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

M.A. Ngo Bieng, Thomas Perot, F. de Coligny, F. Goreaud

► **To cite this version:**

M.A. Ngo Bieng, Thomas Perot, F. de Coligny, F. Goreaud. Spatial pattern of trees influences species productivity in a mature oak-pine mixed forest. *European Journal of Forest Research*, 2013, 132 (5-6), p. 841 - p. 850. 10.1007/s10342-013-0716-z . hal-00920782

**HAL Id: hal-00920782**

**<https://hal.science/hal-00920782>**

Submitted on 19 Dec 2013

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2 **Reference:**

3 **Ngo Bieng, M. A., T. Perot, F. de Coligny and F. Goreaud (2013). "Spatial pattern of**  
4 **trees influences species productivity in a mature oak-pine mixed forest." European**  
5 **Journal of Forest Research 132(5-6): 841-850. DOI 10.1007/s10342-013-0716-z**

6 **Title:**

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

8 **List of authors:**

9 Marie Ange Ngo Bieng\*, Thomas Perot\*, François de Coligny, François Goreaud

10 \* Marie Ange Ngo Bieng and Thomas Perot contributed equally to this work.

11  
12 M. A. Ngo Bieng  
13 CIRAD, UMR SYSTEM, 2 Place Viala Bâtiment 27, 34060 Montpellier Cedex 1, France  
14 e-mail: [marie-ange.ngo\\_bieng@cirad.fr](mailto:marie-ange.ngo_bieng@cirad.fr)

15  
16 T. Perot  
17 Irstea, Forest Ecosystems Research Unit, Domaine des Barres, 45290 Nogent-sur-Vernisson,  
18 France  
19 e-mail: [thomas.perot@irstea.fr](mailto:thomas.perot@irstea.fr)

20  
21 F. de Coligny  
22 INRA, UMR931 AMAP, Botany and Computational Plant Architecture, TA A-51/PS2,  
23 Boulevard de la Lironde, 34398 Montpellier Cedex 5, France  
24 e-mail: [coligny@cirad.fr](mailto:coligny@cirad.fr)

25  
26 F. Goreaud  
27 Irstea, UR LISC Laboratoire d'Ingénierie des Systèmes Complexes, 24 avenue des Landais,  
28 63172 Aubière, France  
29 e-mail: [francois.goreaud@gmail.com](mailto:francois.goreaud@gmail.com)

30  
31 **Corresponding author:**

32 T. Perot  
33 e-mail: [thomas.perot@irstea.fr](mailto:thomas.perot@irstea.fr)  
34 Tél : +33 (0) 2 38 95 09 65  
35 Fax : +33 (0) 2 38 95 03 46

36

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 interspecific 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

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

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

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:

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

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):

$$195 \quad \text{Var}(\varepsilon_{i,k}) = \sigma^2 |(\text{fitted value}_{i,k})|^{2\delta} \quad (2)$$

196 Where  $\delta$  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  $\alpha_k$  et  $\beta_k$   
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  $\{\alpha_k, \beta_k\}$ , 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).

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:

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

226 Where  $y_{ijkl}$  is the basal area productivity of one species,  $\mu$  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,  $\varepsilon_{ijkl}$  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  $\sigma^2$  and the estimate of the variance are  
 233 denoted identically):

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

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  $\sigma_{type}^2$  and  $\sigma_{pp}^2$  was considered to be  
 238 the overall contribution of spatial pattern to productivity variability.

### 239 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  $\lambda_{oak}$  and  $\lambda_{pine}$  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 ( $-0.085 \text{ mm.m}^{-2}$  and  $-0.094 \text{ mm.m}^{-2}$  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  $0.36 \text{ m}^2.\text{ha}^{-1}.\text{year}^{-1}$   
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  $0.35 \text{ m}^2.\text{ha}^{-1}.\text{year}^{-1}$  (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%).

## 263 **4. Discussion**

### 264 ***4.1 Spatial pattern and species productivity***

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

### 281 ***4.2 Influence of spatial and growth interactions***

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

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  $\lambda_{oak}$  and  $\lambda_{pine}$  (Table 3) show  
304 that oak competitors ( $IC_{oak}$ ) have a more negative effect on oak growth than do pine  
305 competitors ( $IC_{pine}$ ) ( $\lambda_{oak}$  is more negative than  $\lambda_{pine}$ ). 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  $\lambda_{oak}$  and  $\lambda_{pine}$ ) 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.

## 332 **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

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.

## 343 **5. Acknowledgments**

344 This work forms part of the PhD traineeships of M. A. Ngo Bieng and T. Perot and was  
345 funded in part by the research department of the French National Forest Office. We are  
346 grateful to the Loiret agency of the National Forest Office for allowing us to install the  
347 experimental sites in the Orléans state forest. Many thanks to the Irstea staff at Nogent-sur-  
348 Vernisson who helped collect the data: Fanck Milano, Sandrine Perret, Yann Dumas,  
349 Sébastien Marie, Romain Vespierre, Grégory Décelière. Many thanks to Victoria Moore for  
350 her assistance in preparing the English version of the manuscript.

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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<br>(ha) | BA <sub>oak</sub><br>(m <sup>2</sup> .ha <sup>-1</sup> ) | BA <sub>pine</sub><br>(m <sup>2</sup> .ha <sup>-1</sup> ) | BA <sub>other</sub><br>(m <sup>2</sup> .ha <sup>-1</sup> ) | BA <sub>total</sub><br>(m <sup>2</sup> .ha <sup>-1</sup> ) | D <sub>oak</sub><br>(cm) | D <sub>pine</sub><br>(cm) | Age <sub>oak</sub> | Age <sub>pine</sub> | Ho <sub>oak</sub><br>(m) | Ho <sub>pine</sub><br>(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 |                     |                |                              |                    |               |
|--------------|---------------|---------------------------|---------------------------------------|---------------------|----------------|------------------------------|--------------------|---------------|
|              |               |                           | $ncl_{pine}$<br>( $ha^{-1}$ )         | $rcl_{pine}$<br>(m) | $dreg$<br>(m)  | $ncl_{oak}$<br>( $ha^{-1}$ ) | $rcl_{oak}$<br>(m) | $drep$<br>(m) |
| Oak and pine | Canopy        | Type 1 (Patchy mixture)   | 13                                    | 18                  | 5              | 7                            | 17                 | 18            |
|              |               |                           | $ncl_{pine}$<br>( $ha^{-1}$ )         | $rcl_{pine}$<br>(m) | $dreg$<br>(m)  | $drep$<br>(m)                | $p$                |               |
| Oak and pine | Canopy        | Type 2 (Intimate mixture) | 38                                    | 8                   | 10             | 4                            | 0.15               |               |
|              |               |                           | $ncl_{und}$<br>( $ha^{-1}$ )          | $rcl_{und}$<br>(m)  | $dattr$<br>(m) | $drep$<br>(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).**

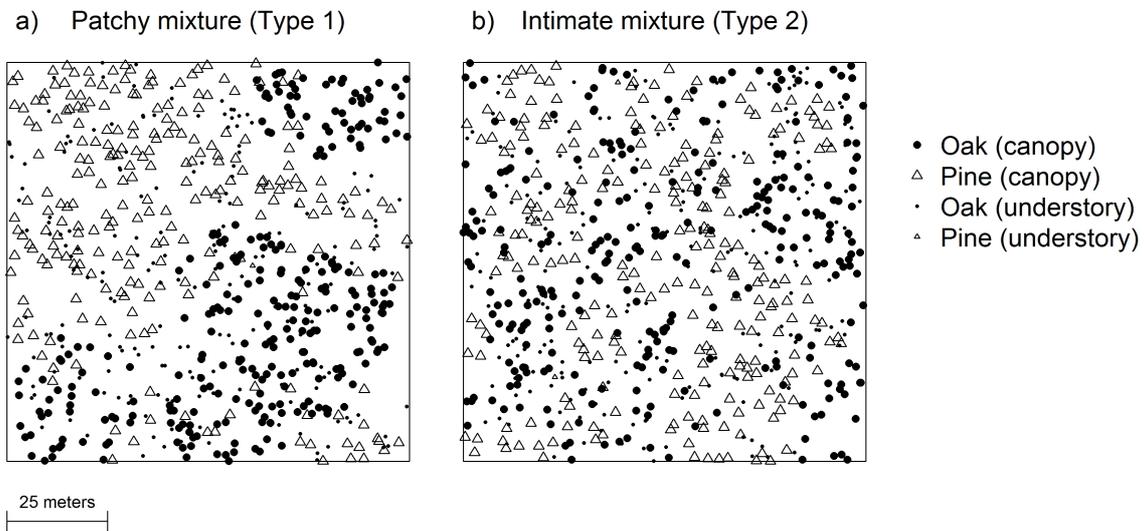
|      |                 | Parameter estimates           |   |  |  | Model statistics |       |     |      |
|------|-----------------|-------------------------------|---|--|--|------------------|-------|-----|------|
|      |                 | Intercept<br>$\alpha$<br>(mm) | <i>girth</i><br>$\beta$<br>(mm.cm <sup>-1</sup> ) | <i>CI</i> <sub>oak</sub><br>$\lambda_{oak}$<br>(mm.m <sup>-2</sup> ) | <i>CI</i> <sub>pine</sub><br>$\lambda_{pine}$<br>(mm.m <sup>-2</sup> ) | $\delta^a$       | 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   |                  |       |     |      |
|      | $\sigma_{plot}$ | 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   |                  |       |     |      |
|      | $\sigma_{plot}$ |                               | 0.0145  |  |  |                  |       |     |      |

<sup>a</sup>  $\delta$  is the parameter of the variance model (see Eq. 2).

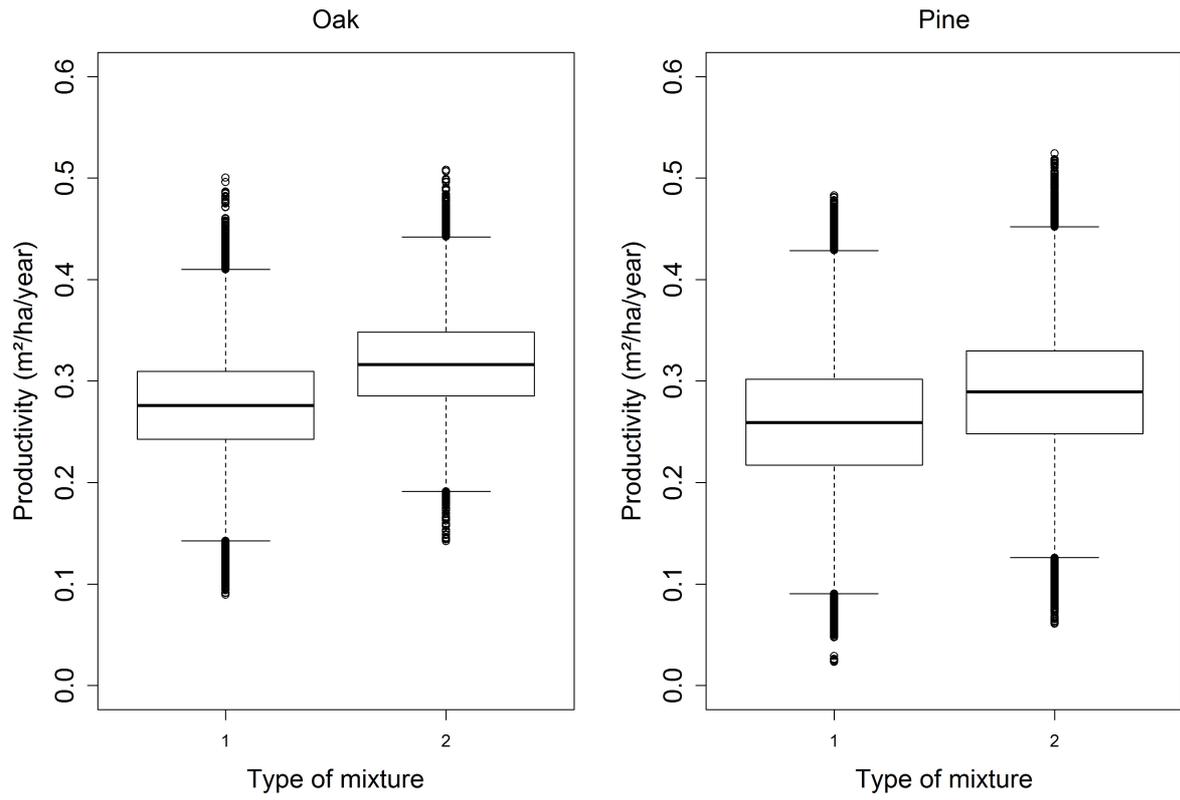
**Table 4 Dendrometric features of the initial stand used in simulations (stand area = 1 ha). For girth, the value in parentheses corresponds to the standard deviation.**

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

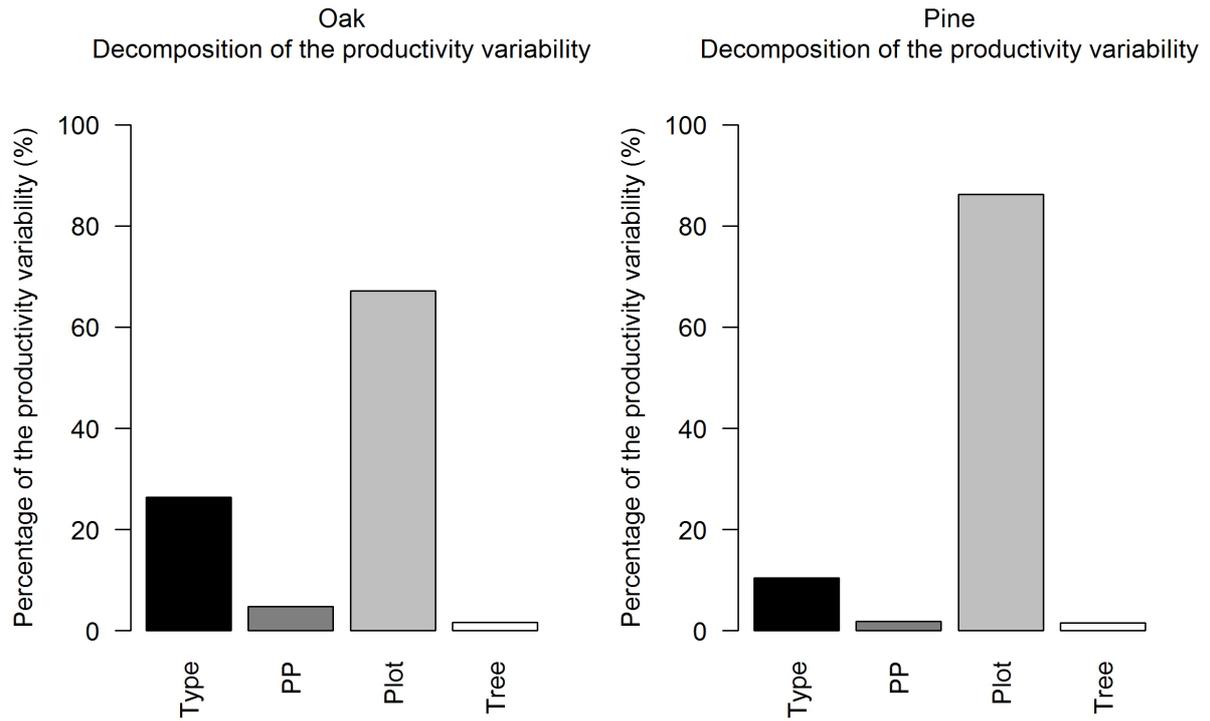
## 8. Figure captions



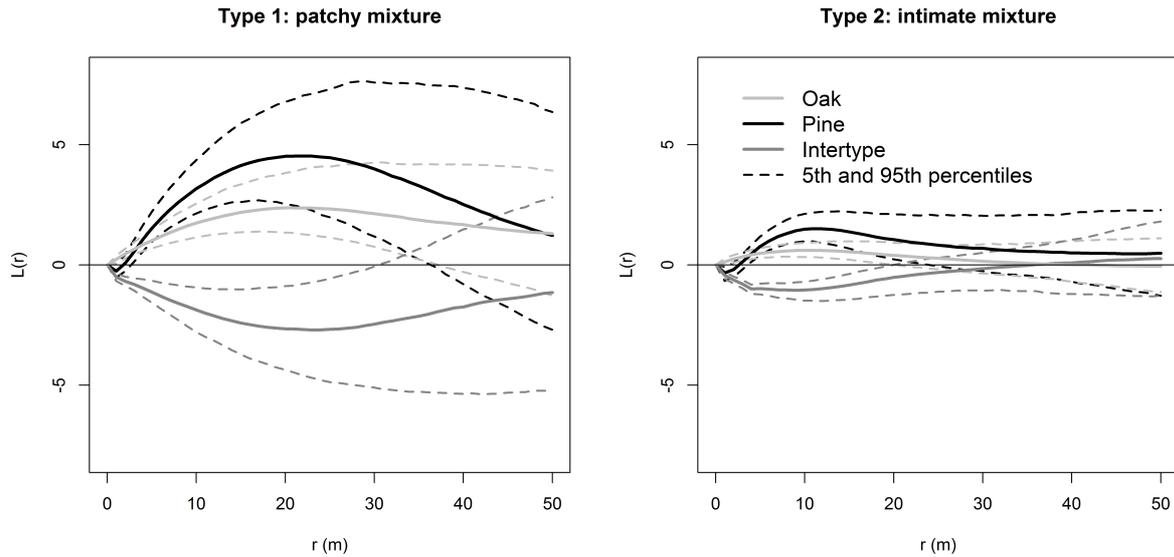
**Fig. 1 a) Patchy mixture (Type 1) simulated with the point process models; b) Intimate mixture (Type 2) simulated with the point process models.**



**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.**