Spatial pattern of trees influences species productivity in a mature oak-pine mixed forest

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1 **Abstract**:

2 Spatial pattern has a key role in the interactions between species in plant communities. These

3 interactions influence ecological processes involved in the species dynamics: growth,

4 regeneration and mortality. In this study, we investigated the effect of spatial pattern on

5 productivity in mature mixed forests of sessile oak and Scots pine. We simulated tree

6 locations with point process models and tree growth with spatially explicit individual growth

7 models. The point process models and growth models were fitted with field data from the

8 same stands. We compared species productivity obtained in two types of mixture: a patchy

9 mixture and an intimate mixture. Our results show that the productivity of both species is

10 higher in an intimate mixture than in a patchy mixture. Productivity difference between the

11 two types of mixture was 11.3% for pine and 14.7% for oak. Both species were favored in the

12 intimate mixture because, for both, intraspecific competition was more severe than

13 interspecific competition. Our results clearly support favoring intimate mixtures in mature

14 oak-pine stands to optimize tree species productivity; oak is the species that benefits the most

15 from this type of management. Our work also shows that models and simulations can provide

16 interesting results for complex forests with mixtures, results that would be difficult to obtain

17 through experimentation.

18

19

20 **Keywords**: Point process model; Spatially explicit growth model; Intimate mixture; Patchy

21 mixture; *Quercus petraea*; *Pinus sylvestris*

22

1. Introduction

Since the beginning of the 1990s when the worldwide fight against biodiversity loss gained

recognition (Earth summit, Rio de Janeiro, 1992), interest in mixed forests has been growing.

Species composition has become a key criterion of sustainable forest management, as defined

at the 2003 Vienna conference on forest protection in Europe (MCPFE et al. 2011).

Moreover, several scientific studies have shown the advantage of setting up mixed stands

compared to pure stands. For example, a mixture of tree species can reduce damage by

phytophagous insects (Jactel and Brockerhoff 2007). Mixing species can also lead to an

increase in stand productivity (Pretzsch and Schutze 2009; Vallet and Perot 2011) thanks to

better resource exploitation and facilitation mechanisms between species (Kelty 2006). More

recently, the question of how ecosystems will adapt to climate change has strengthened the

interest in mixed forests (Lenoir et al. 2008). According to the insurance principle

(McNaughton 1977), mixing tree species could mitigate the consequences of future climatic

changes on forest ecosystem functioning by distributing the risks over the different species. In

Europe, mixed-stand management is also a very important economic issue because the surface

area these stands cover is considerable (MCPFE et al. 2011).

How to optimize the productivity of mixed forests, while at the same time preserving them, is

therefore an important question for forest research. To reach this goal, managers need better

knowledge and a more precise description of the factors that influence trees and species

growth in mixtures. Spatial pattern is known to have a significant impact on species

interactions which in turn impact ecological processes in plant communities (Mokany et al.

2008; Begon et al. 2006; Dieckmann et al. 2000). Spatial pattern refers to the organization of

individuals in space and therefore reflects the local environment around each individual. This

local environment modifies the expression of dynamic natural processes such as growth,

mortality and regeneration (Barot et al. 1999; Courbaud et al. 2001). Thus, spatial pattern can

26 modify species productivity. For herbaceous species, Lamosova et al. (2010) showed that the

27 type of spatial organization affected species productivity in mixtures, and depended on

28 complicated interplay between interspecific and intraspecific competition: generally, in a

29 random pattern the dominant species (superior competitors) increased their productivity,

30 while the aggregated pattern was more favorable for the subordinate species (inferior

31 competitors). However, few studies have dealt with the relationship between spatial pattern

32 and productivity in forest stands, much less in mixed forest stands, partly because

33 experimental approaches which take tree spatial patterns into account is difficult to set up for

34 mixed forests (Vanclay 2006). Some authors used model simulations to overcome this

35 difficulty. For example, Pukkala (1989) studied the effect of spatial pattern type on

36 productivity in monospecific forest stands. To differentiate the effects of intra- and

37 interspecific competitions in mixed stands, spatially explicit models have been developed

38 (e.g. Vettenranta 1999). These growth models use competition indices that require to know

39 the spatial position of trees in the stand. Spatial point processes, which are stochastic models

40 that governs the location of points in space (Cressie 1993), were used to model the spatial

41 structure of mixed forests (e.g. Pretzsch 1997). An approach using simulations with these

42 kinds of realistic models is therefore an interesting way to investigate the impacts of spatial

43 structure on mixed forests productivity (Pretzsch 1997).

44 In our work, we focused on the case of a mixed forest of sessile oak (*Quercus petraea* L.) and

45 Scots pine (*Pinus Sylvestris* L.) in central France. In a previous study, the spatial pattern of

46 these stands had already been accurately described (Ngo Bieng et al. 2006). The authors

47 identified different spatial patterns of canopy trees: the two species showed an intraspecific

48 spatial pattern characterized by a gradient from random to strong aggregation while the

49 interpecific spatial pattern was characterized by a gradient from independence to interspecific

50 repulsion. Moreover, Ngo Bieng et al. (2011) built point process models in order to simulate

4

51   the different spatial patterns identified in these stands. In another previous work in the same

52   forest, Perot et al. (2010) developed individual growth models based on local competition

53   indices and showed that within these stands, intraspecific competition had a more negative

54   effect on growth than interspecific competition for both species. According to these results,

55   species productivity may be enhanced in a mixture where intraspecific competition is

56   minimized.

57   The aim of the present study was to clarify and quantify the impact of tree spatial pattern on

58   species productivity in a mature mixed forest. To do this, we used point process models to

59   simulate two contrasting types of existing spatial pattern that had been identified by Ngo

60   Bieng et al. (2006). We then simulated tree growth with a spatially explicit individual based

61   model using the point process realizations as the initial state, then we compared the

62   productivity obtained in each type of spatial pattern. Finally, we assessed the contribution of

63   spatial pattern to productivity variability of each species.

64   **2. Methods**

65   *2.1 Study site and types of spatial pattern for the simulated oak-pine mixed stands*

66   Our work focused on oak-pine mixed stands in the Orléans forest located in central France

67   (47°51'N, 2°25'E). With 35,000 hectares, the Orléans forest is France's largest public

68   woodland. The forest is dominated by oaks (mainly *Quercus petraea* L.) and Scots pine

69   (*Pinus sylvestris* L.). Between 2004 and 2007, 30 plots in the Orléans forest of between 0.5

70   and 1.25 ha were fully inventoried and mapped so as to run an in-depth study on the

71   horizontal spatial pattern in these stands (Ngo Bieng et al. 2006). These plots were

72   characterized by a mixed canopy composed of oak and pine, and by an understory dominated

73   by oak. Between 2006 and 2007, nine of the 30 plots were selected to study growth in mixed

74   oak-pine stands (Perot et al. 2010). In these plots (Table 1), the mean oak age as determined

75 by cores taken at breast height ranged from 52 to 78 years, and that of pines from 50 to 112

76 years. In any given plot, all the trees of the same species were approximately the same age,

77 thus indicating a single cohort for pines and a single cohort for oaks. Pines were restricted to

78 the canopy of the stands while oaks occupied both the canopy and the understory.

79 In order to quantify the effect of tree spatial pattern on species productivity, in this study we

80 focused on two contrasted types of canopy spatial pattern identified by Ngo Bieng et al.

81 (2006). The first type of mixture is characterized by monospecific clusters (clusters of oaks

82 and clusters of pines) with interspecific spatial repulsion (Fig. 1a). For this first type,

83 repulsion occurs between clusters of individuals. This "patchy mixture" is henceforth called

84 Type 1. In the second type of mixture, individual oaks and pines are randomly scattered (or

85 only slight aggregated) (Fig. 1b). Here, the interspecific structure is characterized by

86 repulsion between individuals at short distances and results in an intimate mixture at the plot

87 scale. This "intimate mixture" is referred to as Type 2 in the following sections.

88 We also took the understory trees into account since they participate in stand productivity and

89 are involved in local competition. In the studied stands, the understory is mainly composed of

90 oak. Several types of spatial pattern have been identified for the understory in these stands

91 (Ngo Bieng 2007). However, in eight of the nine plots where we measured tree growth, the

92 spatial pattern of the understory was the same. Consequently, we chose only one type of

93 spatial pattern for the understory and applied it to both types of mixture (Type 1 and Type 2).

94 *2.2 Point process models of oak-pine mixed stands.*

95 **2.2.1 Point process models**

96 The point process model we used in our study was a combination of classic point processes.

97 In forestry applications, as in this study, the spatial pattern of the trees in a stand is assumed to

98 result from a given point process. We therefore used known point processes to reproduce the

99   spatial features observed in the studied stands. In order to generate clustered or aggregated

100   spatial point patterns, we used the Neyman-Scott (NS) point process (Tomppo 1986; Ngo

101   Bieng et al. 2011). In order to generate the repulsion between individuals or groups of

102   individuals, we used the "soft core" (SC) point process, which is a pairwise interaction

103   process where pairs of points should not be closer than a threshold distance or "soft core"

104   distance (Illian et al. 2008; Ngo Bieng et al. 2011). With the combination of these two point

105   processes, Ngo Bieng et al. (2011) developed point process models fitted on field data to

106   reproduce the spatial patterns of oak-pine mixed stands. These models took into account the

107   spatial pattern of the two species when reproducing the observed spatial features, thus

108   describing the spatial interactions between qualitative marks associated to the simulated

109   spatial point process. For our work, we used the point process models developed by Ngo

110   Bieng et al. (2011) to simulate oak-pine mixed stands. These models are described in the

111   following subsections.

112   **2.2.2 Point process model for spatial pattern of Type 1: patchy mixture**

113   This point process model is a combination of Neyman-Scott processes (NS) and soft core

114   processes (SC). Oak locations were simulated by an NS process. Pines locations were

115   simulated by a NS process with an additional regularity constraint obtained through a SC

116   process. The regularity constraint takes into account regularity at short distances, which is

117   typical of the spatial pattern of pines (Ngo Bieng 2006). The regularity constraint is a

118   threshold distance of regularity ($dreg$) which corresponds to the minimum distance allowed

119   between two pines. To generate a more realistic regularity, if the distance between two pines

120   is below the threshold distance, tree locations can be retained with a probability depending on

121   the distance between the two trees (principle of the SC process). This probability varies

122   linearly from 0 at a null distance to 1 at the threshold distance $dreg$. Interspecific repulsion

123   was also simulated with a SC process and a repulsion distance $drep$. The Type 1 model has

7

124   six parameters (Table 2): the number of oak aggregates (ncl_{oak}), the radius of the oak

125   aggregates (rcl_{oak}), the number of pine aggregates (ncl_{pine}), the radius of pine aggregates

126   (rcl_{pine}), the minimal intraspecific distance between pines or regularity distance ($dreg$), the

127   minimal repulsion distance between oaks and pines or repulsion distance ($drep$).

128   **2.2.3 Point process model for spatial pattern of Type 2: intimate mixture**

129   This model is a combination of a NS process and a SC process. Pine locations were simulated

130   with a NS process with a regularity constraint obtained with a SC process as explained for the

131   previous model. Oak individuals were then randomly simulated with a repulsion distance also

132   ensured with a SC process. Contrary to the previous model, the probability of accepting an

133   oak closer to a pine than the threshold repulsion distance is constant and does not vary with

134   the distance. This model has five parameters (Table 2): the number of pine aggregates

135   (ncl_{pine}), the radius of pine aggregates (rcl_{pine}), the intraspecific minimal distance between

136   pines or distance of regularity ($dreg$), the minimal repulsion distance between oaks and pines

137   ($drep$) and p the constant probability to accept an oak tree at a distance lower than $drep$ from a

138   pine.

139   **2.2.4 Point process model for oak understory**

140   As mentioned previously, the understory was mainly composed of oak, and its spatial pattern

141   did not vary much among the studied plots. We therefore chose to simulated only one type of

142   spatial pattern for understory oaks: the most frequent type in the plots where growth was

143   measured. For Type 1 and Type 2 mixtures, the simulated spatial pattern of understory oaks

144   was therefore identical. As we did for the canopy trees, we used a point process model fitted

145   on field data to simulate the locations of understory oaks (Ngo Bieng et al. 2011). This point

146   process model simulates an attraction with the oaks in the canopy and a repulsion with the

147   pines in the canopy. The point process model for the understory oaks was a combination of

148 NS and SC processes. First, understory oaks were simulated with a NS process. During this

149 simulation, repulsion with the pines in the canopy was ensured with a SC process containing

150 an additional constraint of attraction with canopy oaks. This attraction constraint between

151 understory and canopy oaks was simulated by checking that each understory oak was at a

152 distance below or equal to a given attraction distance. This model had four parameters (Table

153 2): the number of oak aggregates in the understory (ncl_{und}), the radius of oak aggregates in the

154 understory (rcl_{und}), the distance of intraspecific attraction between understory oaks and

155 canopy oaks ($dattr$), the distance of interspecific repulsion between understory oaks and

156 canopy pines ($drep$).

157 Fig. 1 presents simulated stands for the patchy (Type1) and the intimate (Type2) mixtures.

158 *2.3 Spatially explicit individual growth models*

159 As mentioned above, we developed our growth model from data collected from nine plots in

160 the Orleans forest. The nine plots cover the two types of mixture simulated in this work

161 (Table 1). In each plot, we selected 30 oaks and 30 pines based on a stratified sampling

162 method. The stratification variables were tree size and local environment (see Perot et al.

163 2010 for details). Sampled trees were cored to the pith at a height of 1.3 m. The cores were

164 scanned and analyzed using the WinDENDRO software, version 2005a (Regent 2005), and

165 ring width was measured to the nearest 0.01 mm. The COFECHA software (Grissino-Mayer

166 2002) was used to cross-date the individual ring-width series. The ring width analyses were

167 performed on a final total of 230 oaks and 269 pines. Detailed information on past

168 disturbances was not available for our plots (location and size of suppressed trees) so we

169 chose the 6 years period from 2000 to 2005 to study tree growth because there had been no

170 thinnings or storms during that time.

171 The growth model we developed is a spatially explicit individual based model based on local

172 competition indices (Uriarte et al. 2004b). This model is similar to that presented by Perot et

9

173 al. (2010) but for the present study we added a plot random effect to account for factors

174 influencing tree growth at the plot level (soil quality, stand age, stand density). The final

175 model for each species was a linear mixed effect model. For both species, the competition

176 indices were the basal areas of the oaks and pines belonging to the neighborhood of the target

177 tree (CI_{oak} et CI_{pine}). In a previous work on the same plots (Perot et al. 2010), several radii (5,

178 10 and 15m) were tested for the neighborhood so as to cover the range of radii reported in

179 other studies (Canham et al., 2004; Stadt et al., 2007; Uriarte et al., 2004a) and to minimize

180 the influence of edge effects when computing the competition indices. Based on model

181 comparisons, the authors concluded that indices computed with a 10 m radius gave the best

182 results. Based on this work, we defined the neighborhood as a 10 m radius circle around the

183 target tree. These competition indices account for both intra- and interspecific competitions.

184 For each species the final model was written as follows:

185
$$\Delta r_{i,k} = \left(\alpha_0 + \alpha_k\right) + \left(\beta_0 + \beta_k\right) girth_{i,k} + \lambda_{oak} CI_{i,oak} + \lambda_{pine} CI_{i,pine} + \varepsilon_{i,k} \tag{1}$$

186 where $\Delta r_{i,k}$ is the radial increment of tree i for plot k over a growth period of 6 years, $girth_{i,k}$ is

187 the girth of tree i at 1.3 m, $CI_{i,oak}$ and $CI_{i,pine}$ are the competition indices for oak competitors

188 and pine competitors respectively, $\{\alpha_0, \beta_0, \lambda_{oak}, \lambda_{pine}\}$ are the parameters estimated for the

189 fixed effects of the model, $\{\alpha_k, \beta_k\}$ are the parameters corresponding to the random part of the

190 model (plot effect) and $\varepsilon_{i,k}$ is the residual part of the model.

191 Preliminary results showed that the variance of the residuals increased with the adjusted

192 values. To correct for this heteroscedasticity, we modeled the variance of the residuals with

193 the fitted values and a power function (Eq. 2), as suggested by Pinheiro and Bates (Pinheiro

194 and Bates 2000):

195
$$\mathrm{Var}(\varepsilon_{i,k}) = \sigma^2 |(fitted\ value_{i,k})|^{2\delta} \tag{2}$$

196   Where δ is the parameter of the variance model. The model was fitted using the R software

197   version 2.14.0 (R Development Core Team 2011) with the lme function of the nlme package

198   (Pinheiro et al. 2011).

199   *2.4 Simulation experiment design*

200   Initial stands for the two types of mixture were simulated with the point process models

201   presented in section 2.2. Since stand density and tree size influence individual growth (see Eq.

202   1), in order to have exactly the same number of trees of each species and exactly the same

203   dendrometric characteristics for the two types of mixture, we used the same tree list to

204   simulate the initial stands for both mixture types. With this method, we ensured that the only

205   parameter that changed between Type 1 and Type 2 mixtures was the spatial pattern of the

206   trees. We carried out our simulations on a 1-ha plot (Table 4).

207   Both the spatial pattern within a mixture and growth show some variability. This variability

208   was estimated from field data and was included in the point process models as well as in the

209   individual growth model. To account for the different sources of variability, it was necessary

210   to carry out several simulations with each model. We proceeded as follows: a) to account for

211   variability in the spatial pattern within a mixture type, each type was simulated 200 times, b)

212   to account for growth variability at the plot level, for each initial stand the parameters α_k et β_k

213   (Equation 1) were simulated 50 times, c) to account for variability in individual growth

214   (residual variability), for each initial stand and each pair of values {α_k, β_k}, individual tree

215   growth was simulated 10 times following Equation 1. In all, we performed 200,000

216   simulations (2 * 200 * 50 * 10). For each simulation, we calculated the basal area productivity

217   for oak and for pine. All the simulations were performed in the Capsis platform with the

218   oakpine1 module (Dufour-Kowalski et al. 2012).

11

219   *2.5 Decomposition of the basal area productivity variability*

220   Thanks to our simulation design, we were able to estimate the effects of several factors on the

221   productivity of both species: 1) an effect related to the type of mixture, 2) an effect related to

222   the variability in the spatial pattern within the type of mixture, 3) an effect related to the

223   growth variability between plots (plots are nested in the type of mixture) and 4) an effect

224   related to tree growth variability within the plot:

225
$$y_{ijkl} = \mu + type_i + pp_{ij} + plot_{ijk} + \varepsilon_{ijkl} \tag{3}$$

226   Where y_{ijkl} is the basal area productivity of one species, μ is the general mean, $type_i$ is the type

227   of mixture effect, pp_{ij} is the spatial pattern random effect in the type, $plot_{ijk}$ is the plot random

228   effect of the growth model in each point process realization, ε_{ijkl} is the residual and

229   corresponds to tree level variability in the growth model. The structure of our simulation

230   design (balanced nested design) made it possible to decompose the variability of species

231   productivity into different components and to estimate the contribution of each component to

232   variability as follows (for simplicity, the variance σ^2 and the estimate of the variance are

233   denoted identically):

234     $$\sigma_{total}^2 = \sigma_{type}^2 + \sigma_{pp}^2 + \sigma_{plot}^2 + \sigma_{res}^2 \quad \text{with} \quad \begin{cases} \sigma_{res}^2 = MSD_{res} \\ \sigma_{plot}^2 = \left(MSD_{plot} - \sigma_{res}^2 \right) / n_{res} \\ \sigma_{pp}^2 = \left(MSD_{pp} - \sigma_{res}^2 - n_{res}\sigma_{plot}^2 \right) / \left(n_{res} n_{plot} \right) \\ \sigma_{type}^2 = \left(MSD_{type} - \sigma_{res}^2 - n_{res}\sigma_{plot}^2 - n_{res}n_{plot}\sigma_{pp}^2 \right) / \left(n_{res} n_{plot} n_{pp} \right) \end{cases}$$

235   Where *MSD* is the mean square deviation for the different sources of variability, $n_{type} = 2$, n_{pp}

236     $= 200$, $n_{plot} = 50$, and $n_{res} = 10$. We then assessed the importance of spatial pattern variability

237   in the productivity variability of each species. The sum of σ_{type}^2 and σ_{pp}^2 was considered to be

238   the overall contribution of spatial pattern to productivity variability.

3. Results

240 The results of the growth model show that, for oak, the effect of oak competition on growth is

241 about twice higher than the effect of pine competition (see λ_{oak} and λ_{pine} in Table 3). The

242 magnitude of the effect of pine competition on pine growth is close to the effect of pine

243 competition on oak growth (-0.085 mm.m^{-2} and -0.094 mm.m^{-2} respectively). But contrary to

244 oak, the competition index computed on oaks has no significant effect on pine growth.

245 The results of the simulations show that productivity in Type 2 (intimate mixture) is higher

246 than in Type 1 (patchy mixture) for both species (Fig. 2). The difference in productivity

247 between Type 2 and Type 1 is more pronounced for oak than for pine: +14.7% for oak and

248 +11.3% for pine.

249 The productivity values obtained for oak and pine show some variability. If we combine the

250 results from the two types of mixture, oak productivity varies from 0.23 to 0.36 m².ha^{-1}.year^{-1}

251 (first and ninth deciles) with a coefficient of variation of 0.175 (ratio of the standard deviation

252 to the mean). Pine productivity varies from 0.19 to 0.35 m².ha^{-1}.year^{-1} (first and ninth deciles)

253 with a coefficient of variation of 0.228. Variability in pine productivity is thus slightly higher

254 than that of oak.

255 The results also show that most of the productivity variability is explained by plot effect,

256 which represents 86% of the total variability for pine and 67% for oak (Fig. 3). The spatial

257 pattern (type of spatial pattern + random effect in the type) explains 12% of the variability for

258 pine and 31% for oak. The overall effect of spatial pattern on oak productivity is important.

259 Even if the individual growth variability within a plot is high, it has little impact on the

260 overall productivity variability (between 1 and 2% of the total variability). Variability in

261 spatial pattern within a mixture type also has a relatively little impact, though the effect on

262 oak productivity (5%) is slightly higher than on pine productivity (2%).

4. Discussion

4.1 Spatial pattern and species productivity

Spatial pattern plays a key role in the interactions between species in plant communities (Dieckmann et al. 2000). These interactions influence ecological processes involved in the species dynamics: growth, regeneration and mortality (Begon et al. 2006). Our results show that the productivity of sessile oak and Scots pine is higher in an intimate mixture (Type 2) than in a patchy mixture (Type 1). Our work has made it possible to estimate the difference in species basal area productivity between the two types of mixture. This difference was 11.3% for pine and 14.7% for oak (Fig. 2). These figures are comparable to those of Pukkala (1989) who simulated Scots pine productivity in pure stands for different spatial patterns. He found that volume productivity was 10% lower in aggregated spatial patterns compared to regular spatial patterns. Our results also show that the plot effect explains a large part of the productivity variability (Fig. 3). The plot effect, estimated with the growth model, includes several factors that affect tree growth: (i) a site effect - soil conditions vary from one plot to another and affect species productivity, (ii) an age effect - young stands have higher productivity and finally, (iii) a density effect - denser stands generally have higher productivity (Vallet and Perot 2011). The variability obtained for pine productivity is similar to that of oak productivity but is much more influenced by plot effects (Fig. 3).

4.2 Influence of spatial and growth interactions

Intra- and interspecific competition are crucial to understand the effect of mixture on forest productivity and forest dynamic (Kelty 2006; Forrester et al. 2006). As in the study of Perot et al. (2010), our results showed that, for both species, intraspecific competition had a more negative effect on growth than interspecific competition (see parameters λ_{oak} and λ_{pine} in Table 3). Oak had little impact on pine growth probably because pines had a greater girth than oaks

14

287 on average (Table 1). The light interception by the pine foliage is lower than the light

288 interception by the oak foliage (Balandier et al. 2006; Sonohat et al. 2004). This may help to

289 explain that in our oak model, the interspecific competition was lower than the intraspecific

290 competition. The two species involved have different light requirements but also different

291 root distribution patterns (Brown 1992). The complementarity in nutrient and water use could

292 also contribute to explain why intraspecific competition was more severe than interspecific

293 competition. The local competition and the spatial features of each mixture type help to

294 explain the results of this work. Two spatial features vary simultaneously between Types 1

295 and 2: the intraspecific pattern and the interspecific pattern. Ripley's function and inter-type

296 function (Ripley 1977; Lotwick and Silverman 1982; Perot and Picard 2012) can be used to

297 characterized and compare these two dimensions. On average in the patchy mixture (Type1),

298 there are more oaks around an oak tree than in the intimate mixture (Type 2) (see L functions

299 at 10 m for oak in Fig. 4). Consequently, the competition index IC_{oak} is higher, on average, in

300 Type 1 than in Type 2. In contrast, in Type 1 mixture, there are fewer pines on average around

301 an oak tree than in Type 2 (see inter-type functions at 10 m in Fig. 4). Consequently, the

302 competition index IC_{pine} is lower, on average, in Type 1 than in Type 2. In addition, the

303 parameters of the growth model must be examined. Parameters λ_{oak} and λ_{pine} (Table 3) show

304 that oak competitors (IC_{oak}) have a more negative effect on oak growth than do pine

305 competitors (IC_{pine}) (λ_{oak} is more negative than λ_{pine}). In the intimate mixture (Type 2) there

306 are more pines around oaks than in the patchy mixture (Type 1) and pines are less competitive

307 than oaks. This explains why oak productivity is higher, on average, in the intimate mixture

308 than in the patchy mixture. For one particular simulation, the final result is complex because

309 productivity depends on both intra- and interspecific competition (estimated through

310 parameters λ_{oak} and λ_{pine}) and also on intra- and interspecific spatial patterns. Variability in the

311 spatial pattern of a mixture type thus explains why oak productivity in Type 2 is not always

312 higher than in Type 1 (Fig. 2). The reasoning is similar for pine but the result is easier to

313 analyze because there is no interspecific competition parameter in the individual growth

314 model. For pine, productivity depends only on the intraspecific spatial pattern.

315 *4.3 Influence of species assemblage and stand age*

316 The effect of spatial pattern on species productivity in mixed stands should depend on species

317 assemblage. In our study, both oak and pine were favored in the intimate mixture because, for

318 both species, intraspecific competition was more severe than interspecific competition. Other

319 authors have also shown that interspecific competition was lower than intraspecific

320 competition (e.g. Forrester and Smith 2012), while some studies have shown the opposite in

321 some conditions (e.g. Pretzsch et al . 2010). Intensity of interactions may also change with

322 species assemblages. Further works involving other species are therefore necessary to

323 generalize our results. Moreover, for tree species, the competition relationship between

324 species may depend on stand developmental stage (Filipescu and Comeau 2007; Cavard et al.

325 2011). Pine is a fast growing species compared to oak (Duplat and Tran-Ha 1997; Perot et al.

326 2007). In young stage, pine is probably more competitive than oak. Consequently, oak

327 productivity could be favored by a patchy mixture at an earlier stage. In addition, Getzin et al.

328 (2006) showed that interspecific competition is less intense at older stages than at younger

329 stages, probably due to the spatial sharing of resources. In our study, this would explain why

330 the mixture type had less impact on pine productivity than on oak productivity, and why pine

331 is more influenced by plot effects (site, age, density) than oak.

Conclusion

333 Our study is innovative in that we worked on a mature mixed forest. For such complex

334 forests, models and simulations can provide interesting quantitative results that would be

335 difficult to obtain through experimentation. The two mixture types that we tested are realistic

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336 oak-pine mixtures found in central France (Ngo Bieng et al. 2006). Our results show that their

337 spatial differences are contrasted enough to have an impact on the productivity of both species

338 in the mixture. From a practical point of view, our work shows the interest of favoring

339 intimate mixtures in mature oak-pine stands to optimize tree species productivity. Oak is the

340 species that benefits most from this type of management. In order to achieve more general

341 results, further work is needed to determine the change in competition between oak and pine

342 over time.

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7. Tables

Table 1: Dendrometric characteristics of the nine plots used for growth models (Orléans Forest, France). BA = basal area; Other = other broadleaf tree species; D = mean diameter at a height of 130 cm; Age = mean age of the cored trees at a height of 130 cm; Ho = dominant height. Only the height of the sample trees was measured. The dominant height was estimated with a measure of the dominant diameter and a height-diameter relationship fitted for each species and each plot using the sample trees; PP = type of spatial pattern, 1 = patchy mixture, 2 = intimate mixture, 3 = intermediate type with cluster of pines and oaks randomly scattered; For diameters and ages, values represent the mean with the standard deviation in parentheses.

Plot	Area (ha)	BA_{oak} (m².ha^{-1})	BA_{pine} (m².ha^{-1})	BA_{other} (m².ha^{-1})	BA_{total} (m².ha^{-1})	D_{oak} (cm)	D_{pine} (cm)	Age_{oak}	Age_{pine}	Ho_{oak} (m)	Ho_{pine} (m)	PP
P108	0.80	9.6	19.8	1.4	30.8	17.7 (6.74)	36.2 (5.31)	68 (4.3)	66 (2.5)	22.3	23.0	2
P178	1.00	16.5	10.0	1.5	28.0	21.5 (10.49)	36.5 (7.56)	78 (4.6)	77 (1.8)	21.1	22.1	1
P184	0.75	10.9	12.0	2.1	25.1	17.5 (8.88)	36.3 (7.76)	71 (8.6)	68 (4.2)	21.9	20.8	3
P216	0.50	11.2	12.1	0.9	24.1	17.0 (6.39)	27.8 (7.6)	52 (2.8)	50 (2.2)	18.8	19.0	2
P255	1.00	12.6	10.5	1.1	24.2	17.8 (7.54)	31.7 (6.25)	69 (5.9)	62 (4.6)	20.1	19.7	2
P534	0.50	12.2	19.6	1.0	32.7	16.6 (6.54)	37.4 (6.5)	59 (2.3)	83 (3.2)	22.1	22.5	2
P563	0.50	13.6	11.9	0.2	25.7	25.1 (10.12)	35.6 (4.58)	70 (3.1)	69 (2.3)	24.5	23.0	2
P57	1.00	11.2	11.4	0.4	23.0	16.7 (6.36)	34.3 (6.41)	67 (7.1)	62 (3.1)	20.4	21.2	1
P78	0.70	14.7	16.5	1.0	32.2	20.1 (7.48)	42.2 (8.79)	62 (5.2)	112 (17.5)	21.8	25.6	2

Table 2 Parameters in the point process models. ncl_{sp} = number of aggregates for species sp; rcl_{sp} = radius of aggregates for species sp; $dreg$ = distance of regularity which corresponds to the minimum distance allowed between pines; $drep$ = repulsion distance between oaks and pines; und = oak understory; $dattr$ = distance of intraspecific attraction between understory oaks and canopy oaks.

Species	Tree position	Type of spatial pattern	Parameters in the point process model					
			ncl_{pine} (ha^{-1})	rcl_{pine} (m)	$dreg$ (m)	ncl_{oak} (ha^{-1})	rcl_{oak} (m)	$drep$ (m)
Oak and pine	Canopy	Type 1 (Patchy mixture)	13	18	5	7	17	18
			ncl_{pine} (ha^{-1})	rcl_{pine} (m)	$dreg$ (m)	$drep$ (m)	p	
Oak and pine	Canopy	Type 2 (Intimate mixture)	38	8	10	4	0.15	
			ncl_{und} (ha^{-1})	rcl_{und} (m)	$dattr$ (m)	$drep$ (m)		
Oak	Understory	Type 1 and Type 2	37	12	52	2		

Table 3 Parameter estimates of the spatially explicit individual growth model (see Eq. 1).
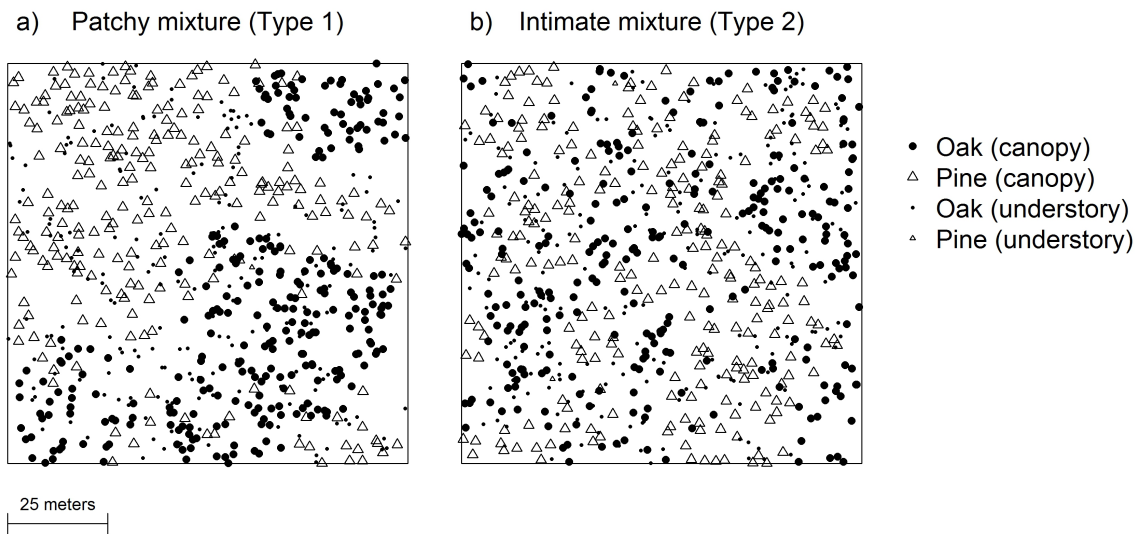
		Parameter estimates					Model statistics		
		Intercept α (mm)	*girth* β (mm.cm^{-1})	CI_{oak} λ_{oak} (mm.m^{-2})	CI_{pine} λ_{pine} (mm.m^{-2})	δ^a	RSE	df	AIC
Oak	Estimates	3.335	0.126	-0.196	-0.094	0.526	1.013	218	1196
	Std. error	1.202	0.018	0.042	0.024				
	P-value	0.006	<0.001	<0.001	<0.001				
	σ_{plot}	2.036	0.048						
Pine	Estimates	2.711	0.0654		-0.0855	0.621	0.838	258	1413
	Std. error	1.054	0.0094		0.0241				
	P-value	0.011	<0.001		<0.001				
	σ_{plot}		0.0145						

[a] δ is the parameter of the variance model (see Eq. 2).

Table 4 Dendrometric features of the initial stand used in simulations (stand area = 1 ha). For girth, the value in parentheses corresponds to the standard deviation.

Species	Number of trees		Girth (cm)		
	Canopy	Understory	mean	min.	max.
Oak	284	208	53.2 (23.2)	23	129
Pine	237	2	97.1 (21.0)	33	160

8. Figure captions

a) Patchy mixture (Type 1)   b) Intimate mixture (Type 2)

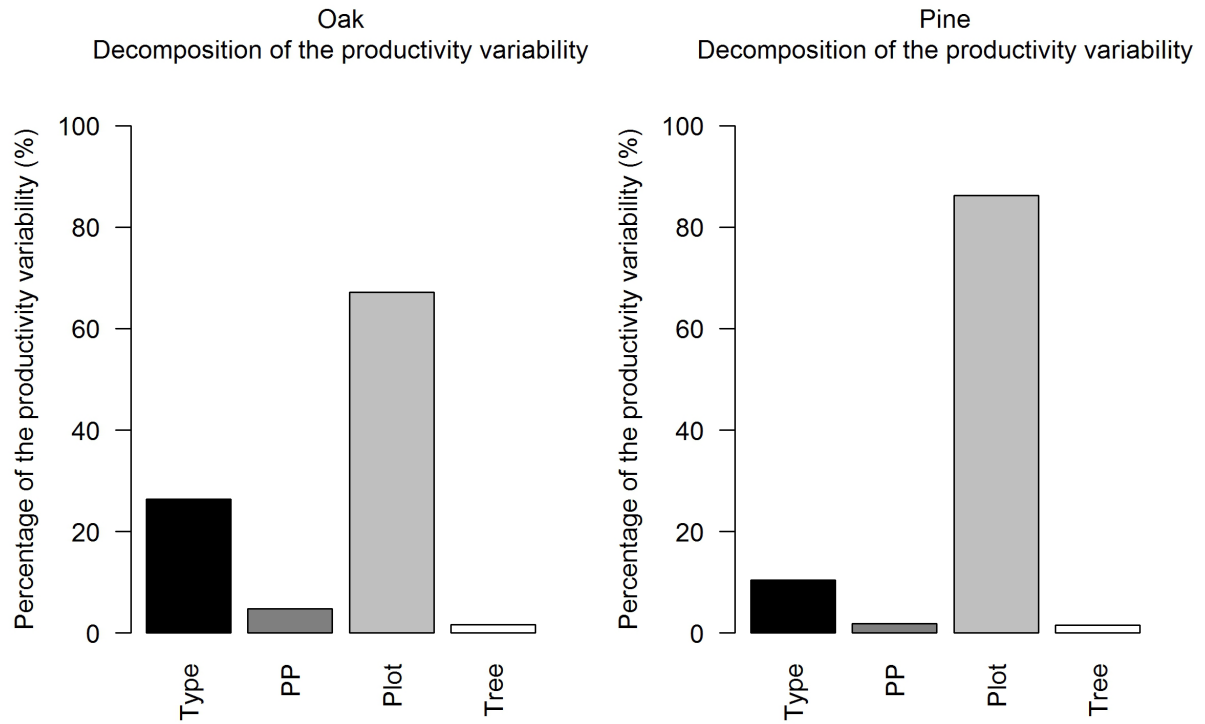- Oak (canopy)
△ Pine (canopy)
· Oak (understory)
▵ Pine (understory)

25 meters

Fig. 1 a) Patchy mixture (Type 1) simulated with the point process models; b) Intimate mixture (Type 2) simulated with the point process models.
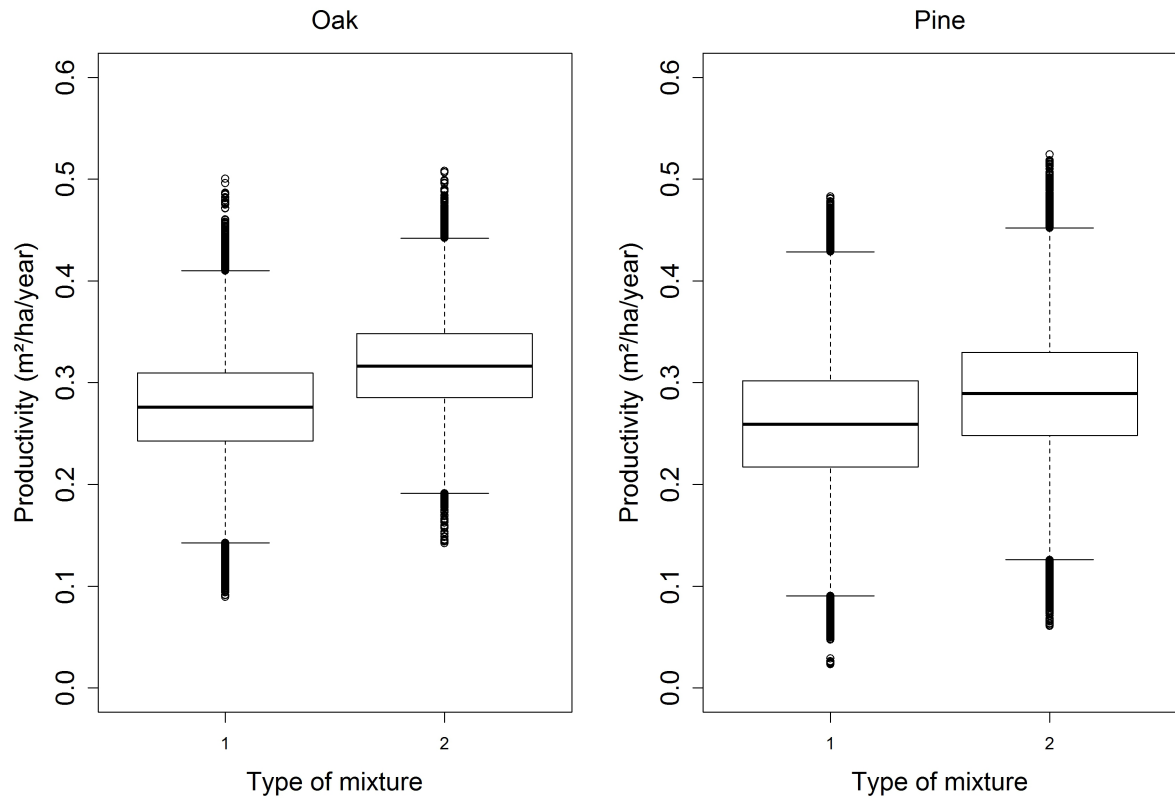
Fig. 2 Productivity comparison between the two mixture types for oak and pine.

Fig. 3 Decomposition of the productivity variability for oak and pine following Equation (3). The different sources of variability are: type of mixture (Type), spatial point pattern within the type (PP), plot random effect (Plot), and tree random effect (Tree).
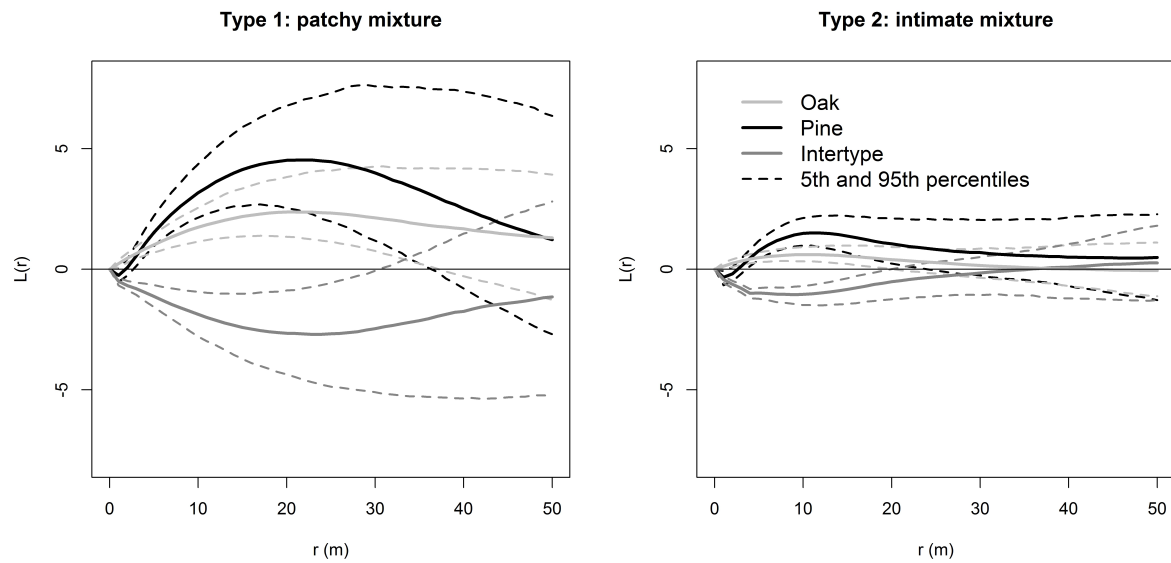
Fig. 4 L function and intertype L function calculated with 1000 simulations of Type 1 and Type 2 mixtures. For the intraspecific L function, L(r) less than 0 indicates spatial regularity, L(r) greater than 0 indicates spatial aggregation. For the intertype L function, L(r) less than 0 indicates spatial repulsion between the two species, L(r) greater than 0 indicates spatial attraction between the two species.