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Original article

A model bridging distance-dependent and distance-independent tree models to simulate the growth of mixed forests

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Mixed stand / oak-pine forest / growth model / neighbourhood distribution

Abstract

• It is widely believed that distance-independent tree models fail to take into account the complexity of mixed stands due to the fact that spatial structure often has a greater impact on growth and dynamics in mixed stands than in pure stands. On the other hand, distance-dependent tree models are difficult to use because they require a map of the stand, which is not only very costly but also impracticable in a routine management context.

• This paper reports the development of a model bridging distance-dependent and distance-independent tree models, and that is designed to simulate the growth of a mixed forest. The model used distributions of the number of neighbours to reconstruct tree neighbourhoods and compute the competition indices needed as inputs to the growth model.

• Data were collected from a mixed forest of sessile oak and Scots pine in central France. The study showed that local competition indices explained a significant proportion of growth variability and that intraspecific competition was greater than interspecific competition. The model based on neighbourhood distributions gave consistent predictions compared to a distance-dependent model.

• This type of model could be used instead of distance-dependent models in management contexts.

Mots-clés :
Peuplement mélangé / mélange chêne-pin / modèle de croissance / distribution de voisinage / indice de compétition

Résumé – Un modèle intermédiaire entre un modèle arbre dépendant et indépendant des distances pour simuler la croissance des peuplements mélangés.

• On considère généralement que les modèles arbre indépendant des distances ne permettent pas de rendre compte de la complexité des peuplements mélangés. En effet, la structure spatiale a souvent un rôle plus important sur la croissance et la dynamique dans ces peuplements que dans les peuplements purs. Les modèles arbre dépendant des distances sont quant à eux difficile à utiliser, car ils nécessitent une cartographie du peuplement qui est une information très coûteuse à obtenir et qui n'est pas disponible dans un cadre de gestion courante.

• Cet article présente un modèle intermédiaire entre un modèle arbre indépendant des distances et un modèle arbre dépendant des distances. Ce modèle a été développé pour simuler la croissance de peuplements mélangés. Il utilise des distributions de nombre de voisins pour reconstruire le voisinage des arbres. Ces voisinages reconstruits permettent ensuite de calculer les indices de compétition nécessaires dans l'équation de croissance.

• Les données ont été récoltées dans des peuplements mélangés de chêne sessile et de pin sylvestre dans le centre de la France. Ce travail montre que des indices de compétition locaux expliquent une part significative de la croissance individuelle et que la compétition intraspécifique est supérieure à la compétition interspécifique. Le modèle basé sur les distributions de voisinage donne des prédictions cohérentes par rapport au modèle arbre dépendant des distances.

• Ce type de modèle pourrait être utilisé à la place des modèles arbre dépendant des distances dans des contextes de gestion.

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1. INTRODUCTION

Interest in mixed forests has been growing steadily, prompted mainly by environmental reasons such as biodiversity conservation or adaptation to global change. In France, mixed forests also represent an economic challenge, since they cover about 50% of the total forest area according to the latest national forest inventory (Morneau et al., 2008) and this figure appears to be on the increase (Ulrich et al., 2006). Nevertheless, forest managers have relatively few tools enabling them to accurately describe or predict mixed forest growth.

Mixed forests are more difficult to understand than pure stands because they are made up of several species that generally present different growth rates. Moreover, the different types of between-species interactions can change during the life of the stand or in response to environmental conditions (Tilman, 1988). Thus, contrary to pure stands for which distance-independent tree models have proven their worth (Munro, 1974), there is no consensus on the best way to model mixed forest growth.

It is widely believed that distance-independent tree models fail to take into account the complexity of these stands due to the fact that spatial structure often has a greater impact on growth and dynamics in mixed stands than in pure stands (Goreaud, 2000; Ngo Bieng, 2007; Porté and Bartelink, 2002). For example, Goreaud et al. (2002) showed that survival of an inferior competitor in a mixed stand was directly dependent on the specific composition of its neighbourhood. Furthermore, many studies have demonstrated the interest of distance-dependent competition indices to explain tree growth in mixed forests (e.g. Canham et al., 2006; Stadt et al., 2007; Zhao et al., 2006). Consequently, more and more models are using spatial characteristics to launch simulations in mixed forests (Porté and Bartelink, 2002).

However, distance-dependent tree models are often difficult to use because they require a map of the stand, which is not only very costly but also impracticable in a routine management context (Munro, 1974; Wimberly and Bare, 1996). Consequently, spatial models are often launched using virtual stands (Illian et al., 2008; Kokkila et al., 2002; Pommerening, 2006; Pretzsch, 1997) generated through point processes (Comas and Mateu, 2007; Stoyan and Penttinen, 2000) whose characteristics can be fitted from real data (e.g. Goreaud et al., 2004; Ngo Bieng, 2007; Pommerening and Stoyan, 2008).

A map of a stand in fact provides a wealth of information that is often under-used in models describing ecological processes. This raises the question of whether it is possible to use less costly information. For example, Phillips et al. (2004) modelled distributions of competition indices for use with a distance-dependent model where each tree had a competition index assigned at random but respecting normal distributions whose parameters were dependent on the species and size of the subject tree.

The aim of this article is to propose a method that combined distributions of the number of neighbours, called neighbourhood distributions, with a list of trees to reconstruct tree neighbourhoods. These reconstructed neighbourhoods make it possible to compute the competition indices needed as inputs in the growth model without knowing the location of every trees. This method allows neighbourhoods to automatically change over time, since each neighbouring tree is itself part of the stand subject to the growth process. However, the individuals have no explicit location, which is what makes the model an intermediary between spatial and non-spatial models. We applied this method to a relatively simple case where only two species are mixed, i.e. sessile oak (*Quercus petraea* L.) and Scots pine (*Pinus sylvestris* L.), in central-northern France. In addition, we focused only on tree radial increments.

This paper begins by presenting the principle of the neighbourhood distribution-based model. Secondly, we present the application of this model in oak-pine forests in central-northern France. We then show how the predictions of this neighbourhood distributions-based model were compared with the predictions of the distance-dependent tree model. Finally, we discuss the limitations of this model and its possibilities for use in routine forest management.

2. MATERIALS AND METHODS

2.1. Stand description and growth data

Data were collected in mixed sessile oak-Scots pine stands from the Orléans state run forest (47° 51′ N, 2° 25′ E), a 35 000 ha forest located in central-northern France. Oak-pine mixed stands hold an important position in the French forests for three main reasons: they cover a relatively large area (Morneau et al., 2008); they have a heritage value for people; and they are well adapted to the sandy and waterlogged soils common to central France.

Between 2004 and 2007, 30 plots of an area between 0.5 and 1.25 ha each were fully mapped in the Orléans state run forest so as to run an in-depth study on the horizontal spatial structure of these stands. Ngo Bieng et al. (2006) described different types of canopy structure corresponding to a gradient from random to strong aggregation of the two species, and from independence to interspecific repulsion. We then selected 9 of the 30 plots to cover this gradient of spatial structure in order to have contrasted competitive conditions between trees of the same species but also between trees of different species. These plots included small proportions of other broadleaved species (mainly *Carpinus betulus* L., *Betula pendula* R. and *Sorbus torminalis* L.) representing 4% of the total basal area (Tab. I).

In each of the selected plots, 20 trees per species were sampled to perform growth measurements. We made the assumption that for a given plot, tree size and local competition were the two factors that had the greatest influence on individual growth. Data corresponding to different tree sizes and different local competitions are necessary to model the effects of these factors. We therefore used a stratified sampling to select the trees to be measured. The stratification variables, tree size and local competition, were characterized using girth at a height of 1.3 m and a competition index (Biging and Dobbertin, 1992), respectively. For each species and each plot, 20 trees were then randomly selected to cover the range of the stratification variables in the plot.

Sampled trees were cored to the pith in two perpendicular directions at a height of 1.3 m. Cores were scanned and analyzed using WinDENDRO software version 2005a (Regent, 2005), and ring width was measured to the nearest 0.01 mm. The individual ring-width series were cross-dated using COFECHA software (Grissino-Mayer,

Table I. Basal area (BA), density (N) and mean diameter (Diam.) for oak, pine and other broadleaved species in the 9 plots.

Plot	Area	Oak			Pine			Other broadleaved species			Total BA	Total *N*
	(ha)	BA (m^2/ha)	*N* (stems/ha)	Diam. (cm)	BA (m^2/ha)	*N* (stems/ha)	Diam. (cm)	BA (m^2/ha)	*N* (stems/ha)	Diam. (cm)	(m^2/ha)	(stems/ha)
D02	0.57	12.1	308	20.5	10.9	113	34.4	1.0	65	13.0	23.9	486
D108	0.48	8.6	327	17.2	25.5	252	35.5	1.5	100	13.4	35.6	679
D20	0.51	9.1	435	15.4	18.4	208	33.1	0.4	38	11.4	28.0	680
D27	0.31	9.7	371	16.6	15.6	140	36.8	3.3	292	11.5	28.6	803
D42	0.24	11.5	467	16.5	15.3	292	24.8	1.0	96	11.3	27.8	854
D49	0.64	13.8	521	16.8	18.5	236	30.9	1.7	77	15.5	34.0	834
D534	0.36	11.5	467	16.5	18.9	167	37.6	0.7	53	12.8	31.2	686
D563	0.24	12.6	229	24.6	21.2	246	32.8	0.2	25	10.9	34.0	500
D78	0.37	14.3	405	20.2	20.4	119	46.2	0.9	57	13.2	35.6	581

2002) to assess the quality of the operation. As some trees were not possible to core and some cores were not usable, the statistical analyses were finally based on a total of 154 oaks and 179 pines.

Detailed information on past disturbances were not available in our plots (location and size of suppressed trees). The period from 2000 to 2005 was therefore chosen to study growth, as there were no human or natural disturbances during this period.

2.2. Principle of the neighbourhood distribution-based model

We considered the general case of a distance-dependent tree model using local competition indices to predict growth:

$$INC_i = f(X_i, CI_i)$$

where INC_i is the size increment of the ith tree between time t and time $t + \Delta t$, X_i corresponds to tree or site characteristics, and CI_i is one or more local competition indices. To compute local competition indices, the neighbourhood of each tree needs to be identified, which is generally done using a map of the stand. However, instead of using the map, the model proposed here uses neighbourhood distributions as a means of reconstructing this local information.

2.2.1. Neighbourhood distributions: definition

Counting the number of neighbours in a disk of radius R for several trees in a stand usually results in different values. To account for this variability, it is necessary to use a distribution of the number of neighbours, similarly to the distribution of diameters used in size class models (see Porté and Bartelink, 2002). In a mixed stand, we have to define several distributions depending on the species of the subject tree and the species considered in the neighbourhood. These distributions are noted $D_{ss,ns}$ where ss is the subject tree species and ns is the neighbourhood trees species. $D_{ss,ns}(x)$ is thus the probability that a tree of species ss has x trees of species ns in its neighbourhood. These distributions are called neighbourhood distributions.

Neighbourhood distributions are directly related to a set of statistics used to characterize the spatial structure of a stand. The spatial structure of a two-species stand can be characterized using Intertype function $K_{12}(R)$ (Lotwick and Silverman, 1982), which is defined as:

$$N_{ns}K_{ss,ns}(R) = E(\text{number of trees of species } ns \text{ at a distance} \leq R \text{ of a tree of species } ss)$$

where N_{ns} is the density of species ns, E the expectation value, and R the radius of the disk centred on the subject tree. Let $\mu_{ss,ns}$ be the expected value of the distribution $D_{ss,ns}$. We then have:

$$N_{ns}K_{ss,ns}(R) = \mu_{ss,ns}.$$

It can be shown that $K_{ss,ns}(R) = K_{ns,ss}(R)$ (Lotwick and Silverman, 1982). Thus if $ss \neq ns$, then $\mu_{ss,ns}/N_{ns}$ characterizes the spatial interaction between species at a distance less than R. If $ss = ns$, then $K_{ss,ss}(R)$ is the Ripley function $K(R)$ (Ripley, 1977) and $\mu_{ss,ss}/N_{ss}$ characterizes the spatial structure of one species at a distance less than R. In the oak-pine mixed stands that we presented, we chose to use four neighbourhood distributions ($D_{\text{oak,oak}}$, $D_{\text{oak,pine}}$, $D_{\text{pine,pine}}$ and $D_{\text{pine,oak}}$) so as to take into account the specific and interspecific spatial interactions between individuals (Fig. 1).

Furthermore, neighbourhood distributions also reflect the variability in the neighbourhoods. Figure 2 shows three examples of neighbourhood distribution in three virtual stands exhibiting the same density but different spatial structures (spatial structures were characterized with the Ripley function, not presented in this article). The three stands have, as expected, different mean values for the number of neighbours, but also very different variability. The stand with a regular pattern shows very low variability while the stand with an aggregated pattern shows very high variability. In regular stands, the mean value of the distribution makes it possible to obtain a good estimator of local competition, whereas the mean value makes little sense in aggregated stands. Neighbourhood distributions thus reflect not only differences in stand spatial structures but also variability of the neighbourhoods in the stand.

2.2.2. Reconstructing neighbourhoods

In a mixed stand, if we assume that we know the neighbourhood distributions as well as the list of trees in the stand, it is possible to reconstruct virtual neighbourhoods, i.e. to give each tree a list of neighbours compatible with the neighbourhood distributions observed (Fig. 3).

For one tree, the first step is to draw a random number of neighbours of each species that conforms to the neighbourhood distributions. In a second step, the neighbouring trees are selected at random from the list of trees. For each subject tree, this selection is done with the full list of the trees without replacement. Thus, two trees may share common neighbours but a subject tree cannot have two times the same neighbour. For the oak-pine mixed stands, two approximations are made here. First, for a given subject tree, oak numbers and

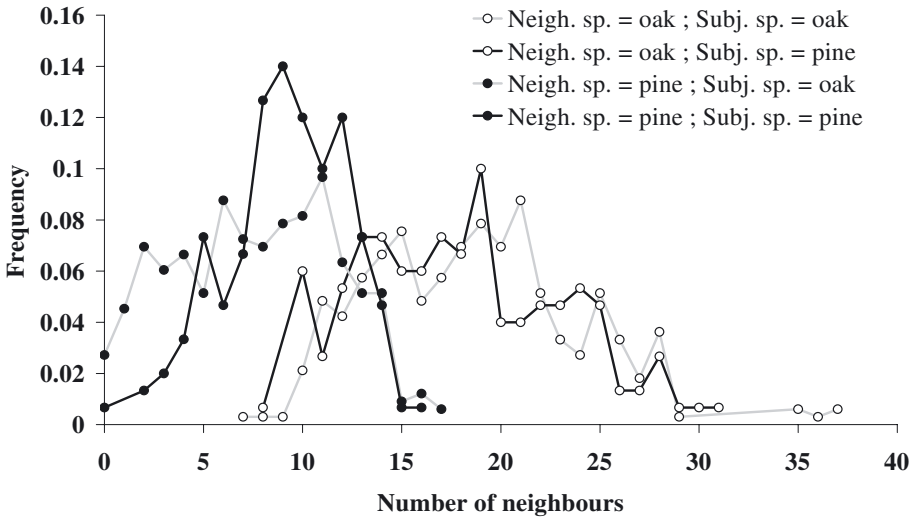

Figure 1. Frequency of number of neighbours at a distance less than 10 m for a plot with two species (plot D49). Subj. Sp. = subject species; Neigh. Sp. = neighbour species. Class width = 1 neighbour.

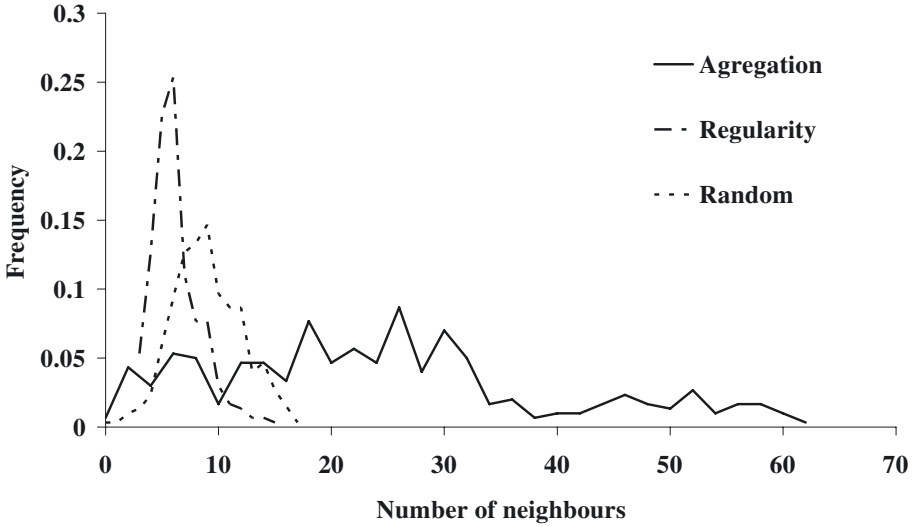

Figure 2. Frequency of number of neighbours at a distance less than 10 m for three simulated stands with one species. The three stands have the same density, but exhibit different spatial structures. Class width = 1 neighbour.

pine numbers were not constrained by the total number of neighbours. Secondly, the neighbours were selected regardless of the size of the subject tree, which corresponds to the assumption of spatial independence between the location of an individual and its size.

At this stage, each tree has a list of neighbours of each species, which makes it possible to compute local competition indices and update the neighbourhoods over time, as indicated below.

2.2.3. Updating neighbourhoods over time

The neighbourhood of a tree in a stand changes over time due to regeneration, growth and mortality, as well as to human impacts. In our study, we did not take mortality or regeneration processes into account, which is why we assumed that a tree's neighbourhood was only influenced by the growth process and thinnings. As stated above, each tree has a list of neighbours that themselves belong to the stand. The growth of a tree between two dates depends on the state of the neighbourhood at the beginning of the growth period. Hence, the neighbourhoods are updated after the growth process when all the trees have grown and their new features are known (Fig. 4). Similarly, neighbourhoods are also updated after a thinning to account for the trees removed. We can thus ensure that reconstructed neighbourhoods change over time according to growth process and thinnings.

To summarize, the neighbourhoods are reconstructed once at the beginning of the first growth period using the neighbourhood distributions and the trees of the stand. Then, as trees of the neighbourhoods are trees of the stand, they change over time according to the growth process and thinnings. Thus, each tree has its own neighbourhood that is consistently changing over time.

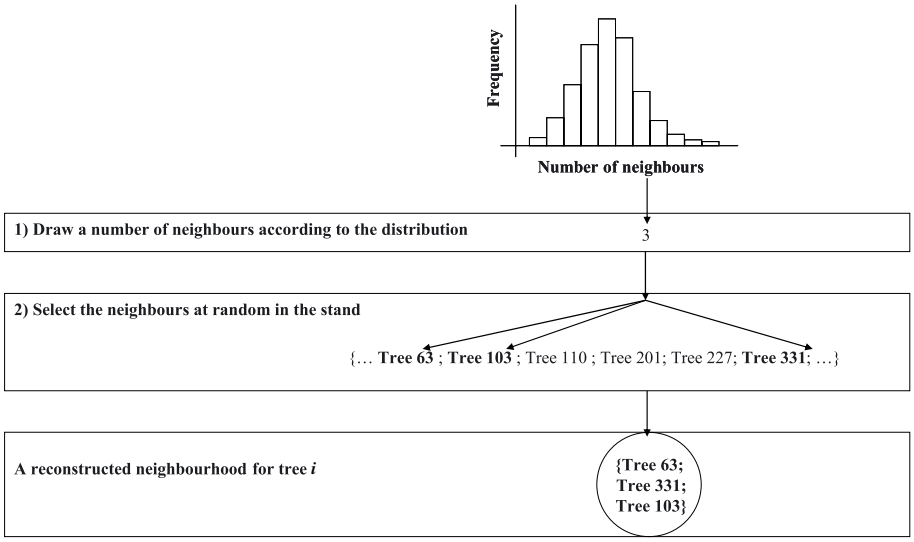

Figure 3. Representation of the way the neighbourhood for one tree in the stand is reconstructed at the beginning of the first growth period (t_0). The neighbourhood is defined by a disk of radius R. In this example, there is three trees in the neighbourhood of tree i.

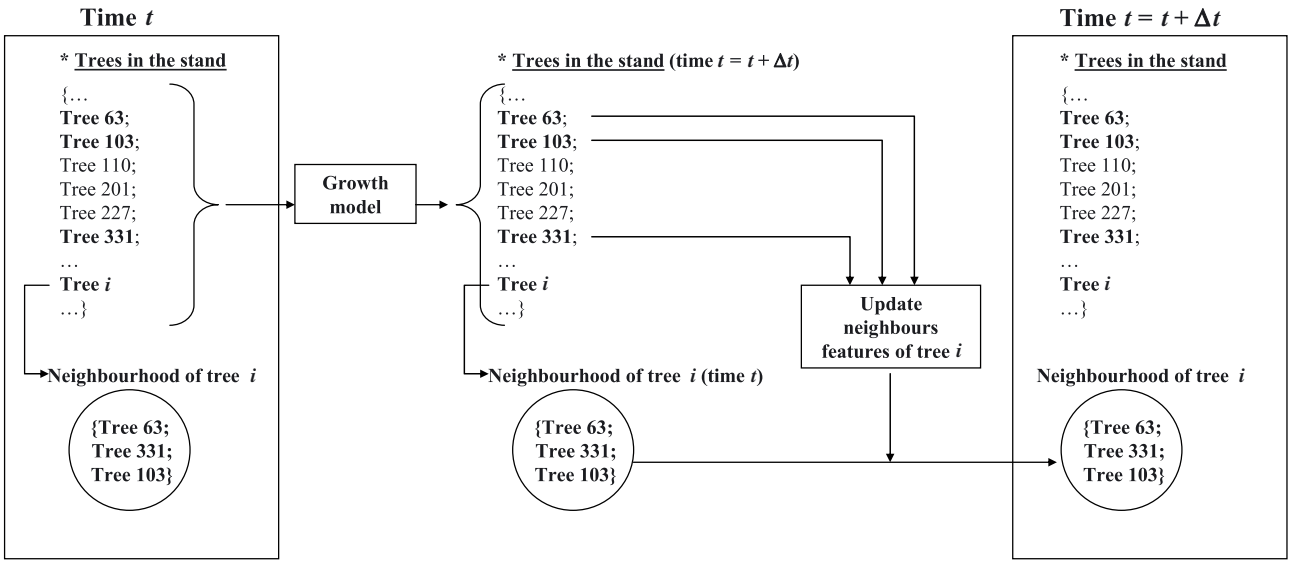

Figure 4. Representation of the way the neighbourhood of a tree is updated at the end of a growth step. All the trees in the stand have a list of neighbours. Tree i has three neighbours called 63, 331 and 103 that belong to the stand. Between time t and time $t + \Delta t$, the model effects tree growth based on the status of the neighbourhoods at time t. The characteristics of the neighbours are updated after the growth step. Trees 63, 331 and 103 at time $t + \Delta t$ make it possible to update the neighbourhood of tree i. The new state of the neighbourhoods will be used for the next growth step.

2.3. Tree size and local competition effects on growth

The growth of a tree is related to its ability to exploit the resources of its environment. We made the classical assumption that the bigger a tree, the greater its potential growth (Wykoff, 1990). To account for tree size, we used tree girth at a height of 1.3 m (Fig. 5).

In a given stand, the neighbours of a tree reduced its growth. In a mixed stand, the type of species in the neighbourhood of a tree could also have an influence on its ability to exploit resources (e.g. Uriarte et al., 2004b; Zhao et al., 2006). Hence, we next assumed that part of the growth variability is linked to differences in neighbourhoods leading to differences in local competition. We considered that a tree's local competition can be characterized by a local competition index.

Competition indices are computed according to characteristics of trees belonging to the neighbourhood of a subject tree. In our application, we want to study the growth between 2000 and 2005. Competition indices should be calculated at the beginning of a growth period (year 1999) if the model is to be used for predictions. Having measured a sample of trees in the stand, we reconstructed the diameters in 1999 for trees in the neighbourhoods in order to estimate the value of

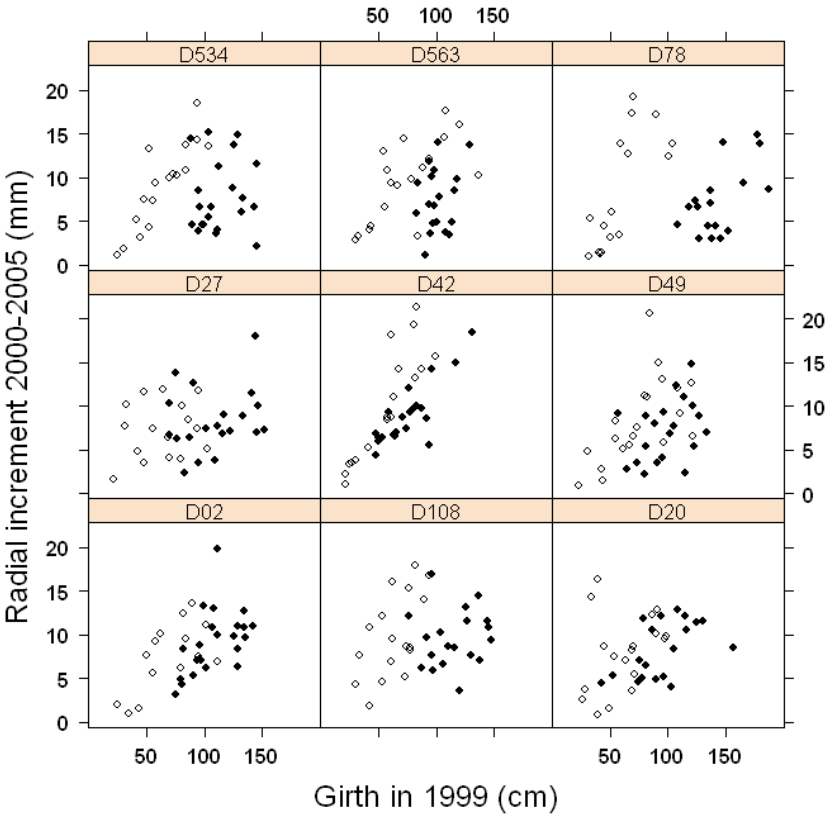

Figure 5. Radial increment (mm) between 2000 and 2005 versus girth in 1999 for the nine plots; o = Sessile oak; • = Scots pine.

the competition indices in 1999. For each plot, we used a relationship between the diameter measured during the inventory (2005 or 2006 depending on the plots) and the circumference in 1999 obtained on the sampled trees. In the absence of mortality or thinning, there is a strong correlation between the neighbourhood at the beginning and the end of a growth period. We therefore assumed that our correction had a small impact on the results about competition indices.

In our work, neighbourhood was defined as a disk of radius R, and three radii were tested in the analyses (R = 5, R = 10 and R = 15 m) so as to cover the range of radii reported in other studies (Canham et al., 2004; Stadt et al., 2007; Uriarte et al., 2004a) and to minimize the influence of edge effects when computing the competition indices. The Crowding index (Canham et al., 2004) was used as predictor variable in the growth model and was calculated in the neighbourhood defined above. This index assumed that the effect of a neighbouring tree on the growth of a target tree varies as a function of the size of the neighbour and as an inverse function of the distance to the neighbour:

$$CI_{i,s} = \sum_{j=1}^{n_s} \frac{dbh_{j,s}^{a}}{l_{ij}^{b}} \quad (1)$$

where $CI_{i,s}$ is the competition index of the target tree i computed for the neighbouring trees belonging to species s, with n_s the number of neighbouring trees belonging to species s, $dbh_{j,s}$ the diameter at a height of 1.3 m of the jth neighbouring tree belonging to species s, and l_{ij} the distance between the target tree i and the jth neighbouring tree. a and b respectively determine the shape of the effect of neighbour diameter and its distance to the target tree on CI (Uriarte et al., 2004b). We tested a limited number of values for a and b ($a \in \{0; 1; 2\}$ and $b \in \{0; 0.5; 1\}$) in order to cover the classical indices of competition, such as local density (a = 0 and b = 0) or local basal area (a = 2 and b = 0), as well as intermediary indices. As stated in the presentation of data, the neighbourhoods may also feature broadleaved species other than oak. Since these other species were very scarce (Tab. I), they were grouped with oak when computing the competition indices.

Tree size and competition indices of each species were added to the growth model (Stadt et al., 2007) so as to create a distance-dependent tree model, otherwise known as a spatially explicit individual-based model:

$$\Delta r_{i,k,s} = \alpha_{k,s} + \beta_{k,s} girth_{i,k,s} + \lambda_{\text{oak}} CI_{i,\text{oak}} + \lambda_{\text{pine}} CI_{i,\text{pine}} + \varepsilon_{i,k,s} \quad (2)$$

where $\Delta r_{i,k,s}$ is the radial increment (mm) of a six-year (2000–2005 period) timespan of tree i, $girth_{i,k,s}$ is the girth (cm) in 1999 of tree i, $\varepsilon_{i,k,s}$ is the residual error, $\alpha_{k,s}$ and $\beta_{k,s}$ are the model parameters for plot k and species s, respectively, and λ_{oak} and λ_{pine} are the coefficients associated with the competition index calculated on the oak competitors and the pine competitors, respectively. For the growth of one species, we considered that a and b were identical for $CI_{i,\text{oak}}$ and $CI_{i,\text{pine}}$. This made it possible to compare the competitive powers of the two species and thus to explore intraspecific and interspecific competition through coefficients λ_{oak} and λ_{pine}. A total of 27 indices were tested (3 radii × 9 competition indices). To select the best competition index, we classified the models using the adjusted R-square. We also adjusted the model with a size effect only in order to assess the improvement made by introducing the competition indices (λ_{oak} = 0 and λ_{pine} = 0).

Table II. Coefficient values of the first 10 competition indices, probability values and adjusted *R*-squares corresponding to Equation (2) model.

Subject tree	Rank	*a*	*b*	*R*	λ_{oak}	$Pr_{oak} > F$	λ_{pine}	$Pr_{pine} > F$	Adj. R^2
Oak	1	0	0.5	10	–0.788	< 0.0001	–0.523	0.0196	0.585
Oak	**2**	**0**	**0**	**10**	**–0.353**	**< 0.0001**	**–0.242**	**0.0129**	**0.580**
Oak	3	1	0	10	–2.431	< 0.0001	–1.123	0.0010	0.576
Oak	4	1	0.5	10	–5.108	< 0.0001	–2.282	0.0035	0.572
Oak	5	1	0.5	15	–4.310	< 0.0001	–1.897	0.0015	0.572
Oak	6	0	0.5	15	–0.535	< 0.0001	–0.356	0.0375	0.547
Oak	7	1	0	15	–1.417	< 0.0001	–0.619	0.0049	0.544
Oak	8	2	0.5	15	–18.474	< 0.0001	–6.636	0.0008	0.542
Oak	9	2	0	15	–26.885	< 0.0001	–9.616	0.0008	0.534
Oak	10	2	0	10	–38.537	< 0.0001	–13.163	0.0025	0.528
Oak	Size effect model (λoak = 0 and λ_{pine} = 0)								0.433
Pine	1	2	0.5	10	–1.459	0.7729	–8.496	0.0002	0.228
Pine	2	2	1	10	–4.304	0.6662	–19.361	0.0001	0.226
Pine	**3**	**2**	**0**	**10**	**–0.750**	**0.9283**	**–12.779**	**0.0005**	**0.223**
Pine	4	1	0.5	10	0.582	0.5349	–2.488	0.0008	0.221
Pine	5	1	0	10	0.320	0.4174	–0.947	0.0019	0.219
Pine	6	2	1	15	–0.969	0.9203	–16.555	0.0005	0.218
Pine	7	1	1	10	0.612	0.7276	–5.684	0.0004	0.216
Pine	8	2	0.5	15	2.070	0.6338	–5.662	0.0037	0.213
Pine	9	1	1	15	0.688	0.6799	–4.977	0.0010	0.213
Pine	10	1	0.5	15	0.711	0.3621	–1.743	0.0044	0.212
Pine	Size effect model (λ_{oak} = 0 and λ_{pine} = 0)								0.155

The plot effect takes into account the possible effects of factors acting at stand level, such as effects of site, total density or stage of development (young or old stand). To test the influence of plot effect on growth, four models were compared: the model given by Equation (2), the model with a plot effect on the α parameter only, the model with a plot effect on the β parameter only, and a model without plot effect. The models were selected using the *F* statistic, which compares the mean squares of two models. When two models had the same degree of freedom, the model with the lower residual sum of squares was selected.

2.4. Methods used to compare models

From the results obtained with the tree distance-dependent model, we developed a model based on neighbourhood distributions adapted to oak-pine mixed stands. We estimated the four neighbourhood distributions for all plots ($D_{oak,oak}$, $D_{oak,pine}$, $D_{pine,pine}$ and $D_{pine,oak}$). To estimate these distributions, it is first necessary to identify the number of neighbours for certain trees in the stand. If a map of the stand is available, the number of neighbours can be calculated for all trees of the stand, which provides a precise distribution. If the map is not available, it is possible to proceed by sampling, for example by randomly selecting trees in the stand for which the number of neighbours is counted. In this case, the distribution will be estimated more or less accurately depending on the sampling size. In our work the distributions were estimated using all the trees of the stand because we did not want to introduce an additional source of variation related to the estimate of the distributions in the predictions of the model. The two models were implemented in the CAPSIS4 simulation platform (Coligny et al., 2003) to run the simulations.

To evaluate the model based on neighbourhood distributions-based model, we investigated how the model behaves compared to the distance-dependent tree model. This investigation was led by comparing simulation results from two model types: the distance-dependent tree model (Eq. (2)) denoted as *S* that uses real tree locations to compute local competition indices, with the model denoted as *I* that uses neighbourhood distributions to reconstruct neighbourhoods of each tree. Our mixed oak-pine stands are thinned roughly every 10 y, which is therefore an appropriate timespan to test the two models. However, in order to respect the time step of our models, we compared the models after six years of growth. We also compared the models after twelve years of growth to check whether the difference between the two models was greater after a longer time projection. Each model was run to simulate six years and twelve years of growth on the 9 plots. For predictions, we did not take into account species other than oak and pine (see Tab. I). For the comparisons, we focused on the predictions of basal area increment at stand level.

For the *I* model, as stated above, a stochastic component was introduced when the neighbourhoods were reconstructed at the beginning of the first growth period. Hence, this model was used to perform 1 000 simulations for each plot to estimate the impact of the stochastic component on the results. From the 1 000 values obtained in a plot, we calculated the average and the 95% confidence interval of the basal area increment for each species. We also computed the relative standard deviation (RSD) to evaluate the variability of the model predictions. We then compared the results of the two models for each plot and each species.

3. RESULTS

3.1. Local competition effect on growth

For oak, the first four indices given in Table II are calculated in a disk of radius 10 m, which leads to the assumption that for this species the radius that gives the best results is 10 m. For

Table III. ANOVA tables, parameter estimates and model statistics for the distance-dependent tree model (Eq. (2)).

	Oak (a = 0 and b = 0 for CI)				Pine (a = 2 and b = 0 for CI)			
Source	SS	d.f.	F value	$Pr > F$	SS	d.f.	F value	$Pr > F$
Intercept	50.48	1	4.939	0.0279	110.75	1	10.647	0.0013
Girth1999	93.95	1	9.194	0.0029	250.38	1	24.071	< 0.0001
Plot	177.99	8	2.177	0.0329				
CI_{oak}	417.87	1	40.89	< 0.0001				
CI_{pine}	64.83	1	6.344	0.0129	137.44	1	13.213	0.0003
Girth1999:Plot	184.87	8	2.261	0.0267	224.02	8	2.692	0.0082
Residuals	1369.24	134			1747.46	168		
Coefficient	Estimate		Standard Error (σ)		Estimate		Standard Error (σ)	
$\alpha_{k,s}$	$4.003 < \alpha_{k,oak} < 13.014$		$2.270 < \sigma < 3.393$		4.602		1.410	
$\beta_{k,s}$	$0.0361 < \beta_{k,oak} < 0.1766$		$0.0256 < \sigma < 0.0434$		$0.0337 < \beta_{k,pine} < 0.0812$		$0.0097 < \sigma < 0.0175$	
λ_{oak}	–0.3539		0.0553					
λ_{pine}	–0.2424		0.0962		–11.364		3.126	
Adjusted R^2	0.5806				0.2117			
Residual S.D.	3.197				3.225			

pine, the result is even clearer, and is also a neighbourhood radius of 10 m. In terms of coefficient a, values 0 and 1 give the best results for oak while values 2 and 1 give the best results for pine. Finally, for coefficient b, values 0 and 0.5 give the best results for oak, while there was no clear trend for pine. In terms of oak growth, the fact that the difference in performance between the first (a = 0 and b = 0.5) and the second index (density local, a = 0 and b = 0) was very low (0.5%) prompted us to choose local density, since this index does not need to factor in the distances to neighbouring trees in the 10 m disc radius. Similarly, for pine growth, since the difference in performance between the first (a = 2 and b = 0.5) and third (a = 2 and b = 0) index was also very low (0.5%), we chose a = 2 and b = 0 corresponding to the local basal area. To simplify, we conclude that in the case of oaks, local competition is related to local density (number of stems in a disc of 10 m radius) while for pines it is related to local basal area. Knowing the location of trees in the disc of 10 m radius does not significantly improve the results.

In the case of oak coefficients λ_{oak} and λ_{pine} were both significant and negative (Tab. II). For the first 10 indices, the absolute values for λ_{oak} were between 1.5 and 3 times greater than λ_{pine}. In the case of pine, the coefficient λ_{oak} was never significant. We can therefore say that for an oak tree, competition exerted by the neighbouring oaks is between 1.5 and 3 times greater than competition exerted by neighbouring pines, while for a pine tree, it is only competition from neighbouring pines that has a significant influence on growth. For both species, and particularly for pine, intra-specific competition is greater than inter-specific competition.

For oak, the plot effect is significant on α and β while for pine the most parsimonious model is the one with a plot effect on β (Tab. III). The distance-dependent tree model explains 58.1% of the growth variability for oak, i.e. a gain of 14.8% compared to a model with a size effect only. For pine, the most parsimonious model explains 21.2% of the growth variability, i.e. a gain of 5.7% compared to a model with a size effect only.

3.2. Comparison between the tree distance-dependent model and the neighbourhood distributions-based model

Model I gives lower predictions than those of model S both after six years and after twelve years (Figs. 6 and 7). For pine, model I predicts a basal area increment greater than the model S for one plot (plot D108). For oak, the predictions of model S are outside the confidence interval of model I. For pine, the predictions of the model S are within the confidence interval of model I for three plots (D02, D27 and D563).

The absolute difference between the two models after six years of growth is 4.4% on average for oak and 3.6% for pine. After twelve years of growth the results remain very similar, with a difference of 4.5% on average for oak and 3.9% for pine.

Variability of basal area increment at stand level obtained from 1 000 repetitions of model I on the same plot was very low and corresponded to an RSD of 1.6% for oak and 1.5% for pine.

4. DISCUSSION

4.1. Local competition effects on growth

We showed that introducing a local competition index significantly improved the proportion of growth variability explained by the model. Compared to a model with a size effect only, the improvement was greater for oak (+14.8% for adjusted R-square) than for pine (+5.7%). Stadt et al. (2007) used the same type of competition index to obtain an improvement of between 10% and 30%. The improvement for pine was low enough to question the usefulness of introducing a local competition index for this species. Finally, we showed that using the distance to neighbouring tree led to small improvement in the performance of competition indices (+0.5% for adjusted R-square). In a given neighbourhood, the presence and diameter at breast height of a neighbouring tree is sufficient information to be able to estimate its contribution to local competition.

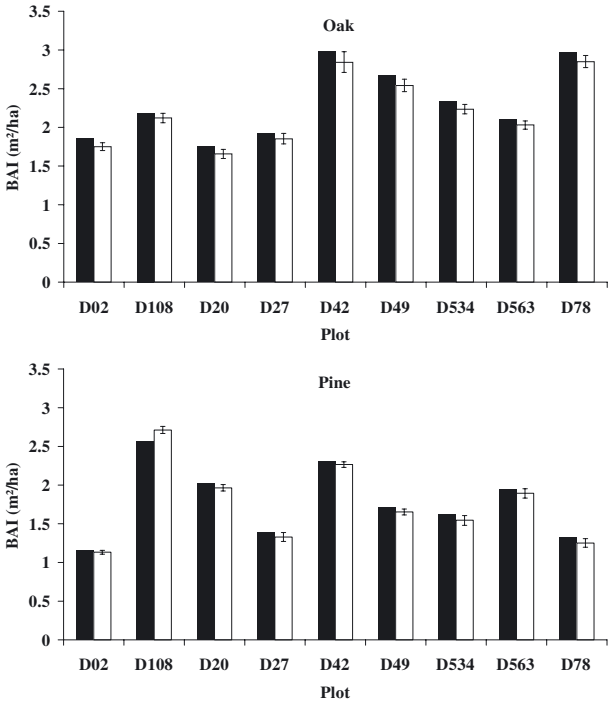

Figure 6. Basal area increment (m^2/ha) for oak and pine after 6 y of growth simulation. For each species, predictions of two models are shown: the distance-dependent model (in black) and the neighbourhood distributions-based model (in white) for which vertical bars represent 95% *CI*.

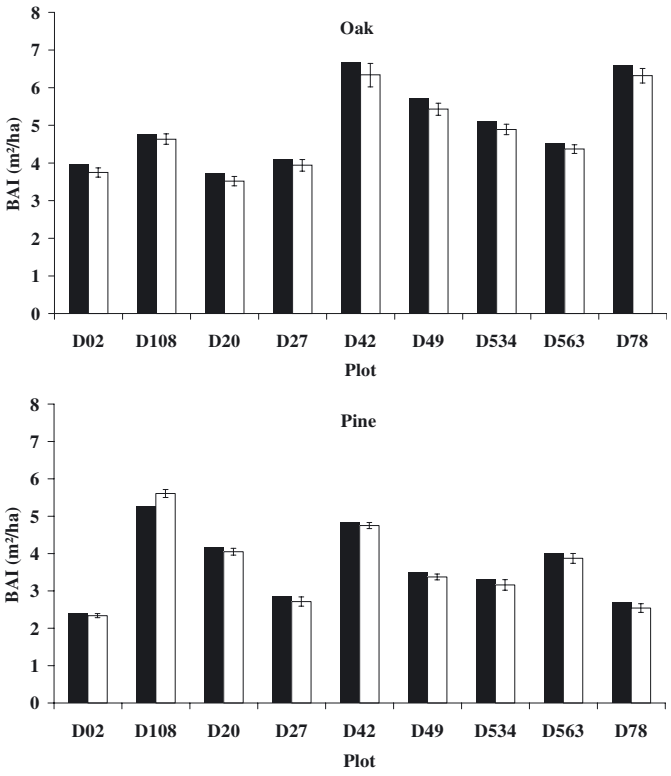

Figure 7. Basal area increment (m^2/ha) for oak and pine after 12 y of growth simulation. For each species, predictions of two models are shown: the distance-dependent model (in black) and the neighbourhood distributions-based model (in white) for which vertical bars represent 95% *CI*.

This work showed that intra-specific competition was more important than interspecific competition. This result is consistent with the "Lotka-Volterra" theoretical model of interspecific competition, which shows that this condition is a requisite for two species to coexist (Begon et al., 1996). We also showed that competition from oak on pine was non-significant. This result is in agreement with Biondi et al. (1992) who found that pine (*Pinus ponderosa* Dougl ex Laws) versus oak (*Quercus gambelii* Nutt) competition was negligible compared with pine versus pine when oak remains mostly in the understorey. Dominant pines were spaced out by the presence of oak trunks and were therefore less affected by crown competition. This situation was also reported by Rio and Sterba (2009) who studied mixed stands of *Pinus sylvestris* L. and *Quercus pyrenaica* Willd. In our study, although not all oaks were in the understorey, the pines on average had a greater girth than oaks, which could explain why there was a non-significant influence of oaks on pines.

4.2. Comparison between the distance dependent model and the neighbourhood distributions-based model

The results obtained with the tree distance-dependent model made it possible to develop a neighbourhood distribution-based model adapted to oak-pine mixed stands. We showed that, the difference between the two models was lower for pine, than for oak. This result can be explained by the fact that the local competition index for pines explained only a very small proportion of pine growth variability. The relative differences between the two models after six and twelve years of growth were very close. This result demonstrates that the predictions of the neighbourhood distributions-based model are little affected by time projection.

However, the predictions of the neighbourhood distributions-based model are lower than those of the distance-dependent model. The approximations we made to reconstruct the neighbourhoods could explain this result. In particular, the number of oaks and the number of pines were not constrained by the total number of neighbours. There is certainly no consequence for pine since the model only uses pine neighbours. In contrast, for oak, the model uses oak neighbours as well as pine neighbours. The approximation could lead to overestimate the total number of neighbours and thus to overestimate the competition. Consequently, the growth predicted with the neighbourhood distributions-based model could be underestimated compared to the distance-dependent model (upper part of Figs. 6 and 7).

Similarly, we made the assumption of spatial independence between the size of a tree and its location. This assumption could have consequences for pine because the competition index for pine involves the size of the neighbours (basal area of pines in a disk of 10 m radius). In a real stand, the size of

a tree can be dependent on other factors that differ from one species to another. For instance, if there is a soil heterogeneity, the size may be different from one place to another, so that the competition indices would be very variable. On the contrary, in some situations with strong competition, only small trees can be found around a big one, so that the competition indices are less variable. In the distance-dependent model, the local competition as well as the result at the stand level would be affected while nothing would change for the model based on neighbourhood distributions.

4.3. Model limitations

A first limitation of the model is that we used approximations to reconstruct the neighbourhoods: the number of oaks and the number of pines were not constrained by the total number of neighbours, and the neighbours were selected regardless of the size of the subject tree. As we have seen, these approximations could affect the model's predictions output, but they remain difficult to avoid. For example, to avoid the first approximation, it is necessary to know the joint distributions that give the probability that a tree of one species will have n_{oak} neighbouring oaks and n_{pine} neighbouring pines at the same time. This solution is feasible (Pommerening, 2006), but a vast amount of data is necessary to have a good estimate of these joint distributions, thus generating a constraint comparable that involved in mapping a stand.

A second limitation of the model comes from the choice of the competition indices. The performance of a local competition index generally depends on the data on which it was tested. It is therefore possible that for another study, other types of indices will prove more relevant than those used here. Some indices, such as those taking into account the spatial organization of trees in the vicinity (Pukkala, 1989), would be quite difficult to recalculate with our method, but it remains possible to assign a distance and azimuth to each neighbouring tree according to field data or assumptions. This prompts the question of how the neighbourhood distributions-based model would behave with other competition indices. In particular, if the competition indices including distance to the neighbouring trees demonstrate very high performance, then the difference with the spatial model could prove more significant than in our study. Another solution would be to work directly with the distributions of the competition indices, but this would make it necessary to model the evolution of these distributions over time (Phillips et al., 2004).

Finally, another limitation of the model is that regeneration and death processes are not taken into account. It is questionable whether these factors can be integrated into the model, especially when neighbourhoods are updated. For mortality due to competition, we can assume that individual mortality depends on tree size and growth in recent years (Wyckoff and Clark, 2000). Neighbourhoods could then easily be updated in the same way as for thinnings. In contrast, modelling the regeneration process generally requires some spatial information not centred on individuals already in place. In addition, the relevant neighbourhood for regeneration can be very different from the neighbourhood used for growth. For these reasons, the regeneration process could be quite difficult to integrate into our model without having to input new spatial information.

4.4. Using the model in routine management contexts

The oak-pine stands we studied are fairly dense, and there is generally no regeneration. Moreover, thinnings are conducted approximately every 10 y, which limits the influence of mortality by competition. Consequently, our model becomes viable in this forest context. We are convinced that neighbourhood distributions can be estimated from data collected during forest management. In France, forest managers carry out inventories via fixed-area plot sampling, often installing temporary plots every quarter of a hectare. The plots may be disks with constant radius on which trees are inventoried and measured. If the species of the tree nearest to the center of the disks is known, these sampling plots could be used to estimate the neighbourhood distributions. Thus, it should be possible to reconstruct neighbourhood distributions without significantly changing the field practices of forest managers.

When we performed several simulations on a plot, the resulting predictions of basal area increment varied little, despite the variability introduced at individual level in the initial step. This was a predictable result, because the characteristics of competition indices (average and variability) remain highly stable since, for each simulation, the numbers of neighbours are drawn from the same distributions and the neighbours are drawn from the same list of trees. From a practical point of view, this means there is no need to run a large number of simulations with this model to achieve good results at stand level.

5. CONCLUSION

In this study we developed a model falling between spatial and non-spatial tree models that takes into account the influence of tree neighbourhoods without using a complete map of the stand. This model uses distributions of the number of neighbours, called neighbourhood distributions, and a list of trees to reconstruct tree neighbourhoods. These distributions take into account the horizontal spatial structure and variability of local neighbourhoods. Moreover, the reconstructed neighbourhoods change consistently over time to account for growth and thinnings. In a mixed forest, local competition between species may be an important factor to input in order to predict growth. Our work in oak-pine mixed stands showed that competition indices computed in a disk of ten-meter radius have a significant effect on individual growth. Moreover, these indices showed that intraspecific competition was greater than interspecific competition. This may affect the dynamics of the stand by impacting on species coexistence. Even if the approximations necessary to reconstruct neighbourhoods do affect the predictions of the neighbourhood distributions-based model, we showed that the model still demonstrated consistent behaviour compared to a distance-dependent model. This type of model could thus be used to replace distance-dependent models in management contexts.

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