instance, the sessile oak (*Quercus petraea*) and European beech (*Fagus sylvatica*) mixed stand is well known for its instability at a local scale. Most of the time its natural dynamics leads to a pure beech stand (Lemée, 1990; Ponttailler et al., 1997). At a broader scale, only disturbances can allow mixed stands of oaks and other species to replace pure beech, leading to a mosaic of patches. The survival of inferior competitors is therefore an important issue for forest management. Leuschner et al. (2001) have recently shown that the competition for soil resources could play a key role in such competitive exclusions.

The spatial structure of a forest stand, that is, the way trees are scattered in the forest, also plays a key role in the dynamics of the ecosystem, especially for mixed stands (Tomppo, 1986; Menaut et al., 1990; Rathbun and Cressie, 1994; Kubota and Hara, 1995; Pretzsch, 1995; Couteron and Kokou, 1997; Batista and Maguire, 1998; Courbaud et al., 2001). Therefore, the classical forest management tools, such as stand growth models built for regular and monospecific stands, are not adapted to predict the dynamics of such complex stands (Houllier et al., 1991; Benjamin and Aikman, 1995; Buongiorno et al., 1995; Pretzsch, 1997). Recent works in forest research have highlighted the need to design individual-based growth models (Judson, 1994; Moeur, 1997; Cescatti and Piutti, 1998; Nagel, 1999; Dubé et al., 2001), that allow to take this spatial structure into account.

The issue of the coexistence of various species in a mixed community has been studied extensively in ecology, mostly for annual plants (Levins and Culver, 1971; Horn and MacArthur, 1972; Mack and Harper, 1977; Hastings, 1980; Weller, 1989; Tilman, 1990, 1993, 1994; Tilman and Pacala, 1993; Huston and DeAngelis, 1994; Kub-

ota and Hara, 1995; Grover, 1997; Connolly et al., 2001; Gullison and Bourque, 2001). This theoretical tradition provides important insights into the functional role of biodiversity in ecosystem functioning (see recent reviews in Tilman, 1999; Loreau, 2000). Many authors have shown how mechanistic models of competition could be used to study these issues (Schoener, 1986; Huston et al., 1988; Huston and DeAngelis, 1994; Pacala and Tilman, 1994; Loreau, 1996, 1998; Grover, 1997; Mikola and Setälä, 1998). We therefore believe that this formalism can also be successfully applied to forest stands.

The impact of the spatial structure on the dynamics of plant populations is becoming a more and more important issue in plant ecology (Pacala and Silander, 1985; Ford and Sorrensen, 1992; Tilman, 1994; Tilman and Kareiva, 1997). However, few spatially explicit models have been used to study the coexistence of various species in a mixed community (Pacala et al., 1996; Berger and Hildenbrandt, 2000; Simioni et al., 2000). As far as mechanistic models of soil competition are concerned, Huston and DeAngelis (1994) have proposed a spatial model that takes into account the limited access to the resource pool for sessile organisms. This model gives interesting results on the survival of inferior competitors, but does not take into account the neighbourhood relationships between plants. In fact, only complex models, such as models from ecological field theory (Wu et al., 1985; Pukkala, 1989; Li et al., 2000) or detailed models of nutrients flows in the soil (Grover, 1997; Leadley et al., 1997; Biondini, 2001; Roose et al., 2001) can explicitly detail the impact of neighbours on the available nutrient pool for each plant.

The aim of this paper is to present a simple mechanistic model of individual tree competition for a soil resource that allows us to study the link between spatial structure and species coexistence in mixed forest stands.

We built this simple individual-based mechanistic model of neighbourhood competition as an extension of the competition models developed by Huston and DeAngelis (1994) and Loreau (1996, Loreau (1998)). We designed this theoretical model for forest stands, but it is a priori relevant to any

plant community as soon as individuals can be defined. In this paper, we first study the model analytically, and then simulate its dynamics for virtual bispecific stands of various structures. We thus show how spatial structure can influence the survival of the less competitive species, and how the dynamics of competition can create some spatial structure. We conclude with a discussion on the link between spatial structure and species coexistence.

2. Model formulation

2.1. Our model (Fig. 1) is a direct extension of the conceptual framework and the models developed by Huston and DeAngelis (1994) and Loreau (1996, 1998)

- (i) It is a mechanistic model, representing the competition between individual plants for a theoretical soil resource;
- (ii) it is a spatial model, which means that each plant has access only to a small amount of the resource, located in a ‘local’ resource depletion zone around its rooting system (Huston and DeAngelis, 1994);
- (iii) it represents the dynamics of the resource level in three different compartments: various plants, each linked to a ‘local’ soil compartment corresponding to its resource depletion zone, and the rest of the soil modelled by a ‘global’ soil compartment.

For the sake of simplicity, we did not add other compartments, such as herbivores or decomposers, which have already been studied in Loreau (1996). We also focused on the short-term dynamics of the ecosystem at the time scale of a tree generation, and therefore did not take regeneration or colonisation processes into account. These assumptions are usually relevant in managed forest stands, because regeneration occurs only in a short period after a long growing period (roughly 100 years).

2.2. The originality of this model is that it explicitly takes the influence of each plant’s neighbourhood into account

In forest or other plant communities, local competition with neighbours plays a key role in the growth and death of each plant (Begon et al., 1990). Indeed, plants with few neighbours usually have a higher growth and a lower mortality than do plants growing in a crowded area. However, many models do not take this phenomenon into account.

As far as the competition for soil resources is concerned, such a local competition is due to the fact that some resources locally available to one plant can also be used by its neighbours, especially more competitive ones. Real local depletion zones are not independent, and can sometimes overlap (Begon et al., 1990). In our simple conceptual framework, we chose to model this local competition with a potential resource exchange, e_{ij} , between the depletion zones of two neighbour-

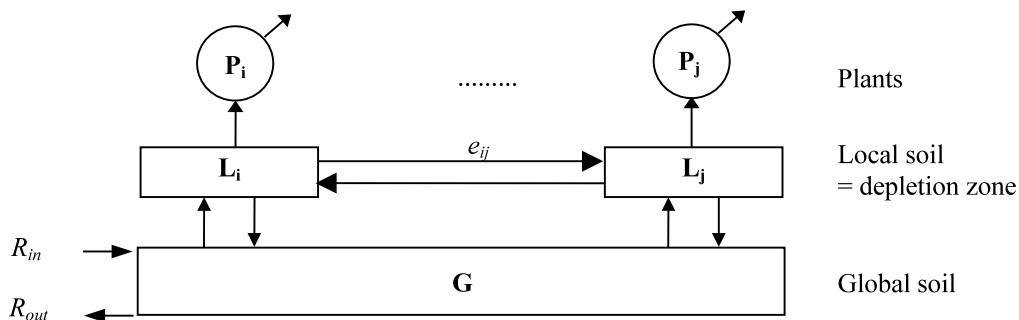


Fig. 1. Flow diagram of the model: each plant P_i has direct access to the resources in its local depletion zone L_i , and slower resource exchanges occur between these local zones and the global soil G . R_{in} and R_{out} represent the quantity of resource coming from the outside and leaving the system, respectively; e_{ij} corresponds to a potential resource exchange between two local depletion zones.

ing plants. This e_{ij} term is thus the main new feature of this model. It represents the intensity of the interaction between two plants, as determined by the difference in their competitive abilities.

The location of individuals is therefore taken into account in the definition of e_{ij} , which implies that this model must be used as a true individual-based model: it is not possible to merge various individuals of the same species into a single compartment as in Huston and DeAngelis (1994) or Loreau (1996) and Loreau (1998).

2.3. The equations of the model correspond to the flows between the various compartments

Let P_i be the amount of resource inside a plant compartment, L_i the concentration of resource in its local soil compartment, and G the concentration of resource in the global soil compartment. Since the model is intended to be theoretical, the resource is not specified (it could be, for instance, water, nitrogen, or phosphorus), and the units of P_i , L_i or G are not specified either. If there are n plants, the resource flows in the various compartments can be modelled by a system of $(2n + 1)$ coupled differential equations Eqs. (1)–(3). These equations are similar to those previously used by Loreau (1996) or Huston and DeAngelis (1994). More discussions on the form of the equations can be found in these papers.

$$\frac{dP_i}{dt} = a_i P_i L_i - b_i P_i = a_i P_i [L_i - c_i]; \quad c_i = \frac{b_i}{a_i} \quad (1)$$

$$\frac{dL_i}{dt} = \frac{q_i}{V_i} [G - L_i] - \frac{a_i}{V_i} P_i L_i + \sum_{j \neq i} \frac{e_{ij}}{V_i} \quad (2a)$$

$$e_{ij} = v_{ij} [L_j - L_i] \quad (2b)$$

$$\frac{dG}{dt} = \frac{[R_{in} - R_{out}]}{V} - \sum_i \frac{q_i}{V} [G - L_i] \quad (3a)$$

$$\frac{dG}{dt} = \frac{q}{V} [G_0 - G] - \sum_i \frac{q_i}{V} [G - L_i] \quad (3b)$$

The dynamics of P_i is modelled by Eq. (1). The first term represents the resource uptake by the plant in its resource depletion zone. We have used a classical Lotka-Volterra form, which leads to recipient control of the local resource concentration (Loreau, 1996; Grover, 1997); a_i measures the

resource uptake rate. The second term corresponds to the loss of resource, for instance through dead leaves (for trees, this also includes the creation of the duramen). We have made the classical hypothesis that this loss is proportional to the instantaneous amount of resource (Grover, 1997); b_i is the resource loss rate. Eq. (1) leads us to define a new variable, c_i , which is equivalent to Tilman's (1982) R^* and is an inverse measure of a plant's competitive ability.

The dynamics of L_i is modelled by Eq. (2). The first term corresponds to the resource exchange between the local and global soil compartments, which we have classically hypothesised to be proportional to the difference between the resource concentration in the two compartments. V_i is the volume of the local soil compartment, which we have assumed to be constant for the sake of simplicity, and q_i represents the exchange flow rate between the local and global soil compartments. The value of q_i is highly dependent on the resource considered (Begon et al., 1990). The second term in Eq. (2) corresponds to the resource uptake by the plant. The last term corresponds to the local competition: for each neighbouring plant, we have assumed that the local interplant competition can be modelled by an exchange of resource e_{ij} between the two depletion zones. As detailed in Eq. (2), we have further assumed that this exchange of resource, e_{ij} , is proportional to the difference between the concentration in the two local soil compartments. The proportionality term, v_{ij} , thus measures the intensity of the interaction between the two plants: if the plants are very close to each other the competition is very intense, and v_{ij} is high. For non-neighbouring plants, v_{ij} is zero.

The dynamics of G is modelled by Eq. (3). The first term corresponds to the quantity of resource coming from the outside, which we have assumed to be constant (R_{in}), or leaving the system, for instance through infiltration (R_{out}). We have assumed this loss of resource to be proportional to the resource concentration in the global soil compartment, so that $R_{out} = qG$, where q represents the output flow rate. Using a simple change in notation, we can write $R_{in} = qG_0$. G_0 is then a measure of the fertility of the site; it corresponds

to the equilibrium value of G when there are no plants. The second term corresponds to the resource exchange between the global soil compartment and all the local soil compartments.

3. Methods

All computer programs, implemented in C language, are available on request.

3.1. Model simulation

3.1.1. We used a discrete version of the model to simulate the dynamics of a forest stand

The discrete equations of the model are detailed in Eq. (4). During the simulations, the time discretisation step Δt has to be small enough to avoid discretisation artefacts, without being too time consuming. We also added a mortality threshold, M , in order to take into account the fact that declining trees cannot survive when their level of resource is too low.

if $P_i < M$ then

$$P_i = 0 \text{ and } \frac{\Delta P_i}{\Delta t} = 0 \quad (\text{death of } P_i)$$

if $P_i \geq M$ then (4a)

$$\frac{\Delta P_i}{\Delta t} = a_i P_i (L_i - c_i) \quad (4b)$$

$$\frac{\Delta L_i}{\Delta t} = \frac{q_i}{V_i} (G - L_i) - \frac{a_i P_i L_i}{V_i} + \sum_{j \neq i} \frac{v_{ij}}{V_i} (L_j - L_i) \quad (4c)$$

$$\frac{\Delta G}{\Delta t} = \frac{q}{V} (G_0 - G) - \sum_i \frac{q_i}{V_i} (G - L_i) \quad (4d)$$

3.1.2. We defined relevant parameter values for the simulation

We chose to study the behaviour of the model with simple bispecific virtual stands of 1 ha, simulated with a generalised Gibbs process (see below). We used a very simple definition of the neighbourhood: we considered that 2 trees are neighbours when their distance is lower than a threshold D_{\max} . For such neighbours, we used a

constant value of the interaction intensity: $v_{ij} = v$. For non-neighbouring trees, $v_{ij} = 0$. For an arbitrary level of resource around $G_0 = 10$, we defined a highly competitive species 1 with a competitive ability $c_1 = 4$, and a less competitive (but still able to survive) species 2 with $c_2 = 8$. We chose realistic values for the other parameters using results from the literature, expertise of foresters and dimensional analysis. We especially set q_i and V_i to 1, and therefore considered that the time unit would correspond to the time necessary for the local compartment L_i to renew its resource. Table 1 summarises the values used in the simulations presented in this article.

In this article, we considered a mean theoretical resource, with an intermediate transfert rate, and therefore used a time unit corresponding to 0.1 year. During the simulations, we used a time discretisation step $\Delta t = 0.1 \times \text{time unit}$, so that each iteration corresponds to a 0.01 year period. Finally, for each simulation, we computed 10000 iterations of the discrete equations, corresponding to a 100-year time period, which is the mean life span of a managed stand. Longer simulations would not be appropriate because our model does not take regeneration processes into account.

3.2. Analysis of spatial structure

The spatial structure of an ecosystem is a complex concept, which involves both vertical and horizontal components of space utilisation by its elements (Begon et al., 1990). In this article, we focus on the horizontal location of the centre of each individual, which can be represented by a point pattern (Cressie, 1993).

3.2.1. We used the $L(r)$ function to describe the spatial structure of univariate point patterns

Many methods can be found in the literature to analyse the spatial structure of a point pattern (e.g. Ripley, 1981; Diggle, 1983; Cressie, 1993). We chose to use Ripley's $K(r)$ function and other similar functions, which have the advantage of describing the spatial structure at different ranges simultaneously (Cressie, 1993), and have been used recently in many plant ecological studies (Duncan, 1991; Skarpe, 1991; Moeur, 1993; Szw-

Table 1
Parameters of the model, and their values used for the simulations

Parameter	Description	Possible range	Values used
n	Number of trees	From 10 000 to 100 per ha	200 on 1 ha
G_0	A measure of the intrinsic fertility of the site	Arbitrary set around 10	Mainly 10.4 (middle fertility); and from 5 (low fertility) to 40 (high fertility)
P_i	Amount of resource in a tree	>0	Initial value set to G_0
L_i	Concentration of resource in a local soil compartment	From 0 to G_0	Initial value set to G_0
G	Concentration of resource in the global soil compartment	From 0 to G_0	Initial value set to G_0
a_1	Resource uptake rate for species 1		0.05
a_2	Resource uptake rate for species 2		0.05
c_1	Inverse measure of the competitive ability for species 1		4
c_2	Inverse measure of the competitive ability for species 2		8
b_1	Resource loss rate for species 1		0.2
b_2	Resource loss rate for species 2		0.4
V_i	Volume of a local soil compartment	Arbitrary set to 1	1
V	Volume of the global soil compartment	Bigger than the sum of V_i	2000
q_i	Exchange flow rate between the global soil compartment and a local soil compartment	arbitrary set to 1	1
q	Output flow rate for the global soil compartment	Bigger than the sum of q_i	400
D_{\max}	Maximal distance between two competing trees	From 1 m to 20 m	10 m
v_{ij}	Interaction parameter between two trees	Depending on the mean number of neighbours	1/12 if the 2 trees are neighbours; 0 otherwise
M	Mortality threshold	From 0.1 to 1	0.5

grzyk and Czerwczak, 1993; Haase et al., 1996; Pélissier, 1998; Barot et al., 1999; Goreaud et al., 1999; Pélissier and Goreaud, 2001). This function is therefore complementary to classical methods based on the distance to nearest neighbours (Clark and Evans, 1954).

Under the assumptions of stationarity and isotropy (that is, invariance by translation and rotation), and for a point process of intensity λ , Ripley's $K(r)$ function is defined so that $\lambda K(r)$ is the expected number of neighbours in a circle of radius r centred on an arbitrary point of the pattern (Ripley, 1977). Therefore, for each range r it is possible to compare this function to the expected number of neighbours for a random pattern, and to detect regularity or aggregation. In this paper we used the modified $L(r)$ function (Besag, 1977), whose classical estimator $\hat{L}(r) =$

$\sqrt{\hat{K}(r)/\pi} - r$ has a more stable variance than does $\hat{K}(r)$ and is easier to interpret. Indeed, $L(r) = 0$ under the classical null hypothesis of complete spatial randomness (CSR), which corresponds to a Poisson pattern. $L(r) < 0$ indicates that the pattern is regular at range r (there are fewer neighbours within distance r of an arbitrary point than expected under CSR). $L(r) > 0$ indicates that the pattern is clustered at range r (there are more neighbours within distance r of an arbitrary point than expected under CSR). Fig. 2 illustrates the $L(r)$ function obtained for three typical patterns.

3.2.2. We used the $L_{1,2}(r)$ intertype function to describe the spatial structure of bispecific patterns

For a bispecific pattern, and under the same assumptions, it is also possible to define an intertype function, $K_{1,2}(r)$, that characterises the rela-

tive location of one species with respect to another. $K_{1,2}(r)$ is proportional to the expected number of neighbours of species 2, in a circle of radius r , centred on an arbitrary tree of species 1 in the stand (Lotwick and Silverman, 1982). In this paper, we used the modified $L_{1,2}(r)$ function (Diggle, 1983), whose classical estimator $\hat{L}_{1,2}(r) = \sqrt{\hat{K}_{1,2}(r)/\pi} - r$ has a more stable variance than does $\hat{K}_{1,2}(r)$ and is easier to interpret. Indeed, $L_{1,2}(r) = 0$ under the null hypothesis of independence. $L_{1,2}(r) < 0$ indicates a repulsion between the two species at range r (there are fewer neighbours of species 2 within distance r of an arbitrary point of species 1 than expected under the hypothesis of independence). $L_{1,2}(r) > 0$ indicates an attraction between the two species at range r

(there are more neighbours of species 2 within distance r of an arbitrary point of species 1 than expected under the hypothesis of independence). Fig. 3 illustrates the function $L_{1,2}(r)$ obtained for three typical bispecific patterns.

More details on the computation of these $L(r)$ and $L_{1,2}(r)$ functions, including edge effect correction, can be found in Goreaud and Pélissier (1999).

3.3. Virtual stand simulation

We used the classical point process formalism to simulate virtual stands (see e.g. Diggle, 1983; Tomppo, 1986; Cressie, 1993).

Estimation of $L(r)$ for 3 typical patterns

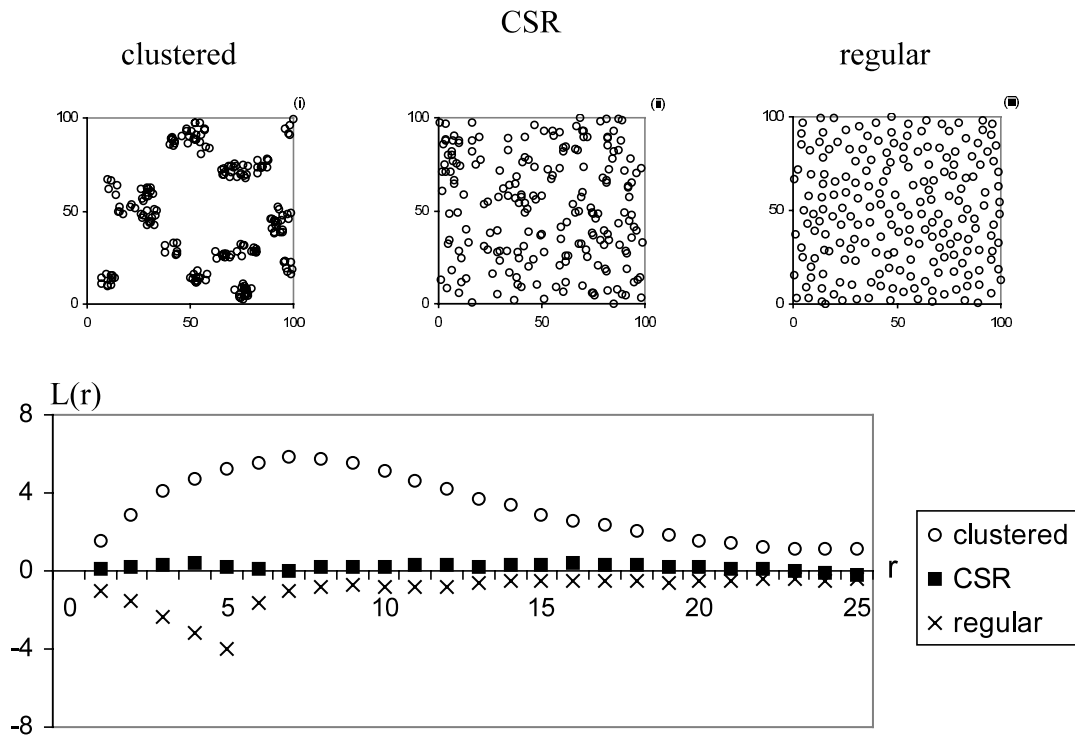


Fig. 2. Estimation of the $L(r)$ function obtained for 3 virtual stands: a clustered pattern obtained with a Neyman-Scott process (Diggle, 1983); a Poisson pattern corresponding to the null hypothesis of CSR, and a regular pattern simulated with a Gibbs process (Diggle, 1993).

Estimation of $L_{1,2}(r)$ for 3 bispecific patterns

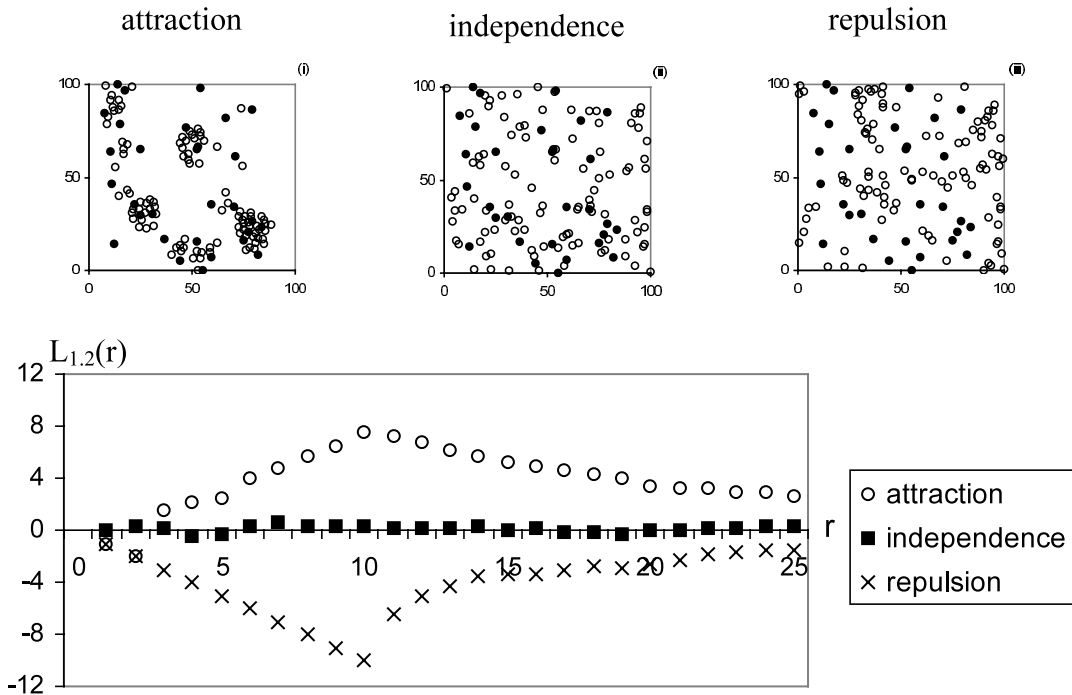


Fig. 3. Estimation of the $L_{1,2}(r)$ function obtained for 3 virtual bispecific stands, where species 1 (in black) has a Poisson pattern, and species 2 (in white) is obtained either through another independent Poisson process (ii), or through an interspecific Gibbs process with a negative (i) or positive (iii) interaction function.

3.3.1. *In order to obtain as many different structures as possible, we used a generalised Gibbs process to simulate the virtual stands used as initial conditions of the model*

For each simulation, we first generated the location of 100 trees of species 1 in a 1 ha area, using a classical Gibbs process with a random interaction function and a random number of iterations. A Gibbs process is defined by a pairwise interaction function $f(r)$, that represents somehow the cost associated with the presence of two points at a distance r . Simply speaking, we can consider that the realisations of this process minimise the global cost F , defined as the sum of the costs associated with each pair of points (Eq. (5)). Therefore, negative values of the cost function lead to clustered patterns, and positive values to regular patterns. We simulated such Gibbs

processes with a classical stepwise depletion-replacement algorithm (Ripley 1979). More details on Gibbs processes can be found in Diggle, (1983) or Tomppo (1986).

$$F = \sum_{i \neq j} f(r_{ij}) \quad (5)$$

Our random interaction function $f(r)$ used three constant values: $f(r) = 100$ for $r < 1$ m, $f(r) = \theta_1$ for $1 < r < 5$ m, and $f(r) = \theta_2$ for $5 < r < 10$ m. The first positive value ensured a short-distance regularity so that trees were not superimposed on one another. The other two values θ_1 and θ_2 were random parameters, chosen between -100 and $+100$, so that the final pattern of species 1 presented a high variability of spatial structure, from clusters of various sizes to regularity of various intensities. The random number of simulations

(between 1 and 1000) allowed us to obtain weakly structured patterns, close to CSR, as well as highly structured ones.

We then used the same principle to simulate the location of 100 trees of species 2 with an interspecific Gibbs process, again with a random interaction function and a random number of iterations. The interaction function $g(r)$ was similar to $f(r)$, with $g(r) = 100$ for $r < 1$ m, $g(r) = \theta_3$ for $1 < r < 5$ m, and $g(r) = \theta_4$ for $5 < r < 10$ m. The final pattern of species 2 also presented a high variability of spatial structure, and the intertype structure (that is, the relative positions of species 1 and species 2) was also very variable, from independence to attraction or repulsion. We thus obtained virtual stands covering the potential variability of structure of real stands.

4. Results

4.1. *At individual scale, the survival of a tree directly depends on the specific composition of its neighbourhood*

4.1.1. *For each tree, there are two possible equilibrium states*

We calculated the equilibrium state of the model by setting to zero the time derivative of each variable (Eq. (6)). We thus obtained two possible equilibrium states for each tree, which is classical with such models (Grover, 1997). This dynamics could also be compared with more general results in theoretical ecology, for instance the feasibility of food webs (e.g. May, 1973). The first equilibrium corresponds to the death of the tree, and the concentration in its depletion zone is then equal to a weighted mean of the equilibrium concentrations in the neighbours' depletion zones and in the global soil compartment: C_i^{mean} (Eq. (7)). The second equilibrium corresponds to the survival of the tree, and the concentration in its depletion zone is then equal to c_i (Eq. (8)). The equilibrium concentration in the global soil compartment depends on the intrinsic fertility of the site and the state of each depletion zone (Eq. (9)).

$$\frac{dP_i}{dt} = 0 \quad ; \quad \frac{dL_i}{dt} = 0 \quad ; \quad \frac{dG}{dt} = 0 \quad (6)$$

$$P_i^* = 0 \quad \text{and} \quad L_i^* = C_i^{\text{mean}} = \frac{q_i G^* + \sum_{j \neq i} v_{ij} L_j^*}{q_i + \sum_{j \neq i} v_{ij}} \quad (7)$$

$$L_i^* = c_i \quad \text{and} \quad P_i^* = \frac{q_i + \sum_{j \neq i} v_{ij}}{a_i} \left[\frac{C_i^{\text{mean}}}{c_i} - 1 \right] \quad (8)$$

$$G^* = \frac{qG_0 + \sum_i q_i L_i^*}{q + \sum_i q_i} \quad (9)$$

At stand level, there are 2^n possible global equilibrium states, whose stability depends on the sign of the eigenvalues of the corresponding Jacobian matrix. As it is often the case with complex systems (see for instance Loreau, 1996), we did not succeed in calculating those eigenvalues, and thus were not able to conclude on the global stability of the various possible equilibrium states. However, we can show that if $c_i < C_i^{\text{mean}}$ then any equilibrium state where the corresponding tree i dies (Eq. (7)) is unstable (Appendix A). Moreover, if $c_i > C_i^{\text{mean}}$ then any equilibrium state where the corresponding tree i does not die (Eq. (8)) is biologically impossible, because it would correspond to a negative biomass. Finally, we can formulate a necessary condition that must be fulfilled by every stable and biologically relevant equilibrium state (Eq. (10)).

$$\forall i, \begin{cases} \text{if } c_i \leq C_i^{\text{mean}} & \text{then } P_i^* > 0 \\ \text{if } c_i > C_i^{\text{mean}} & \text{then } P_i^* = 0 \end{cases} \quad (10)$$

In order to explore the dynamics of the system at stand level, we also used some simulations (Fig. 4). We always obtained a convergence of the variables towards an equilibrium fulfilling a similar condition. However, because of the mortality threshold in the discrete model, this condition is slightly different (Eq. (11)).

$$\text{if } c_i \leq C_i^{\text{mean}} \left(1 - \frac{Ma_i}{q_i + \sum_{j \neq i} v_{ij} + Ma_i} \right) \text{ then}$$

$$P_i^* \geq M \tag{11a}$$

$$\text{if } c_i > C_i^{\text{mean}} \left(1 - \frac{Ma_i}{q_i + \sum_{j \neq i} v_{ij} + Ma_i} \right) \text{ then}$$

$$P_i^* = 0 \tag{11b}$$

4.1.2. We obtained an individual survival condition that confirms the importance of the neighbourhood

As with all theoretical models, our model is a simplified representation of the complex reality of forest stands that cannot be used to predict precisely the behaviour of a real stand. We can assume, however, that it does reveal the main effects of local competition for a soil resource. Therefore, we have considered that the stable equilibrium of the model corresponds to the direc-

tion of the probable dynamics of the stand. If, for a tree, the stable equilibrium state is death, then probably a real tree with the same neighbourhood will not survive for a very long time. On the contrary, if the stable equilibrium state is survival, a real tree with the same neighbourhood will probably survive longer.

With this interpretation, the necessary condition (Eq. (10)) or (Eq. (11)) can be translated into a survival condition, at the individual scale, linking the ability of a tree to survive to its neighbourhood (Eq. (12)).

$$P_i \text{ survive} \Leftrightarrow c_i \leq C_i^{\text{mean}} = \frac{q_i G^* + \sum_{j \neq i} v_{ij} L_j^*}{q_i + \sum_{j \neq i} v_{ij}} \tag{12}$$

The originality of this result is the explicit roles of the concentration in the depletion zone of neighbouring trees and of the parameters v_{ij} , which point out the importance of neighbourhood in survival when taking into account local competition for soil resources.

Typical evolution of a few trees

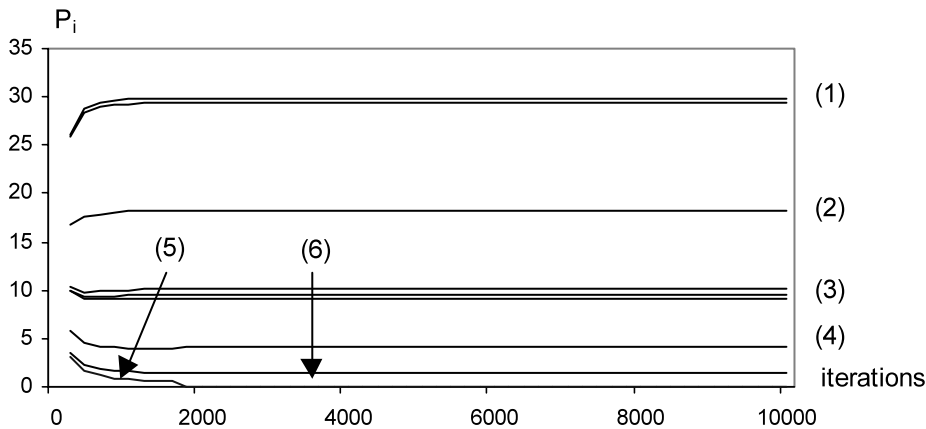


Fig. 4. Typical dynamics of the amount of resource in a few trees of a virtual mixed stand. (1) Two trees of species 1, which is highly competitive ($c_1 = 4$), quickly converging towards a high level of resource. The equilibrium state is slightly different for the 2 trees, because they have different neighbourhoods. (2) A tree of species 2 ($c_2 = 5$), which is competitive but less than species 1. (3) Three trees of species 3, with an intermediate competitive ability ($c_3 = 6$), converging towards an intermediate level of resource. (4) A tree of species 4, which is less competitive ($c_4 = 7$) but still surviving, converging towards a low level of resource. (5) A tree of species 5, with a very low competitive ability ($c_5 = 8$), which dies because of its too competitive neighbourhood. (6) Another tree of species 5, surviving at a very low level of resource thanks to its favourable neighbourhood.

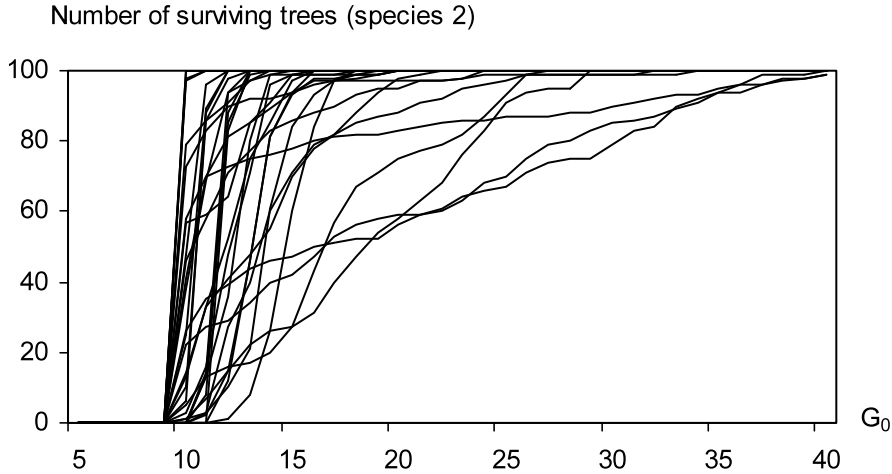


Fig. 5. Number of surviving trees of species 2 after 10000 iterations of our discrete model, for 30 virtual stands with different spatial structures and values of the intrinsic fertility of the site varying from $G_0 = 5$ to $G_0 = 40$. Each curve corresponds to a virtual stand, and describe how its number of surviving trees varies with the fertility.

4.1.3. This survival condition is easy to interpret in the case of a bispecific stand

Let us now consider the simple case of a bispecific stand, and suppose that the parameter c_i of a tree is species-specific. With the simple definition of the neighbourhood used for the simulations (see above), it is possible to simplify the survival condition as in Eq. (13). $N_{i,1}$ represents the number of living neighbours (of the studied tree) that belong to species 1, $N_{i,2}$ the number of living neighbours of species 2, and $N_{i,M}$ the number of dead neighbours. C_i^{mean} is the average value of C_i^{mean} for dead trees.

P_i survives \Leftrightarrow

$$c_i \leq \frac{q_i G^* + v(N_{i,1}c_1 + N_{i,2}c_2 + N_{i,M}C_i^{\text{mean}})}{q_i + v(N_{i,1} + N_{i,2} + N_{i,M})} \quad (13)$$

With this simplified survival condition, it is easy to show that all trees of species 1 can survive as soon as $G_0 \geq c_1$. Indeed, in this case, c_1 is lower than G^* , c_2 and all possible C_i^{mean} . This result can be generalised in a multi-specific context: the most competitive species can always fulfil the survival condition provided it can survive alone.

For the trees of species 2, it is again possible to simplify the survival expression as detailed in Eq. (14): their survival depends directly on the numbers of neighbours of species 1, $N_{i,1}$, and of dead

neighbours, $N_{i,M}$. More generally, in a multi-specific context, the survival of each species depends on the specific composition of its neighbourhood.

P_i (species2) survives \Leftrightarrow

$$c_2 \leq \frac{q_i G^* + v(N_{i,1}c_1 + N_{i,M}C_i^{\text{mean}})}{q_i + v(N_{i,1} + N_{i,M})} \quad (14)$$

We can thus calculate the maximum number of neighbours of species 1, N_{max} , that a tree of species 2 can endure without dying (Eq. (15)).

P_i (species2) survives $\Leftrightarrow N_{i,1} < N_{\text{max}}$ (15a)

$$N_{\text{max}} = \frac{q_i(G^* - c_2) + vN_{i,M}(C_i^{\text{mean}} - c_2)}{v(c_2 - c_1)} \quad (15b)$$

4.1.4. The model also points out the positive effect of fertility on the survival of a less competitive species

Indeed, G^* is an increasing function of G_0 (Eq. (9)), which is a measure of the fertility. For higher values of G_0 , G^* is higher as well, and the survival condition (Eq. (13)) is easier to fulfil.

This positive effect appears clearly in the simulation results. Fig. 5 illustrates the relation between the number of trees of species 2 that survived after 10000 iterations of our discrete model, and the value of the parameter G_0 . The model presents three intervals of behaviour. First,

for low a fertility ($G_0 < 9.3$), no tree of species 2 can survive whatever the spatial structure. Then, for intermediate fertilities, some trees can survive because they have a less competitive neighbourhood. For most of the virtual stands, the number of surviving trees increases rapidly with fertility, and reaches 100% for values of G_0 ranging from 12 to 20, depending on spatial structure. For a few virtual stands corresponding to unfavourable structures, 100% survival is only achieved for $G_0 = 40$. For higher fertilities, all trees can survive whatever their neighbourhood.

4.2. At stand scale, we obtained an explicit relation between the number of surviving trees and the spatial structure of the stand

4.2.1. In the bispecific case, the survival condition leads to a negative relation between the mean number of surviving trees (of the less competitive species) and the intertype function

In the simplified survival condition (Eq. (14)), the variables $N_{i,1}$ and $N_{i,M}$ are directly linked to the intertype function described earlier (Eq. (16)). Indeed, $K_{2,1}(D_{\max})$ is proportional to the mean number of trees of species 1 around a tree of species 2, and it is also possible to define $K_{2,M}(D_{\max})$, which is proportional to the mean number of dead trees around a tree of species 2.

$$\overline{N_{i,1}} = \lambda_1 K_{2,1}(D_{\max}) \tag{16a}$$

$$\overline{N_{i,2M}} = \lambda_{2M} K_{2,M}(D_{\max}) \tag{16b}$$

Therefore, the mean number of survivors of the less competitive species is highly dependent on the interspecific structure of the stand. In the case of interspecific repulsion at range $r = D_{\max}$, which corresponds to low values of $K_{2,1}(D_{\max})$, the survival condition is easier to fulfil because the mean value of $N_{i,1}$ is smaller. On the contrary, in the case of interspecific attraction, which corresponds to high values of $K_{2,1}(D_{\max})$, the survival condition is more difficult to fulfil because the mean value of $N_{i,1}$ is larger.

4.2.2. There is, however, a high variability around this mean relation depending on spatial structure

In order to study this relation and its variability, we simulated our discrete model with 1000 1 ha virtual stands with various spatial structures. Fig. 6 illustrates how the number of survivors (of species 2) of each stand after 10000 iterations of the discrete model varies with the initial value of $L_{2,1}(D_{\max})$. The trend in the figure corresponds to the mean negative relation previously described. However there is a high variability around this trend, especially for the intermediate values of $L_{2,1}(D_{\max})$ (from -1 to 10). This phenomenon is

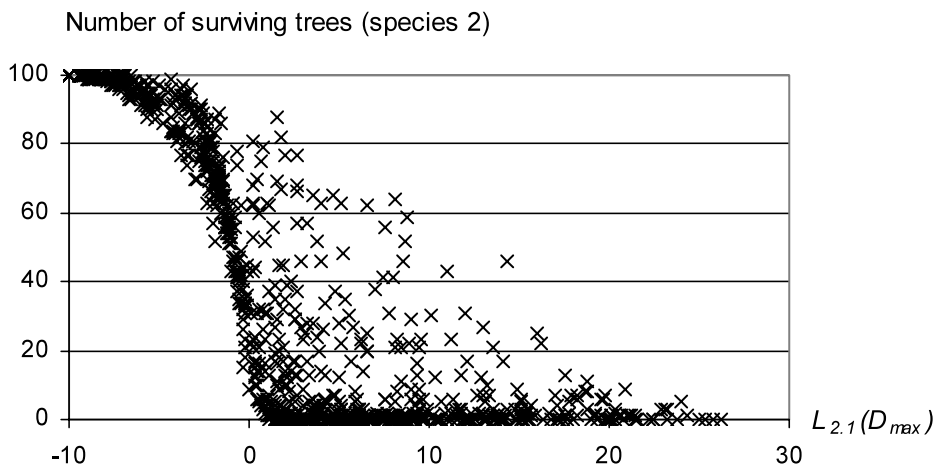


Fig. 6. Relation between the intertype function $L_{2,1}(r)$ at range $r = D_{\max} = 10$ m and the number of surviving trees of species 2 after 10000 iterations of the discrete model, for 1000 virtual stands of various spatial structures, composed of 100 trees of species 1 (superior competitor) and 100 trees of species 2 (inferior competitor), randomly scattered on 1 ha. We used a middle fertility ($G_0 = 10.4$) for these simulations.

Table 2
Results of the linear regression model (17) for 1000 virtual stands

Parameter	Coefficient	Value	Standard error	P
Intercept	α	36.75	0.850	$< 10^{-5}$
$L_{2,1}(10\text{ m})$	β	-4.67	0.086	$< 10^{-5}$
$L_2(10\text{ m})$	γ	0.46	0.010	10^{-5}
$L_1(10\text{ m})$	δ	1.55	0.065	$< 10^{-5}$

(17)). The number of surviving trees (of species 2) is thus described as a sum of various terms proportional to: (i) $L_{2,1}(10\text{ m})$, the interspecific structure at range $D_{\max} = 10\text{ m}$, (ii) $L_2(10\text{ m})$, the spatial structure of species 2 at range $D_{\max} = 10\text{ m}$, and (iii) $L_1(10\text{ m})$, the spatial structure of species 1 at range $D_{\max} = 10\text{ m}$, respectively. The results of the linear regression, achieved on the 1000 same virtual stands, are presented in Table 2. All parameters have a significant effect ($P < 10^{-5}$) on the number of survivors, and the overall model is very highly significant ($P < 10^{-5}$, $R^2 = 0.79$). The negative value of β corresponds to the negative relation previously described between the survival of species 2 and the intertype function. The positive values of γ and δ show that the survival of the less competitive species is easier in aggregated stands.

Number of surviving trees

$$= \alpha + \beta L_{2,1}(10\text{ m}) + \gamma L_2(10\text{ m}) + \delta L_1(10\text{ m}) \quad (17)$$

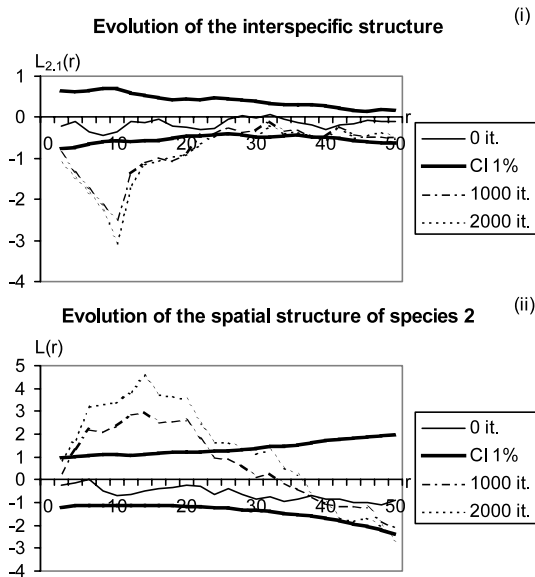


Fig. 7. (i) Intertype function $L_{2,1}(r)$, and (ii) specific spatial structure $L(r)$ for species 2, computed for 1 virtual stand, in the initial state (black plain line) and after 1000 or 2000 iterations of the discrete model (black dotted lines). The two grey bold lines define the confidence interval (CI) for the null hypotheses of Independence (i) or CSR (ii), respectively.

due to the variability of the other parameters of the spatial structure of the stands. Indeed, 2 virtual stands sharing the same value of $L_{2,1}(D_{\max})$ have the same mean interspecific structure at range $r = D_{\max}$, but they can have different local patterns, different interspecific structures at lower or higher ranges, and very different specific spatial structures of the two species.

In order to illustrate this impact of other parameters of the spatial structure on the survival of the less competitive species, we made an analysis of variance with a simple linear model (Eq.

4.2.3. The competition process in turn modifies the spatial structure of the stand

By eliminating some trees of species 2, local competition in turn changes the spatial structure of the stand. Fig. 7 illustrates these changes in the $L_{2,1}(r)$ intertype function and the $L(r)$ function for species 2, which are both computed in the initial state and after 1000 or 2000 iterations of the model, for a particular virtual stand. There is a progressive decrease in $L_{2,1}(r)$ around $r = 10\text{ m}$, which corresponds to a shift towards interspecific repulsion. In parallel, the spatial structure of species 2 shifts towards higher values of $L(r)$, corresponding to a more aggregated structure. These changes are the direct consequence of differences in the mortality of trees depending on their neighbourhood. As trees of species 2 with few neighbours of species 1 are more likely to survive, the mean value of neighbours of species 1 around living trees of species 2 decreases with time, leading to smaller and negative values of $L_{2,1}(r)$ for $r = D_{\max} = 10\text{ m}$. Most of the time, trees having few neighbours of species 1 have many neighbours of species 2, thus building a kind of aggregate in terms of specific spatial structure. Such aggregates

will have a higher probability of survival than isolated trees, often surrounded by trees of species 1. Therefore, the mean number of neighbours of species 2 around living trees of species 2 increases.

5. Discussion

5.1. The simplicity of our model must be taken into account in analysing its results

Firstly, as already mentioned, our model is intended to be a theoretical model to explore and understand a general ecological question, thus not a detailed model to make precise predictions on individual plant growth (Levins, 1966). Fitting of such a model to real stands is difficult because some variables (such as the concentration of a resource in a local depletion zone) are notoriously difficult to measure (Vogt et al., 1989). In the absence of relevant data, we had to use arbitrary values for some of the parameters in our theoretical simulations.

Secondly, the model explores a specific question, i.e. the influence of spatial structure on the short-term survival of inferior competitors. Accordingly, it focuses on local neighbourhood competition. Many other processes, such as regeneration, colonisation, mortality, light competition, nutrient recycling, herbivory or thinning, are not taken into account, and would need adaptations of the model (Kenkel, 1988; Dhôte, 1994; Loreau, 1994, 1995; Rathbun and Cressie, 1994; Fröhlich and Quednau, 1995; de Mazancourt et al., 1998; Courbaud et al., 2001). However, our approach in which we take neighbourhood explicitly into account using resource exchanges between local depletion zones is general and can be easily applied to other models.

Thirdly, we have used several strong hypotheses, whose impact on the model requires further investigation. For instance, the neighbourhood definition used in the simulations is obviously far from the complex reality of the local competition between tree root systems (Kuiper and Coutts, 1992; Büttner and Leuschner, 1994; Drexhague et al., 1999). However, the qualitative results of the model were not different when we used other definitions, such as values of v_{ij} decreasing with distance, or

different ranges of interaction D_{\max} . Another strong hypothesis is the choice to keep V_i constant throughout the dynamics of the stand, which was necessary to ensure some consistency with the definition of the competition term e_{ij} . It is not realistic when taking young trees into account, because root length increases rapidly from the regeneration phase (a few cm) to the mature tree state (a few m). More research is required to take into account this dynamics of the root system (e.g. Biondini, 2001). Finally, the model implicitly concerns even-aged stands, where all individuals have similar age and size, and no regeneration needs to be taken into account to study their short-term dynamics. When studying uneven-aged stands, or longer time periods, the relation between adult and young trees is more complicated than local competition (Szwagrzyk, 1990; Skovsgaard and Johannsen, 1996; Péliissier, 1998; Barot et al., 1999), and would need to be incorporated in the analysis. More details on these hypotheses are discussed in Goreaud (2000).

5.2. The model provides explicit relations between the spatial structure of a plant community and the survival of inferior competitors

Many authors have studied how some factors, such as the spatial heterogeneity of resources, the temporal variability of climatic conditions, the existence of resource depletion zones, or the recycling of nutrients could improve the survival of a less competitive species in a mixed community (see a review in Begon et al., 1990). In this paper, we show how the spatial structure, and more precisely the composition of the local neighbourhood, can also influence this survival through local competition. At an individual scale, it is well known that each plant's survival depends on the composition of its neighbourhood (Pacala and Silander, 1985; Begon et al., 1990; Kubota and Hara, 1995; Otto, 1998). With our model, it is possible to formulate this relation explicitly, and even analytically, and to show that plants of a competitive inferior species that are located together within an aggregate are more likely to survive than plants surrounded by more competitive species. These results are consistent with the results of other models. With the

TREEGRASS model, a fine scale 3D model of light and water resource use by plants in savanna ecosystem, Simioni et al. (2000) have shown that grass production was higher when trees are aggregated. Moreover, using an understory light environment model, Martens et al. (2000) have shown that the variability of the understory light increases when the spatial structure of trees is aggregated, which could facilitate the survival of various species of plants.

Because the mortality process is highly non-linear, it is generally difficult to find a relation between spatial structure and survival at the community scale. With our model, it was possible to take this complexity into account, and to derive a threshold number of more competitive neighbours that a plant can endure, N_{\max} , as well as an explicit link between the classical parameters describing the spatial structure (such as the intertype function) and the number of survivors. The influence of spatial structure on survival appears to be stronger for intermediate values of soil fertility. With either a very low or a very high fertility, the constraint is either too difficult or too easy to fulfil, and spatial structure then has little influence on survival.

The origin of the structure of an ecosystem is another important issue in theoretical ecology. Many authors have studied how various factors, such as soil heterogeneity, catastrophic events, regeneration processes or competition, can create structure (Oldeman, 1983; Huston and DeAngelis, 1987; Begon et al., 1990; Menaut et al., 1990; Lefever and Lejeune, 1997; Pontailier et al., 1997). Our model illustrates how local competition for a

soil resource in a mixed community can lead to some specific structures. By eliminating plants that have too many more competitive neighbours, local competition modifies the interspecific structure of the community towards interspecific repulsion, which progressively decreases the intensity of competition. In such situations, foresters sometimes say that the stress of the stand decreases with its age (Otto, 1998). As far as the specific structure is concerned, aggregates of less competitive species are more likely to survive, leading to a more aggregated structure. The presence of aggregates in a forest stand is usually explained by some constraints on the regeneration process, such as the proximity of the mother tree (for heavy seeds) (Collinet, 1997). Our model shows how it can also be the result of local competition in mixed communities.

5.3. The qualitative results of our model are consistent with some observations in mixed stands, and could be applied in forest management

As discussed above, the validation of our theoretical model on forest data is very difficult, because no measures of resource concentrations in soil or tree compartments are available in classical forest stand databases. However, more qualitative comparisons of the dynamics of simulated and real stands are possible, especially using the spatial structure as a criteria (Goreaud et al., 1999). For this purpose, we used the 1 ha 'Beau Poirier' plot, located in a 150-year-old sessile oak (*Quercus petraea*) and European beech (*Fagus sylvatica*) mixed stand near Nancy (France) (Pardé, 1981). Between 1950 and 1995, more than 33% of the oaks have been eliminated through competition with beech. In such mixed stands, the competition between fine roots is very important (Leuschner et al., 2001), so that our model of soil nutrient competition is relevant. Actually the changes in the spatial structure of the plot (Fig. 8) are consistent with the qualitative results of the model: the values of the intertype function $L_{O,B}(r)$ have decreased between 1950 and 1995, which corresponds to a shift of the structure towards interspecific repulsion.

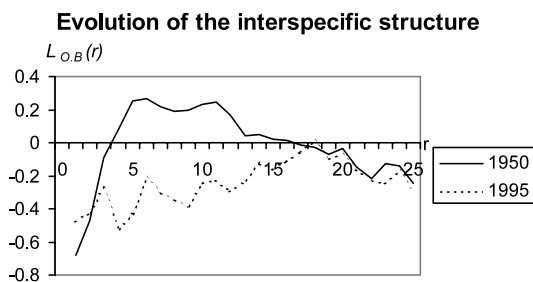


Fig. 8. Intertype function between oak and beech $L_{O,B}(r)$, computed on the data of the Beau Poirier plot in 1950 and 1995.

On the same plot, aggregated trees have a higher survival rate than do isolated ones. Some forestry practices already recommend to specifically manage groups of less competitive trees in order to improve their growth and survival (Staschel and Greger, 1993; Duchiron, 1994; Otto, 1998). The advantages of aggregates can be explained by our neighbourhood competition model. More studies on the dynamics of such aggregates, and especially on the maximum number of neighbours, could lead to some justification and generalisation of these practices (Bastien and Otto, 1998).

At stand level, the relation between the spatial structure of a stand and the survival of less competitive trees could become a useful tool in forest management, by predicting the dynamics of the composition of mixed stands, which is still a real problem for foresters (McTague and Stansfield, 1995; Vanclay et al., 1997; Jogiste, 1998; Pretzsch, 2000). For instance, comparing the dynamics of different types of spatial structure could allow the optimisation of the location of trees before their plantation. On existing stands, predicting the survival of less competitive species could help to define thinning scenarios. However, such applications require an important phase of model fitting, which means that foresters have to create long-term experimental plots in mixed stands with spatially explicit measures of individual trees.

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Appendix A. Stability of the equilibrium states

Let us consider a global equilibrium state of the model, and let P_i^* , L_i^* and G^* be the equilibrium

values of the variables. The stability of this equilibrium state depends on the sign of the eigenvalues of the corresponding Jacobian matrix (Eq. (18)).

$$J^* = \begin{pmatrix} A_1 & B_{12} & \dots & B_{1i} & \dots & \begin{pmatrix} 0 \\ \frac{q_1}{V_1} \end{pmatrix} \\ B_{21} & q_2 A_2 & \dots & B_{2i} & \dots & \begin{pmatrix} 0 \\ \frac{q_2}{V_2} \end{pmatrix} \\ \vdots & \vdots & \ddots & \vdots & \ddots & \vdots \\ B_{i1} & B_{i2} & \dots & A_i & \dots & \begin{pmatrix} 0 \\ \frac{q_i}{V_i} \end{pmatrix} \\ \vdots & \vdots & \ddots & \vdots & \ddots & \vdots \\ \left(0 \ \frac{q_1}{V_1}\right) & \left(0 \ \frac{q_2}{V_2}\right) & \dots & \left(0 \ \frac{q_i}{V_i}\right) & \dots & \left(-\frac{q}{V} - \sum_{i=1}^n \frac{q_i}{V_i}\right) \end{pmatrix}$$

$$A_i = \begin{pmatrix} a_i(L_i^* - c_i) & a_i P_i^* \\ -\frac{a_i}{V_i} L_i^* & -\frac{\left(q_i + a_i P_i^* + \sum_{j \neq i} v_{ij}\right)}{V_i} \end{pmatrix}$$

and
$$B_{ij} = \begin{pmatrix} 0 & 0 \\ 0 & \frac{v_{ij}}{V_i} \end{pmatrix} \tag{18}$$

Let us consider a tree i whose equilibrium state is death. For this tree $P_i^* = 0$ and $L_i^* = C_i^{\text{mean}}$ (Eq. (7)). Therefore, all terms of the corresponding line $(2i - 1)$ of the Jacobian matrix are zero, except the diagonal term, which is $a_i(C_i^{\text{mean}} - c_i)$. We can then conclude that $\lambda_i = a_i(C_i^{\text{mean}} - c_i)$ is an eigenvalue of the Jacobian matrix.

The sign of λ_i depends of the relation between c_i and C_i^{mean} . If, for this tree i , $c_i < C_i^{\text{mean}}$, then λ_i is positive, which implies that the equilibrium state is unstable.

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