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

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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

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

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

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

30
31 **Corresponding author:**

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

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_{umd}), the radius of oak aggregates in the
154 understory (rcl_{umd}), 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 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 $\{\alpha_k, \beta_k\}$, 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, 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):

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

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 σ_{type}^2 and σ_{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 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 $\text{m}^2.\text{ha}^{-1}.\text{year}^{-1}$
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 λ_{oak} and λ_{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 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.

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.

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352 **6. References**

- 353 Balandier P, Sonohat G, Sinoquet H, Varlet-Grancher C, Dumas Y (2006) Characterisation,
354 prediction and relationships between different wavebands of solar radiation
355 transmitted in the understorey of even-aged oak (*Quercus petraea*, *Q-robur*) stands.
356 *Trees-Struct Funct* 20 (3):363-370
- 357 Barot S, Gignoux J, Menaut JC (1999) Demography of a savanna palm tree: Predictions from
358 comprehensive spatial pattern analyses. *Ecology* 80 (6):1987-2005

359 Begon M, Townsend CR, Harper JL (2006) Ecology: from individuals to ecosystems. 4th ed.
360 Blackwell Publishing, Oxford

361 Canham CD, LePage PT, Coates KD (2004) A neighborhood analysis of canopy tree
362 competition: effects of shading versus crowding. *Can J For Res* 34 (4):778-787

363 Cavard X, Bergeron Y, Chen HYH, Paré D, Laganière J, Brassard B (2011) Competition and
364 facilitation between tree species change with stand development. *Oikos* 120
365 (11):1683-1695

366 Courbaud B, Goreaud F, Dreyfus P, Bonnet FR (2001) Evaluating thinning strategies using a
367 tree distance dependent growth model: some examples based on the CAPSIS
368 software "uneven-aged spruce forests" module. *For Ecol Manag* 145 (1-2):15-28

369 Cressie NAC (1993) Statistics for spatial data. John Wiley and sons, New York

370 Dieckmann U, Law R, Metz JAJ (2000) The Geometry of Ecological Interactions:
371 Simplifying Spatial Complexity. Cambridge University Press, Cambridge

372 Dufour-Kowalski S, Courbaud B, Dreyfus P, Meredieu C, de Coligny F (2012) Capsis: an
373 open software framework and community for forest growth modelling. *Ann For Sci*
374 69 (2):221-233

375 Duplat P, Tran-Ha M (1997) Modélisation de la croissance en hauteur dominante du chêne
376 sessile (*Quercus petraea* Liebl) en France Variabilité inter-régionale et effet de la
377 période récente (1959-1993). *Ann For Sci* 54 (7):611-634

378 Filipescu CN, Comeau PG (2007) Competitive interactions between aspen and white spruce
379 vary with stand age in boreal mixedwoods. *For Ecol Manag* 247 (1-3):175-184

380 Forrester DI, Bauhus J, Cowie AL, Vanclay JK (2006) Mixed-species plantations of
381 Eucalyptus with nitrogen-fixing trees: A review. *For Ecol Manag* 233 (2-3):211-230

382 Forrester DI, Smith RGB (2012) Faster growth of *Eucalyptus grandis* and *Eucalyptus pilularis*
383 in mixed-species stands than monocultures. *For Ecol Manag* 286:81-86

384 Getzin S, Dean C, He FL, Trofymow JA, Wiegand K, Wiegand T (2006) Spatial patterns and
385 competition of tree species in a Douglas-fir chronosequence on Vancouver Island.
386 *Ecography* 29 (5):671-682

387 Grissino-Mayer HD (2002) Research report evaluating crossdating accuracy: a manual and
388 tutorial for the computer program COFECHA. *Tree-Ring Research* 57 (2):205-221

389 Illian J, Penttinen A, Stoyan H, Stoyan D (2008) *Statistical Analysis and Modelling of Spatial*
390 *Point Patterns*. Wiley, Chichester

391 Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. *Ecol Lett*
392 10 (9):835-848

393 Kelty MJ (2006) The role of species mixtures in plantation forestry. *For Ecol Manag* 233 (2-
394 3):195-204

395 Lamosova T, Dolezal J, Lanta V, Leps J (2010) Spatial pattern affects diversity-productivity
396 relationships in experimental meadow communities. *Acta Oecol-Int J Ecol* 36
397 (3):325-332

398 Lenoir J, Gégout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in
399 plant species optimum elevation during the 20th century. *Science* 320 (5884):1768-
400 1771

401 Lotwick HW, Silverman BW (1982) Methods for analysing spatial processes of several types
402 of points. *Journal of the Royal Statistical Society B* 44 (3):406-413

403 McNaughton SJ (1977) Diversity and stability of ecological communities - comment on role
404 of empiricism in ecology. *Am Nat* 111 (979):515-525

405 MCPFE, UNECE, FAO (2011) *State of Europe's forests 2011*. MCPFE, Warsaw

406 Mokany K, Ash J, Roxburgh S (2008) Effects of spatial aggregation on competition,
407 complementarity and resource use. *Austral Ecol* 33 (3):261-270

408 Ngo Bieng MA (2007) Construction de modèles de structure spatiale permettant de simuler
409 des peuplements virtuels réalistes. Application aux peuplements mélangés Chêne
410 sessile - Pin sylvestre de la région Centre. Doctorat thesis in Forestry Science,
411 ENGREF-Cemagref, Nogent-sur-Vernisson

412 Ngo Bieng MA, Ginisty C, Goreaud F (2011) Point process models for mixed sessile forest
413 stands. *Ann For Sci* 68 (2):267-274

414 Ngo Bieng MA, Ginisty C, Goreaud F, Perot T (2006) A first typology of Oak and Scots pine
415 mixed stands in the Orleans forest (France), based on the canopy spatial structure. *N*
416 *Z J For Sci* 36 (2):325-346

417 Perot T, Goreaud F, Ginisty C, Dhôte JF (2010) A model bridging distance-dependent and
418 distance-independent tree models to simulate the growth of mixed forests. *Ann For*
419 *Sci* 67 (5):502p501-502p511

420 Perot T, Perret S, Meredieu C, Ginisty C (2007) Prévoir la croissance et la production du Pin
421 sylvestre : le module Sylvestris sous Capsis 4. *Revue Forestiere Francaise* 59 (1):57-
422 84

423 Perot T, Picard N (2012) Mixture enhances productivity in a two-species forest: evidence
424 from a modelling approach. *Ecol Res* 27:83-94

425 Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Statistics and
426 Computing. Springer, New York

427 Pinheiro JC, Bates DM, DebRoy S, Sarkar D, the R Development Core Team (2011) nlme:
428 linear and nonlinear mixed effects models. R package version 3.1-101.

429 Pretzsch H (1997) Analysis and modeling of spatial stand structures. Methodological
430 considerations based on mixed beech-larch stands in Lower Saxony. *For Ecol Manag*
431 97 (3):237-253

432 Pretzsch H, Schutze G (2009) Transgressive overyielding in mixed compared with pure
433 stands of Norway spruce and European beech in Central Europe: evidence on stand
434 level and explanation on individual tree level. *Eur J For Res* 128 (2):183-204

435 Pretzsch H, Block J, Dieler J, Hoang Dong P, Kohnle U, Nagel J, Spellmann H, Zingg A
436 (2010) Comparison between the productivity of pure and mixed stands of Norway
437 spruce and European beech along an ecological gradient. *Ann For Sci* 67 (7):712

438 Pukkala T (1989) Methods to describe the competition process in a tree stand. *Scand J Forest*
439 *Res* 4:187-202

440 R Development Core Team (2011) R: A language and environment for statistical computing.
441 R Foundation for Statistical Computing, Vienna, Austria

442 Regent I (2005) Windendro 2005a: manual for tree-ring analysis. Université du Quebec à
443 Chicoutimi

444 Ripley BD (1977) Modelling spatial patterns. *Journal of the royal statistical society B* 39:172-
445 212

446 Sonohat G, Balandier P, Ruchaud F (2004) Predicting solar radiation transmittance in the
447 understory of even-aged coniferous stands in temperate forests. *Ann For Sci* 61
448 (7):629-641

449 Stadt KJ, Huston C, Coates KD, Feng Z, Dale MRT, Lieffers VJ (2007) Evaluation of
450 competition and light estimation indices for predicting diameter growth in mature
451 boreal mixed forests. *Ann For Sci* 64:477-490

452 Tomppo E (1986) Models and methods for analysing spatial patterns of trees.
453 *Communicationes Instituti Forestalis Fenniae* (No. 138)

454

455 Uriarte M, Canham CD, Thompson J, Zimmerman JK (2004a) A neighborhood analysis of
456 tree growth and survival in a hurricane-driven tropical forest. *Ecol Monogr* 74
457 (4):591-614

458 Uriarte M, Condit R, Canham CD, Hubbell SP (2004b) A spatially explicit model of sapling
459 growth in a tropical forest: does the identity of neighbours matter? *J Ecol* 92 (2):348-
460 360

461 Vallet P, Perot T (2011) Silver fir stand productivity is enhanced when mixed with Norway
462 spruce: evidence based on large-scale inventory data and a generic modelling
463 approach. *J Veg Sci* 22 (5):932-942

464 Vanclay JK (2006) Experiment designs to evaluate inter- and intraspecific interactions in
465 mixed plantings of forest trees. *For Ecol Manag* 233 (2-3):366-374

466 Vettenranta J (1999) Distance-dependent models for predicting the development of mixed
467 coniferous forests in Finland. *Silva Fenn* 33 (1):51-72

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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} (m ² .ha ⁻¹)	BA _{pine} (m ² .ha ⁻¹)	BA _{other} (m ² .ha ⁻¹)	BA _{total} (m ² .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)	<i>girth</i> β (mm.cm ⁻¹)	<i>CI</i> _{oak} λ_{oak} (mm.m ⁻²)	<i>CI</i> _{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		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

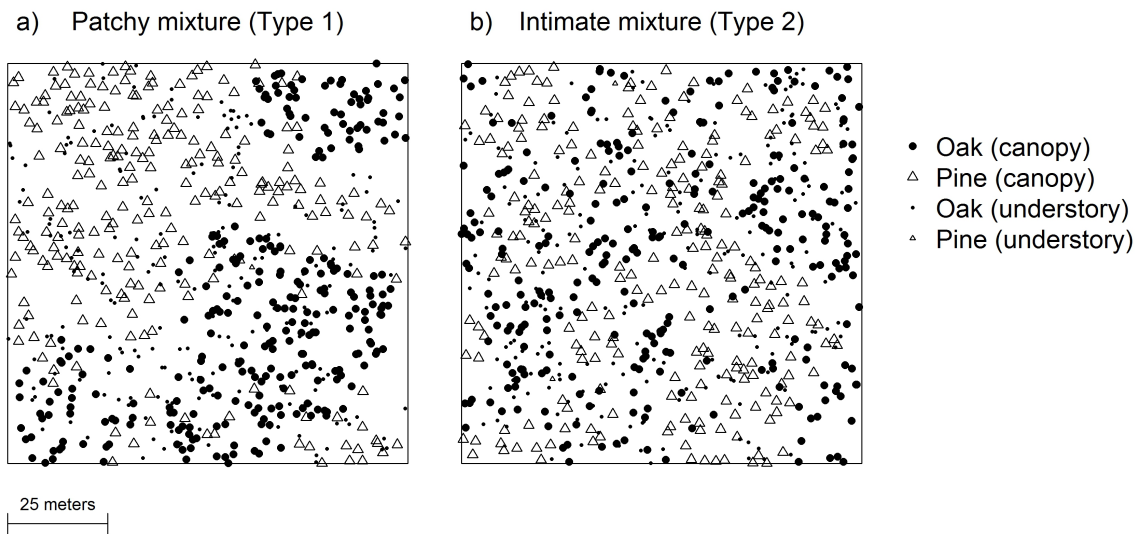


Fig. 1 a) Patchy mixture (Type 1) simulated with the point process models; b) Intimate mixture (Type 2) simulated with the point process models.

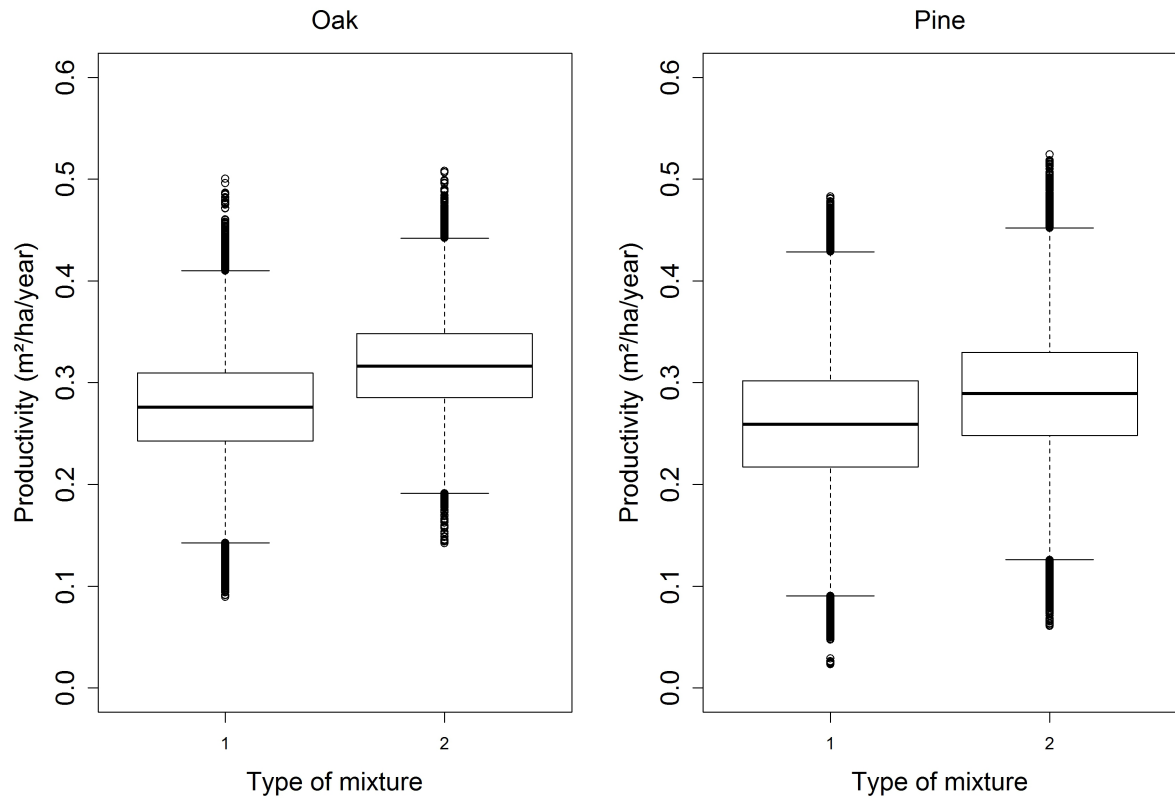


Fig. 2 Productivity comparison between the two mixture types for oak and pine.

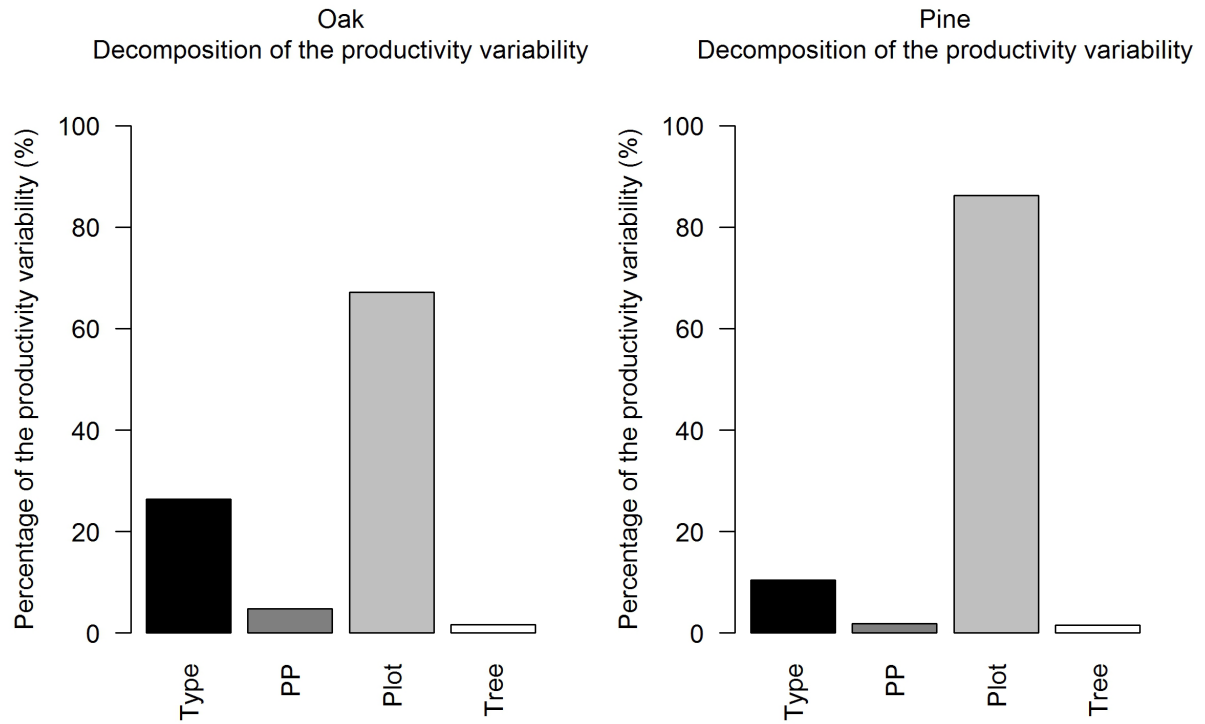


Fig. 3 Decomposition of the productivity variability for oak and pine following Equation (3). The different sources of variability are: type of mixture (Type), spatial point pattern within the type (PP), plot random effect (Plot), and tree random effect (Tree).

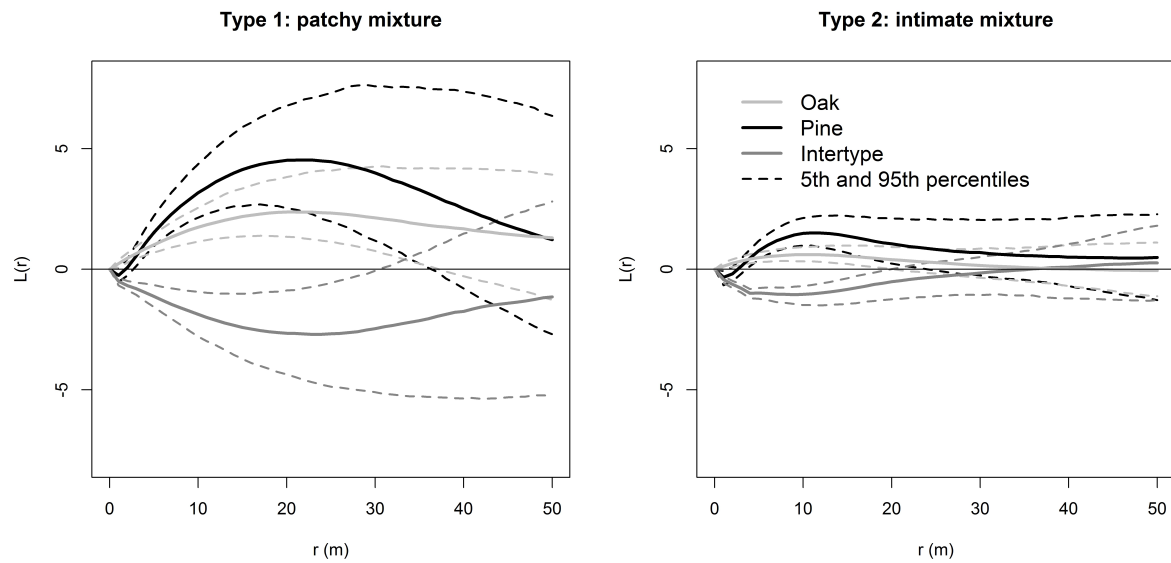


Fig. 4 L function and intertype L function calculated with 1000 simulations of Type 1 and Type 2 mixtures. For the intraspecific L function, $L(r)$ less than 0 indicates spatial regularity, $L(r)$ greater than 0 indicates spatial aggregation. For the intertype L function, $L(r)$ less than 0 indicates spatial repulsion between the two species, $L(r)$ greater than 0 indicates spatial attraction between the two species.