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# Mixture enhances productivity in a two-species forest: evidence from a modeling approach

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6  
7 **Title:**

8 Mixture enhances productivity in a two-species forest: evidence from a modelling  
9 approach

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21     **Abstract:**

22     The effect of mixture on productivity has been widely studied for applications related to  
23     agriculture but results in forestry are scarce due to the difficulty of conducting experiments.  
24     Using a modelling approach, we analysed the effect of mixture on the productivity of forest  
25     stands composed of sessile oak and Scots pine. To determine whether mixture had a positive  
26     effect on productivity and if there was an optimum mixing proportion, we used an  
27     aggregation technique involving a mean-field approximation to analyse a distance-dependent  
28     individual-based model. We conducted a local sensitivity analysis to identify the factors  
29     which influenced the results the most. Our model made it possible to predict the species  
30     proportion where productivity peaks. This indicates that transgressive over-yielding can occur  
31     in these stands and suggests that the two species are complementary. For the studied growth  
32     period, mixture does have a positive effect on the productivity of oak-pine stands. Depending  
33     on the plot, the optimum species proportion ranges from 38% to 74% of oak and the gain in  
34     productivity compared to the current mixture is 2.2% on average. The optimum mixing  
35     proportion mainly depends on parameters concerning intra-specific oak competition and yet,  
36     intra-specific competition higher than inter-specific competition was not sufficient to ensure  
37     over-yielding in these stands. Our work also shows how results obtained for individual tree  
38     growth may provide information on the productivity of the whole stand. This approach could  
39     help us to better understand the link between productivity, stand characteristics and species  
40     growth parameters in mixed forests.

41     **Keywords: Mixed forest - Niche complementarity - Overyielding - Individual-based**  
42     **model - Model Aggregation**

## 43 **1 Introduction**

44 It is currently admitted that plant diversity and ecosystem functioning are interrelated, and  
45 that greater plant diversity can lead to greater productivity (Hector et al. 1999; Loreau et al.  
46 2002; Hooper et al. 2005; Thebault and Loreau 2006). One of the mechanisms that has been  
47 put forward to explain the greater productivity at higher diversity is the "niche  
48 complementarity" (Loreau et al. 2001) that may result from inter-specific differences in  
49 resource requirements and uses or from positive interactions between species.

50 The principle of complementarity has been widely studied for herbaceous species in  
51 applications related to agriculture (de Wit 1960; Vandermeer 1989). However, although  
52 mixed forests are being promoted more and more, results on tree species complementarity are  
53 quite scarce particularly because of the difficulty of conducting long-term experiments (Kelty  
54 and Larson 1992; Piotta 2008; Pretzsch 2009). A classical way to study the effect of mixing  
55 proportion on productivity is to establish "replacement series" experiments (Jolliffe 2000). In  
56 these experiments, rather well-adapted to the study of two-species mixtures, the proportions  
57 of species vary while the overall density is maintained constant. This type of experiment can  
58 also be applied in forestry (Luis and Monteiro 1998; Garber and Maguire 2004) but they are  
59 more difficult to conduct because, for most tree species, results are available only after a  
60 period of many years. The use of large-scale forest inventory data (Vila et al. 2007; del Rio  
61 and Sterba 2009) and studies based on modeling (Pretzsch and Schutze 2009) are two  
62 alternative approaches to fill in the gaps in knowledge of the mixed-forest productivity.

63 Here we focused on the case of mixed forests with two species which are widely  
64 distributed throughout Europe (MCPFE et al. 2007). For a two-species mixed stand, we can  
65 use replacement diagrams to define and represent three main types of productivity response to  
66 the mixing proportion (Figure 1).

67

Figure 1 here

68 The effect of mixing proportion on productivity clearly depends on the species that are  
69 combined (Kelty 2006). For a given pair of species, the first issue is to know what kind of  
70 response occurs (positive, negative or no influence on productivity). The second challenge is  
71 to determine whether the productivity of the mixture can exceed the productivity of the most  
72 productive species in a pure stand - in other words, whether productivity peaks when an  
73 optimum mixing proportion is reached (right side of Figure 1). This phenomenon is called  
74 "transgressive over-yielding" and reflects mechanisms of facilitation or a strong  
75 complementarity between species for resource use (Hector et al. 2002; Hector 2006; Schmid  
76 et al. 2008).

77 The answers to these questions should be strongly linked to the relationship between intra-  
78 specific and inter-specific competition (Harper 1977). For example, based on the Lotka-  
79 Volterra theoretical model of inter-specific competition, Loreau (2004) showed that inter-  
80 specific competition for both species must be lower than intra-specific competition for  
81 transgressive over-yielding to occur. Intra- and inter-specific competition can be quantified  
82 empirically using local competition indices in a distance-dependent individual-based model  
83 (Biging and Dobbertin 1992; Canham et al. 2004; Uriarte et al. 2004; Stadt et al. 2007). The  
84 challenge is to link the results obtained at the individual tree level with the results that  
85 concern the whole stand. That is what we did in the present study.

86 In this article, we investigate whether the mixture of two tree species can improve the  
87 productivity of the stand. To address this question we used a distance-dependent individual-  
88 based model developed in a previous study for mixed stands of sessile oak (*Quercus petraea*  
89 L.) and Scots pine (*Pinus sylvestris* L.) (Perot et al. 2010). We used an aggregation technique  
90 to analyse this model and to answer the following questions: 1) Does mixture have a positive

91 effect on stand productivity? 2) What is the optimum mixing proportion in terms of  
92 productivity? 3) What are the factors that most influence the results for questions 1) and 2)?

## 93 **2 Materials and methods**

### 94 **2.1 Growth data from mixed oak-pine stands**

95 We collected the growth data in mixed oak-pine stands from the Orléans state forest. This  
96 forest is located in north-central France (47°51'N, 2°25'E) and covers 35 000 ha. Mixed oak-  
97 pine stands occupy an important position in French forests for three main reasons: they cover  
98 a relatively large area (Morneau et al. 2008); they have a heritage value for the public; and  
99 they are well-adapted to the sandy, water-logged soils common to central France.

100 Between 2006 and 2007, we established 9 plots (ranging in size from 0.5 to 1 ha) to study  
101 the growth of mixed oak-pine stands (Table 1). The nine plots included other broadleaved  
102 species (mainly *Carpinus betulus* L., *Betula pendula* R. and *Sorbus torminalis* L.) but they are  
103 in very small proportion (4% of the total basal area on average) and were not considered in  
104 the present study. These plots had been fully mapped in a previous in-depth study on  
105 horizontal spatial structure (Ngo Bieng et al. 2006). In each plot, we sampled 20 trees per  
106 species to take growth measurements. Sampled trees were cored twice to the pith in  
107 perpendicular directions at a height of 1.3 m. Cores were scanned and ring widths were  
108 measured to the nearest 0.01 mm (see Perot et al. 2010 for details). Because some trees were  
109 impossible to core and some cores were not usable, the growth analyses were based on a final  
110 total of 154 oaks and 179 pines. The mean oak age per plot ranged from 50 to 90 years, and  
111 that of pines from 50 to 120 years. In a plot, all trees of a species had approximately the same  
112 age indicating a single cohort for pines and a single cohort for oaks. Pines occupied the upper  
113 stratum of the stand while oaks occupied both the upper stratum and the understory, excepted  
114 in plot D78 where oaks were more abundant in the understory. Oak and pine populations had

115 mainly experienced artificial thinnings but some natural perturbations may also have occurred  
 116 (*i.e.* storms, fires, and pest damages). Detailed information on past disturbances (natural or  
 117 artificial) was not available in our plots (location and size of suppressed trees) so we chose the  
 118 period from 2000 to 2005 to study growth because there were no human or natural  
 119 disturbances during that time.

120 Table 1 here

## 121 2.2 The distance-dependent individual-based model

122 A distance-dependent individual-based model was developed in a previous work from the  
 123 growth data presented above (Perot et al. 2010). We briefly recall model equations and refer  
 124 to Perot et al. (2010) for details on model fitting and equation selection. Subscripts 1 and 2 are  
 125 used in equations and in the following sections to indicate oak and pine species respectively.  
 126 The distance-dependent individual-based model uses tree size and local competition indices  
 127 calculated inside a circle centred on a focal tree to predict the radial increment of its trunk.  
 128 Different competition indices and circle radii were compared for their ability to explain  
 129 individual growth (see Perot et al. 2010 for details on competition index selection). A radius  
 130 of 10 meters around the focal tree (neighbourhood radius) best explained growth variability.  
 131 A plot effect was introduced to take into account the possible effects of factors acting at stand  
 132 level such as site effect, total density or stage of development (young or old stand). The model  
 133 was fitted separately for oaks and pines using the ordinary least squares method to obtain an  
 134 individual growth equation for each species:

135 for oaks, 
$$\Delta r_{i,k,1} = \alpha_{k,1} + \beta_{k,1} girth_{i,k,1} + \lambda_{1,1} N_{i,1,1} + \lambda_{1,2} N_{i,1,2} + \varepsilon_{i,k,1} \quad (1)$$

136 for pines, 
$$\Delta r_{i,k,2} = \alpha_2 + \beta_{k,2} girth_{i,k,2} + \lambda_{2,2} G_{i,2,2} + \varepsilon_{i,k,2} \quad (2)$$

137 where  $\Delta r_{i,k}$  is the radial increment (mm) over a six-year interval (2000-2005) of the  $i$ th tree  
 138 in plot  $k$ ,  $girth$  is the girth (cm) in 1999 and  $\varepsilon$  is the residual error.  $\alpha_k$  and  $\beta_k$  are model

139 parameters for plot  $k$ . For pine, results showed no plot effect on  $\alpha$  which we simply denote  $\alpha_2$   
140 (see Table 2).  $\lambda_{j,1}$  and  $\lambda_{j,2}$  are the coefficients associated with the competition indices  
141 calculated for oak and pine, respectively.  $N_{i,1,1}$  is the number of oaks in the neighbourhood  
142 (*i.e.* at a distance less than 10 meters) of a focal tree  $i$  belonging to the oak species.  $N_{i,1,2}$  is the  
143 number of pines in the neighbourhood of a focal tree  $i$  belonging to the oak species.  $G_{i,2,2}$  is  
144 the basal area of pines in the neighbourhood of a focal tree  $i$  belonging to the pine species. For  
145 simplicity,  $N_{i,1,1}$ ,  $N_{i,1,2}$  and  $G_{i,2,2}$  will be called the local density of oaks, the local density of  
146 pines and the local basal area of pines, respectively. These competition indices account for  
147 both intra- and inter-specific competition. The coefficient  $\lambda_{2,1}$  associated with the competition  
148 index calculated for the neighbouring oaks of a pine focal tree was not significantly different  
149 from zero and does not appear in equation 2. This result suggests that the growth of pine is  
150 weakly influenced by oak. One may also notice that  $\lambda_{i,i} < \lambda_{i,j}$ , which means that intra-specific  
151 competition is higher than inter-specific for both species.

152 Table 2 here

### 153 **2.3 Aggregating the individual-based model to obtain analytical results at stand level**

154 The distance-dependent individual-based model mimics the dynamics of each tree, but for  
155 predictions at the stand level, simulations are necessary. To obtain analytical results at the  
156 stand level, we aggregated the individual model. This operation was hindered somewhat by  
157 the presence of local competition indices that introduce a spatial dependence; we therefore  
158 proceeded in two steps. We first applied the mean field approximation to obtain a distance-  
159 independent individual-based model (Levin and Pacala 1997; Dieckmann et al. 2000; Picard  
160 and Franc 2001). Secondly, we aggregated this distance-independent model into a model  
161 predicting the basal area increment of the whole stand. We call this aggregated model “the  
162 stand model”.



163 The mean field approximation is particularly well suited to simplify the spatial dependence  
 164 in distance-dependent individual-based models. To apply this method to the model presented  
 165 above (equations 1 and 2), we considered that the spatial pattern of trees was a point process  
 166 realization. The mean field approximation assumes that all trees are affected in the same way  
 167 by their neighbourhood. We can then replace the specific expression of a competition index  
 168 for a given spatial pattern by its expected value across all possible outcomes of the point  
 169 process. To calculate this expected value, we assumed that the point process is ergodic, which  
 170 implies that the mean across several realizations equals the spatial average over one  
 171 realization (Cressie 1993; Illian et al. 2008). Under this assumption, we replaced the average  
 172 of a competition index by its spatial average calculated from all the trees in the stand. We thus  
 173 obtained equations 3 and 4 which correspond to a distance-independent individual-based  
 174 model:

$$\Delta r_{i,k,1} = \alpha_{k,1} + \beta_{k,1} \text{girth}_{i,k,1} + \lambda_{1,1} \langle N_{i,1,1} \rangle + \lambda_{1,2} \langle N_{i,1,2} \rangle \quad (3)$$

$$\Delta r_{i,k,2} = \alpha_2 + \beta_{k,2} \text{girth}_{i,k,2} + \lambda_{2,2} \langle G_{2,2} \rangle \quad (4)$$

177 where  $\langle N_{1,1} \rangle$  and  $\langle N_{1,2} \rangle$  are the spatial averages of the local density of oaks and pines for an  
 178 oak focal tree, and  $\langle G_{2,2} \rangle$  is the spatial average of the local basal area of pines for a pine focal  
 179 tree. Under appropriate assumptions on the point process (homogenous and isotropic), the  
 180 spatial averages of these indices can be related to Ripley's  $K$  function (Ripley 1977) and to the  
 181 inter-type  $K$  function (Lotwick and Silverman 1982). In this way, we can link the growth to  
 182 the spatial structure of the stand. Let us call  $K_{1,2}$  the inter-type function between species 1 and  
 183 2. If  $1 = 2$ ,  $K_{1,1}$  is known to be the Ripley's function for species 1. If  $d_2$  is the density of  
 184 species 2,  $d_2 K_{1,2}(r)$  is the expectation of the number of trees of species 2 found at a distance  
 185 less than or equal to  $r$  from a randomly chosen tree of species 1. These functions are often  
 186 used to test the null hypothesis of complete spatial randomness. For oak, we directly obtain  
 187 the following relationships:

188 
$$\langle N_{1,1} \rangle = \frac{N_1}{S} K_{1,1}(10)$$

189 
$$\langle N_{1,2} \rangle = \frac{N_2}{S} K_{1,2}(10)$$

190 where  $N_1$  and  $N_2$  are the total number of oaks and the total number of pines in the stand,  $S$   
 191 is the plot area,  $K_{1,1}(10)$  is the value of the Ripley's function at ten meters for the oak  
 192 population, and  $K_{1,2}(10)$  is the value of the inter-type function at ten meters for oak and pine  
 193 populations. To simplify, we will call these variables  $K_{1,1}$  and  $K_{1,2}$  in the following sections.  
 194 Equation 3 can now be written as follows:

195 
$$\Delta r_{i,k,1} = \alpha_{k,1} + \beta_{k,1} \text{girth}_{i,k,1} + \lambda_{1,1} \frac{N_1}{S} K_{1,1} + \lambda_{1,2} \frac{N_2}{S} K_{1,2} \quad (5)$$

196 In the case of pine, we have to calculate the spatial average of the local basal area which  
 197 implies taking into account the correlation between the individual basal area and the location  
 198 of the trees. To simplify, we assumed that the individual basal area of a tree was independent  
 199 of its location on the plot. We then calculated the average local basal area around a pine tree  
 200 by multiplying the average individual basal area of a pine ( $\bar{g}_2$ ) by the average local density of  
 201 pines ( $\langle N_{2,2} \rangle$ ). The average individual basal area of a pine is the ratio between the total basal  
 202 area of pines in the stand and the total number of pines. The spatial average of the local basal  
 203 area can thus be written as follows:

204 
$$\langle G_{2,2} \rangle = \bar{g}_2 \langle N_{2,2} \rangle = \frac{G_2}{N_2} \frac{N_2}{S} K_{2,2}(10) = \frac{G_2}{S} K_{2,2}(10)$$

205 where  $K_{2,2}(10)$  is the value of the Ripley's function at ten meters for the pine population,  
 206 called  $K_{2,2}$  in the following sections. Equation 4 can now be written as follows:

207 
$$\Delta r_{i,k,2} = \alpha_2 + \beta_{k,2} \text{girth}_{i,k,2} + \lambda_{2,2} \frac{G_2}{S} K_{2,2} \quad (6)$$

208 Equations 5 and 6 represent a distance-independent individual-based model resulting from  
 209 the mean field approximation of equations 1 and 2. However, this model includes some

210 spatial information on the populations through the Ripley functions at ten meters and the  
 211 inter-type function at ten meters. These functions were calculated for the 9 plots from the  
 212 observed spatial pattern of the trees (Table 3).

213 Table 3 here

214 We then proceeded to the second step and aggregated the individual-based model into a  
 215 stand model. As all variables now characterize a plot, we can drop the  $k$  index without any  
 216 risk of confusion. The principle of the aggregation is to sum the individual dynamics defined  
 217 by equations 5 and 6. We chose basal area increment, denoted  $\Delta G$ , to account for stand  
 218 productivity. We did not choose volume increment, because volume requires data on tree  
 219 height that were not available in our study. Next, we showed (see Appendix) that the stand  
 220 model can be written as follows:

$$221 \begin{cases} \Delta G = \Delta G_1 + \Delta G_2 \\ \Delta G_1 = A(\gamma_1)N_1 + B(\gamma_1, \beta_1)N_1\bar{r}_1 + C(\beta_1)G_1 \\ \Delta G_2 = A(\gamma_2)N_2 + B(\gamma_2, \beta_2)N_2\bar{r}_2 + C(\beta_2)G_2 \end{cases} \quad (7)$$

222 where  $\bar{r}_j$  is the mean tree radius for species  $j$ , functions  $A$ ,  $B$  and  $C$  are defined by:

$$223 \begin{cases} A(\mu) = \pi\mu^2 \\ B(\mu, \nu) = 2\pi\mu(1 + 2\pi\nu) \\ C(\mu) = 4\pi\mu(1 + \pi\mu) \end{cases}$$

224 and:

$$225 \begin{cases} \gamma_1 = \alpha_1 + \lambda_{1,1} \frac{N_1}{S} K_{1,1} + \lambda_{1,2} \frac{N_2}{S} K_{1,2} \\ \gamma_2 = \alpha_2 + \lambda_{2,2} \frac{G_2}{S} K_{2,2} \end{cases}$$

226 Here,  $\Delta G$  corresponds to the basal area increment of all trees alive in 2005. For this  
 227 population of trees, no mortality or recruitment occurred during the study period 2000-2005.  
 228 Thus, the growth process was sufficient to define the productivity of the population over the  
 229 6-year interval.

230 To check for consistency, we compared the stand model to the individual-based model. We  
 231 simulated the stand basal area increment over the 2000-2005 period for the 9 plots using both  
 232 models, starting from the same initial state. We then calculated the mean absolute difference  
 233 between the predictions of the two models for each species as follows:

$$234 \quad E_s = \frac{1}{9} \sum_{k=1}^9 |\Delta G_{k,s,IBM} - \Delta G_{k,s,SM}|$$

235 where  $E_s$  is the mean absolute difference between the two models for species  $s$ ,  $\Delta G_{k,s,IBM}$  is  
 236 the stand basal area increment of species  $s$  predicted by the individual-based model for plot  $k$   
 237 and  $\Delta G_{k,s,SM}$  is the stand basal area increment of species  $s$  predicted by the stand model for  
 238 plot  $k$ . We also used a Wilcoxon signed rank test on  $\Delta G_{k,s}$  to see if there was a significant  
 239 difference between the two models.

#### 240 **2.4 Introducing the mixing proportion into the stand model**

241 To determine the proportion of each species in a mixed stand, we must define a reference  
 242 variable that quantifies its abundance in the stand. For example, one can choose the number of  
 243 stems, but in this case, the small individuals of a species and the large ones of another species  
 244 would have the same weight and this is generally not acceptable in forest ecosystems. To  
 245 avoid such problems, it is preferable to choose variables that are related to the volume or  
 246 biomass of populations (Pretzsch 2005). In this study, we used basal area which takes into  
 247 account both the number and size of individuals. For a forest composed of two tree species,  
 248 the proportion of a species  $j$  is defined as the ratio between the basal area of the species and  
 249 the total basal area:  $x_j = G_j/G$ . In addition, we introduced the quadratic mean radius  $\bar{r}_{G,j}$  so as  
 250 to link the density of a species  $j$  to its basal area:  $G_j = N_j \pi \bar{r}_{G,j}^2$ . We chose the proportion of oak  
 251 ( $x_1$ ) to define the mixing proportion of the stand, noted  $x$ . The proportion of pine then is  $1 - x$ .

252 With these new variables included, the stand model has 6 stand state variables: the total  
 253 basal area  $G$ , the mixing proportion for oak  $x$ , the quadratic mean radius for oaks  $\bar{r}_{G,1}$ , the

254 quadratic mean radius for pines  $\bar{r}_{G,2}$ , the mean radius for oaks  $\bar{r}_1$ , and the mean radius for  
 255 pines  $\bar{r}_2$ . State variables are the minimum set of variables that are required to know the state  
 256 of a forest stand. Every point  $(G, x, \bar{r}_{G,1}, \bar{r}_{G,2}, \bar{r}_1, \bar{r}_2)$  in  $\mathbb{R}^{+6}$  potentially defines a forest stand.  
 257 The mean radius can be seen as the first moment of the diameter distribution, whereas the  
 258 quadratic mean radius corresponds to the non-centred second moment of the diameter  
 259 distribution. For most statistical distributions, the variance is related to the mean, which  
 260 means that  $\bar{r}_{G,j}$  and  $\bar{r}_j$  will generally be related. On the contrary, no relationship is a priori  
 261 expected between  $x$  and the other 5 state variables. To check this, we tested the 9 plots to see  
 262 if there was a significant correlation between  $x$  and any of the other state variables: all  
 263 Pearson's correlation coefficients turned out to be non significantly different from zero.

264 The six state variables are complemented by 4 secondary variables that follow from them  
 265 directly: the basal area of oaks  $G_1 = xG$ , the basal area of pines  $G_2 = (1 - x)G$ , the number of  
 266 oaks  $N_1 = xG/(\pi\bar{r}_{G,1}^2)$ , and the number of pines  $N_2 = (1-x)G/(\pi\bar{r}_{G,2}^2)$ . The model also includes 10  
 267 parameters  $(\alpha_1, \alpha_2, \beta_1, \beta_2, \lambda_{1,1}, \lambda_{1,2}, \lambda_{2,2}, K_{1,1}, K_{2,2}, K_{1,2})$  and 1 constant (the plot area  $S$ ).

268 We introduced the mixing proportion  $x$  into equation 7 and we used the basal area and the  
 269 quadratic mean radius to replace the density. The stand model can then be written as a  
 270 function of the mixing proportion, the total basal area and the average dendrometric  
 271 characteristics of each species:

$$272 \left\{ \begin{array}{l} \Delta G = \Delta G_1 + \Delta G_2 \\ \Delta G_1 = A(\gamma_1) \frac{Gx}{\pi\bar{r}_{G,1}^2} + B(\gamma_1, \beta_1) \bar{r}_1 \frac{Gx}{\pi\bar{r}_{G,1}^2} + C(\beta_1) Gx \\ \Delta G_2 = A(\gamma_2) \frac{G(1-x)}{\pi\bar{r}_{G,2}^2} + B(\gamma_2, \beta_2) \bar{r}_2 \frac{G(1-x)}{\pi\bar{r}_{G,2}^2} + C(\beta_2) G(1-x) \end{array} \right. \quad (8)$$

273 with:

274

$$\begin{cases} \gamma_1 = \alpha_1 + \lambda_{1,1} \frac{1}{S} K_{1,1} \frac{Gx}{\pi \bar{r}_{G,1}^2} + \lambda_{1,2} \frac{1}{S} K_{1,2} \frac{G(1-x)}{\pi \bar{r}_{G,2}^2} \\ \gamma_2 = \alpha_2 + \lambda_{2,2} \frac{1}{S} K_{2,2} G(1-x) \end{cases}$$

275 Since a forest stand is characterized by 6 state variables, 6 dynamics equations are required  
 276 to define its change over time. Equation 8 is equivalent to 2 independent equations for  $G$  and  
 277  $x$ . The dynamics equations for  $\bar{r}_{G,1}$  and  $\bar{r}_{G,2}$  follow from  $\Delta N_1 = 0$  and  $\Delta N_2 = 0$ , since, as  
 278 previously mentioned, the number of trees remained constant (no mortality, no recruitment).  
 279 The dynamics equations for  $\bar{r}_1$  and  $\bar{r}_2$  can also be derived from the individual-based distance-  
 280 dependent model (see Appendix) but we did not use them in the calculations described below.

## 281 2.5 "Transgressive over-yielding" and optimum mixing proportion

282 Every value of the vector  $(G, x, \bar{r}_{G,1}, \bar{r}_{G,2}, \bar{r}_1, \bar{r}_2)$  defines a state of the forest stand. To  
 283 determine the mixing proportion  $x$  that maximizes productivity, we considered  $(G, \bar{r}_{G,1}, \bar{r}_{G,2},$   
 284  $\bar{r}_1, \bar{r}_2)$  to be known variables, with  $x$  the only unknown state variable. This is equivalent to  
 285 searching for the optimum in a subspace of the space of states. This approach is similar to  
 286 "replacement series" experiments that compare pure and mixed stands while keeping the total  
 287 density constant (Jolliffe 2000). With this condition, the basal area increment  $\Delta G$  defined by  
 288 equation 8 can be considered as a function of the mixing proportion  $x$ . By definition, there is  
 289 "transgressive over-yielding" if  $x$  is such that  $\Delta G(x) > \max\{\Delta G(0), \Delta G(1)\}$ ; in other words,  
 290  $\Delta G(x)$  has a maximum value between 0 and 1. The optimum mixing proportion  $x_{max}$  then  
 291 becomes the value of  $x$  where the derivative of  $\Delta G(x)$  with respect to  $x$  is null, while ensuring  
 292 that the derivative is positive for  $x < x_{max}$  and negative for  $x > x_{max}$ .

293 A local sensitivity analysis was conducted to assess how  $x_{max}$  varied when one of the  
 294 parameters was changed. As the different parameters were not expressed in the same units, we

295 computed elasticities rather than sensitivities. The elasticity of  $x_{max}$  to that of the parameter  $p$   
296 is defined as  $\partial \ln(x_{max}) / \partial \ln(p)$ .

## 297 **3 Results**

### 298 **3.1 Difference between the individual-based model and the stand model**

299 The predictions of the individual-based model and those of the stand model were very  
300 similar (Figure 2). The mean absolute difference between the two models for the 2000-2005  
301 period was 0.051 m<sup>2</sup>/ha for oak ( $E_1$ ) and 0.023 m<sup>2</sup>/ha for pine ( $E_2$ ). This corresponds to a  
302 difference of 2.4% and 1.7% respectively between the two models.

303  Figure 2 here

304 However, the Wilcoxon signed rank test showed significant differences between the two  
305 models (for oak  $V = 44$  and  $p$ -value = 0.00781; for pine  $V = 45$  and  $p$ -value = 0.00390). The  
306 stand model gives values slightly lower than the individual model. However, despite these  
307 results, we considered that the difference between the two models was small enough to allow  
308 us to use the aggregated model to study the effect of mixing proportions on stand  
309 productivity.

### 310 **3.2 Optimum mixing proportion formula**

311 Since  $\Delta G'(x) = \Delta G'_1(x) + \Delta G'_2(x)$ , we calculated the derivative of the oak growth function and  
312 the derivative of the pine growth function separately. Let us pose  $m_{1,s1} = 2(1 + 2\pi\beta_{s1})$ ,  
313  $m_{2,s1} = 4\pi\beta_{s1}(1 + \pi\beta_{s1})$ ,  $n_{1,s1} = \lambda_{s1,s1} K_{s1,s1}/S$ , and  $n_{2,s1} = \lambda_{s1,s2} K_{s1,s2}/S$ , where  $s1$  is one of the species  
314 and  $s2$  the other one. For oaks we then obtained  $\Delta G'_1(x) = a_1x^2 + b_1x + c_1$  with:

$$\begin{aligned}
315 \quad a_1 &= \frac{3G^3}{\pi^2 \bar{r}_{G,1}^2} \left( \frac{n_{1,1}}{\bar{r}_{G,1}^2} - \frac{n_{2,1}}{\bar{r}_{G,2}^2} \right)^2 \\
b_1 &= \frac{2G^2}{\pi \bar{r}_{G,1}^2} \left( \frac{n_{1,1}}{\bar{r}_{G,1}^2} - \frac{n_{2,1}}{\bar{r}_{G,2}^2} \right) \left( 2\alpha_1 + \frac{2Gn_{2,1}}{\pi \bar{r}_{G,2}^2} + \bar{r}_1 m_{1,1} \right) \\
c_1 &= \frac{G}{\bar{r}_{G,1}^2} \left( \alpha_1 + \frac{Gn_{2,1}}{\pi \bar{r}_{G,2}^2} \right) \left( \alpha_1 + \frac{Gn_{2,1}}{\pi \bar{r}_{G,2}^2} + \bar{r}_1 m_{1,1} \right) + Gm_{2,1}
\end{aligned}$$

316 And for pines we obtained  $\Delta G'_2(x) = a_2 x^2 + b_2 x + c_2$  with:

$$\begin{aligned}
317 \quad a_2 &= -\frac{3n_{1,2}^2 G^3}{\bar{r}_{G,2}^2} \\
b_2 &= \frac{2G^2 n_{1,2}}{\bar{r}_{G,2}^2} (2\alpha_2 + 3Gn_{1,2} + \bar{r}_2 m_{1,2}) \\
c_2 &= -\frac{G}{\bar{r}_{G,2}^2} \left[ (\alpha_2 + Gn_{1,2})^2 + 2Gn_{1,2} (\alpha_2 + Gn_{1,2} + \bar{r}_2 m_{1,2}) + \bar{r}_2 m_{1,2} \alpha_2 \right] - Gm_{2,2}
\end{aligned}$$

318 We can show (see Appendix) that the mixing proportion  $x_{max}$  corresponding to a maximum  
319 for the function  $\Delta G(x)$  is the solution given by:

$$320 \quad x_{max} = \frac{-b - \sqrt{b^2 - 4ac}}{2a} \quad (9)$$

321 with  $a = a_1 + a_2$ ,  $b = b_1 + b_2$  and  $c = c_1 + c_2$ .

322 Thanks to model aggregation, we obtained an explicit expression for the optimum mixing  
323 proportion ( $x_{max}$ ) as a function of the parameters of the stand model, the average dendrometric  
324 characteristics of each species, the total basal area and the spatial characteristics of the stand.

### 325 3.3 Mixing effect on stand productivity

326 For each plot, a mixing proportion between 0 and 1 was found that maximized the stand  
327 basal area increment. This mixing proportion varied between 38% and 74% depending on the  
328 plot (Figure 3).

329 

330 The difference between the optimum mixing proportion ( $x_{max}$ ) and the mixing proportion  
331 actually observed in the plots ( $x_{plot}$ ) varied from 0 to 34% (Table 4). The productivity gain



332 between these two proportions over the 6-year period was relatively low: 2.2% on average  
333 with a maximum of 9% (Table 4).

334 Table 4 here

335 Although the elasticities of  $x_{max}$  to the parameters of the model varied from one plot to  
336 another, a similar pattern was found across plots (Figure 4). The optimum mixing proportion  
337  $x_{max}$  was the most sensitive to the oak parameters, then to the pine parameters, then to the  
338 inter-specific parameters. The parameters to which  $x_{max}$  was the most sensitive on average  
339 were  $K_{1,1}$  and  $\lambda_{1,1}$ . For  $K_{1,1}$  the elasticity is negative, meaning that an increase in  $K_{1,1}$  brings a  
340 decrease in  $x_{max}$ . For  $\lambda_{1,1}$  the elasticity is also negative but, as  $\lambda_{1,1}$  is negative, it means that an  
341 increase in  $\lambda_{1,1}$  brings an increase in  $x_{max}$ . The parameter to which  $x_{max}$  was the least sensitive  
342 on average was  $K_{1,2}$ , with a positive or negative sign that varied depending on the focal plot.  
343 From a quantitative point of view, a 1% increase in  $K_{1,1}$  (or a 1% decrease in  $\lambda_{1,1}$ ) led to a  
344 decrease in  $x_{max}$  of between 1 and 1.2% while a 1% increase in  $K_{1,2}$  led to a variation in  $x_{max}$  of  
345 between 0 and 0.2% depending on the plots.

346 The parameter  $K_{1,1}$  indicates the degree of aggregation of oaks. When  $K_{1,1}$  increases the  
347 oaks are more aggregated and this leads to an increase in intra-specific competition.  $\lambda_{1,1}$  is the  
348 parameter that directly indicates the intensity of the intra-specific competition of oak because  
349 it is associated to the competition index calculated on oak competitors. Since  $\lambda_{1,1}$  is negative,  
350 if this parameter decreases, it means that the intensity of the intra-specific competition  
351 increases. We can therefore conclude that the optimum mixing proportion depends mainly on  
352 the characteristics of the oak population and more particularly on parameters involved in the  
353 intra-specific competition of oak ( $K_{1,1}$  and  $\lambda_{1,1}$ ).

## 354 **4 Discussion**

### 355 **4.1 Complementarity between species**

356 Our results suggest a positive effect of mixture on the productivity of oak-pine stands  
357 (Figure 3). This result is consistent with those of Brown (1992) established for young oak-  
358 pine stands in an experimental design. Unlike Brown's study (1992), we showed that, for  
359 some mixing proportions, stand productivity reached a maximum; this indicates a situation of  
360 "transgressive overyielding" (Figure 3). The gain between optimum productivity and current  
361 productivity of the plots ranged from 0 to 9%. Our individual model was developed for  
362 mixing proportions varying between 28% and 59%. Within this range, we can have  
363 confidence in the stand model predictions. However, outside this range, and particularly for  
364 extreme mixing proportions, the behaviour of the stand model is not guaranteed and may give  
365 unrealistic predictions (see for example, plot D20 on Figure 3). The results obtained here  
366 assume that the relationships fitted on mixed stands can be extrapolated to pure stands.

367 The effect of mixture on productivity is based on two main assumptions: "niche  
368 complementarity" and "sampling effects" (Tilman et al. 2001). As we worked with only two  
369 species and a variable mixing proportion, the "niche complementarity" hypothesis is more  
370 likely to explain our findings. We studied a conifer-broadleaf forest with species having very  
371 contrasting traits for light interception. Consequently, the complementarity of the two species  
372 for the use of light is a strong hypothesis to explain a productivity increase in our mixed  
373 stands (Ishii et al. 2004; Ishii and Asano 2010). Common oak is able to grow in the different  
374 strata of the stand in contrast to Scots pine because oak is a more shade tolerant species than  
375 Scots pine (Niinemets and Valladares 2006). Moreover, in our model there was a non-  
376 significant influence of oaks on pines (equation 2) probably because the pines had a greater  
377 girth than oaks on average (Table 1). These two arguments may explain why a pure stand of

378 pine could be less productive than a pine stand where oaks were able to colonize the lower  
379 strata. We also know that the light interception by the pine foliage is lower than the light  
380 interception by the oak foliage (Balandier et al. 2006; Sonohat et al. 2004). This may help to  
381 explain that in our oak model, the inter-specific competition was lower than the intra-specific  
382 competition (equation 1) which contributes to a higher productivity in mixtures than in pure  
383 stands of oak. The two species involved have different light requirements but also different  
384 root distribution patterns (Brown 1992). The complementarity in nutrient and water use could  
385 also contribute to a higher productivity in the mixture. The positive effect of mixture on stand  
386 productivity that we found could thus be explained by spatial segregations in the aerial and  
387 underground compartments. Our results concern the basal area productivity which does not  
388 include differences in wood density of both species (Pretzsch 2005). To go further in the  
389 study of the species complementarity, it would be interesting to estimate the effect of mixture  
390 on biomass productivity. Further research is also necessary to identify the ecological  
391 mechanisms that can explain the complementarity between these two species.

## 392 **4.2 Over-yielding in mixed forests: a dynamic state**

393 It is important to note that our models were developed from growth data corresponding to a  
394 given time period (2000-2005). It is likely that the parameters of these models change with  
395 time. For example, growth in juvenile Scots pine can be much faster than that of sessile oak  
396 (Brown 1992) and it is possible that the ratio between intra- and inter-specific competition  
397 changes over time for these species. This could explain why a situation of transgressive over-  
398 yielding could occur in mature stands and not in young stands. The impact of the temporal  
399 dimension on our results can also be seen through the optimum mixing proportion formula.  
400 Indeed, we calculated the optimum mixing proportion in the subspace of the state space  
401 defined by known values for  $(G, \bar{r}_{G,1}, \bar{r}_{G,2}, \bar{r}_1, \bar{r}_2)$ . This means that  $x_{max}$  can be considered as a

402 function of the state variables:  $x_{max}(G, \bar{r}_{G,1}, \bar{r}_{G,2}, \bar{r}_1, \bar{r}_2)$ . As all these quantities, including the  
403 mixing proportion itself, change with time, a pending question is whether

404 
$$x(t) = x_{max}(G(t), \bar{r}_{G,1}(t), \bar{r}_{G,2}(t), \bar{r}_1(t), \bar{r}_2(t)) \quad (10)$$

405 at a given time ensures that

406 
$$x(t + \Delta t) = x_{max}(G(t + \Delta t), \bar{r}_{G,1}(t + \Delta t), \bar{r}_{G,2}(t + \Delta t), \bar{r}_1(t + \Delta t), \bar{r}_2(t + \Delta t))$$

407 at the subsequent time. There is actually no reason that this should be the case. This brings  
408 up two questions: (1) Are there any initial values for  $(G, \bar{r}_{G,1}, \bar{r}_{G,2}, \bar{r}_1, \bar{r}_2)$  such that equation 10  
409 would be verified at all times? (2) What type of silviculture - that is, an artificial modification  
410 of  $N_1$  and  $N_2$  - would make it possible to verify equation 10 starting from arbitrary values for  
411  $(G, \bar{r}_{G,1}, \bar{r}_{G,2}, \bar{r}_1, \bar{r}_2)$ ? The effect of mixture on stand productivity could be different for other  
412 periods not only quantitatively but also qualitatively. Including the time factor in our results  
413 will be the subject of future work.

### 414 **4.3 Factors that influence the optimum mixing proportion**

415 By simplifying and aggregating a distance-dependent individual-based model, we were  
416 able to express the productivity of the stand as a function of the stand characteristics, the  
417 model parameters and the mixing proportion (equation 8). Moreover, we have shown that it is  
418 possible to explicitly express the optimum mixing proportion as a function of the mean  
419 dendrometric characteristics of each species and the parameters of the individual model  
420 (equation 9). After applying the stand model to the 9 plots in the study, our results showed  
421 that there is some variability in the optimum value (Table 4). The optimum mixing proportion  
422 ( $x_{max}$ ) ranged from 38% to 74% of oak depending on the plot. We can explain this variability  
423 among plots by studying the qualitative impact of the different factors on the optimum  
424 provided by the local sensitivity analysis (Figure 4). For example the elasticity of  $x_{max}$  to the  
425 spatial structure of oak (index  $K_{1,1}$ ) was negative. It means that the less aggregated the oaks

426 are, the fewer oaks there are within distance of 10 m on average, and consequently the more  
 427 their growth is promoted. The optimum then moves towards a stand where oak is more  
 428 represented. The same explanation can be used for pines and for the other factors. Finally, any  
 429 change in a factor that promotes the productivity of a species moves the optimum towards a  
 430 mixing proportion where the species is more represented. The local sensitivity analysis gave  
 431 us also quantitative results. For a given set of dendrometric characteristics, the optimum  
 432 mixing proportion was more sensitive to parameters involving oak - especially those  
 433 concerning its intra-specific competition ( $K_{1,1}$  et  $\lambda_{1,1}$ ) - than to those involving pine (Figure 4).  
 434 When the oak intra-specific competition increases, the optimum moves towards a stand with a  
 435 higher proportion of pine. In other words, the more intra-specific competition decreases  
 436 (decrease in  $K_{1,1}$  or increase in  $\lambda_{1,1}$ ), the more the optimum for productivity moves towards a  
 437 pure stand of oak. Our plots had different spatial patterns (Table 3) because they probably  
 438 experienced different ecological processes and different human actions (Ngo Bieng et al.  
 439 2006). As it has been recently shown for coexistence issues (see Hart and Marshall 2009), this  
 440 spatial structure has a direct impact on the optimum mixing proportion by changing intra and  
 441 inter-specific competition.

442 The mathematical equations that we developed can also inform us about the conditions  
 443 leading to a situation of over-yielding. For oak, the term  $(\lambda_{1,1}K_{1,1}/\bar{r}_{G,1}^2 - \lambda_{1,2}K_{1,2}/\bar{r}_{G,2}^2)$  is a  
 444 multiplicative factor for parameters  $a_1$  and  $b_1$  of the derivative of  $\Delta G_1(x)$ . Therefore, if  
 445  $\lambda_{1,1}K_{1,1}/\bar{r}_{G,1}^2 = \lambda_{1,2}K_{1,2}/\bar{r}_{G,2}^2$  the relationship between oak productivity and the mixing proportion is  
 446 a straight line which means that there would be no effect of mixture on oak productivity. In  
 447 the special case where we have the same average size for both sub-populations ( $\bar{r}_{G,1} = \bar{r}_{G,2}$ ), a  
 448 random distribution of oaks and no spatial interaction between oak and pine ( $K_{1,1} = K_{1,2} = \pi 10^2$ ),  
 449 this condition corresponds to equality between intra-specific competition and inter-specific

450 competition ( $\lambda_{1,1} = \lambda_{1,2}$ ). The same result would have been achieved for pine if the parameter  
451  $\lambda_{2,1}$  had been different from zero when the individual model was fitted (section 2.2). This  
452 finding is consistent with a known theoretical result: for two species *A* and *B* growing in a  
453 mixture, if the effect of *A* on *B* is the same as that of *B* on *B* and if the effect of *B* on *A* is the  
454 same as that of *A* on *A*, then the productivity of a species in a mixture is the product of its  
455 proportion by its productivity in a pure stand (Harper 1977). In this case, the relationships  
456 between the productivity of species and the mixing proportion are straight lines (left side of  
457 Figure 1). However, our results also show that spatial structure and average size of sub-  
458 populations play a role in the conditions leading to over-yielding. This complements the  
459 results obtained from the Lotka-Volterra theoretical model of inter-specific competition  
460 (Loreau 2004). This means that, in the case of our two-species mixed forest, the condition  
461 "intra-specific competition greater than inter-specific competition" is not sufficient to ensure  
462 over-yielding.

## 463 **5 Conclusion**

464 Our results show that mixture has a positive effect on the productivity of oak-pine stands  
465 and that transgressive over-yielding can occur in these stands. These findings indicate good  
466 complementarity between these two species. Our modelling-based approach allowed us to  
467 express the optimum mixing proportion as a function of stand characteristics and parameters  
468 from a distance-dependent individual-based model. We showed that, for a given set of  
469 dendrometric characteristics, the optimum mixing proportion depends mainly on parameters  
470 involving the oak species, and especially those concerning its intra-specific competition.  
471 However, the mathematical equation for the optimum mixing proportion indicated that an  
472 intra-specific competition higher than inter-specific competition was not a sufficient condition  
473 to ensure over-yielding. We also showed how to use results obtained at the individual level to

474 obtain results on the behaviour of the whole system. As part of the issue on productivity in  
475 mixed forests, this kind of approach can help us to better understand the link between  
476 productivity, stand characteristics and growth parameters of species.

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589

590 **Tables**

591

592 Table 1. Dendrometric characteristics of the plots.  $S$  = plot area;  $\bar{r}_{G,1}$  = quadratic mean radius for oak;  $\bar{r}_{G,2}$  =  
 593 quadratic mean radius for pine;  $\bar{r}_1$  = mean radius for oak;  $\bar{r}_2$  = mean radius for pine; (sd) = standart deviation;  $N_1$   
 594 = number of oaks per hectare;  $N_2$  = number of pines per hectare;  $G_1$  = oak basal area per hectare;  $G_2$  = pine basal  
 595 area per hectare.

<b>Plot</b>	<b>S (ha)</b>	$\bar{r}_{G,1}$ (cm)	$\bar{r}_{G,2}$ (cm)	$\bar{r}_1$ (sd) (cm)	$\bar{r}_2$ (sd) (cm)	$N_1$ (trees.ha <sup>-1</sup> )	$N_2$ (trees.ha <sup>-1</sup> )	$G_1$ (m <sup>2</sup> .ha <sup>-1</sup> )	$G_2$ (m <sup>2</sup> .ha <sup>-1</sup> )
D02	0.951	11.1	17.7	10.0 (4.9)	17.3 (3.5)	354.3	96.7	13.8	9.5
D108	0.800	8.5	16.9	8.0 (3.0)	16.7 (2.6)	353.8	231.3	8.1	20.8
D20	1.015	8.1	16.2	7.5 (3.0)	15.9 (3.1)	481.7	162.5	9.9	13.4
D27	0.625	8.2	17.7	7.3 (3.6)	17.3 (3.8)	396.8	128.0	8.3	12.6
D42	0.500	8.2	12.5	7.7 (2.8)	12.0 (3.5)	472.0	280.0	9.8	13.6
D49	0.994	8.7	15.2	8.0 (3.5)	14.8 (3.1)	493.0	237.4	11.8	17.2
D534	0.500	8.2	18.1	7.6 (3.0)	17.9 (3.1)	488.0	170.0	10.2	17.6
D563	0.500	12.3	16.2	11.4 (4.6)	16.1 (2.2)	242.0	212.0	11.4	17.4
D78	0.700	9.7	20.9	9.1 (3.2)	20.5 (4.1)	407.1	112.9	12.0	15.6

596

597 Table 2. Parameter estimates for the distance-dependent individual-based model (equations 1 and 2).

Plot	Oak				Pine		
	$\alpha_{k,1}$ (mm)	$\beta_{k,1}$ (mm.cm <sup>-1</sup> )	$\lambda_{1,1}$ (mm)	$\lambda_{1,2}$ (mm)	$\alpha_2$ (mm)	$\beta_{k,2}$ (mm.cm <sup>-1</sup> )	$\lambda_{2,2}$ (mm.cm <sup>-2</sup> )
D02	5.99	0.1026	-0.354	-0.242	4.60	0.0566	-0.000361
D108	12.08	0.0896	-0.354	-0.242	4.60	0.0620	-0.000361
D20	12.45	0.0427	-0.354	-0.242	4.60	0.0633	-0.000361
D27	12.73	0.0361	-0.354	-0.242	4.60	0.0512	-0.000361
D42	9.62	0.1633	-0.354	-0.242	4.60	0.0813	-0.000361
D49	13.01	0.0600	-0.354	-0.242	4.60	0.0511	-0.000361
D534	7.73	0.1357	-0.354	-0.242	4.60	0.0476	-0.000361
D563	6.00	0.1066	-0.354	-0.242	4.60	0.0491	-0.000361
D78	4.00	0.1766	-0.354	-0.242	4.60	0.0337	-0.000361

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600

601 Table 3. Values of the Ripley's function for oak ( $K_{1,1}$ ) and for pine ( $K_{2,2}$ ), and values of the inter-type function  
602 ( $K_{1,2}$ ) at a distance of 10 m in each plot. The 99% confidence limits under the null hypothesis are also given  
603 (upper and lower bounds). For the Ripley's function, the null hypothesis corresponds to complete spatial  
604 randomness. For the inter-type function, the null hypothesis corresponds to population independence.

$K$ (m <sup>2</sup> )		Plot								
		D02	D108	D20	D27	D42	D49	D534	D563	D78
$K_{1,1}$	Observed	349.4	330.8	350.7	346.0	346.0	328.4	312.9	304.9	333.8
	Upper	338.4	337.4	327.4	338.1	336.8	328.9	336.1	359.3	336.3
	Lower	293.1	293.5	298.6	293.5	293.8	300.4	293.6	277.3	292.3
$K_{2,2}$	Observed	444.3	321.4	404.0	504.8	323.3	381.5	364.9	321.0	378.2
	Upper	392.2	349.5	356.2	389.5	352.9	349.3	386.7	364.7	391.7
	Lower	245.0	283.6	277.0	250.8	280.9	287.7	259.6	269.7	248.9
$K_{1,2}$	Observed	281.9	294.3	291.1	308.0	316.2	311.7	343.9	308.8	304.7
	Upper	376.4	342.4	349.9	449.2	341.1	331.0	342.2	339.1	365.1
	Lower	255.7	289.3	275.3	206.9	291.8	287.6	286.7	296.1	278.8

605

606 Table 4. Optimum mixing proportion ( $x_{max}$ ) and observed mixing proportion ( $x_{plot}$ ) for each plot;  $\Delta G(x_{max}) =$   
 607 stand basal area increment for  $x = x_{max}$ ;  $\Delta G(x_{plot}) =$  stand basal area increment for  $x = x_{plot}$ ; Gain = relative  
 608 difference between  $\Delta G(x_{max})$  and  $\Delta G(x_{plot})$ .

Plot	$x_{max}$ (%)	$\Delta G(x_{max})$ (m <sup>2</sup> /ha/an)	$x_{plot}$ (%)	$\Delta G(x_{plot})$ (m <sup>2</sup> /ha/an)	Gain (%)
D02	59.3	0.477	59.2	0.477	0.00
D108	43.1	0.591	28.0	0.561	4.91
D20	37.5	0.555	42.6	0.552	0.61
D27	46.5	0.295	39.8	0.292	0.96
D42	45.7	0.374	41.9	0.373	0.21
D49	46.2	0.647	40.8	0.642	0.64
D534	40.8	0.291	36.7	0.290	0.40
D563	73.6	0.320	39.6	0.291	9.05
D78	57.3	0.401	43.6	0.387	3.41

609



610 **Figure captions**

611

612 Figure 1. The three main types of productivity response for a mixed stand composed of two species A and B  
613 according to the mixing proportion (adapted from Harper, 1977). Total density is assumed to be constant for the  
614 different mixing proportions. On the left, mixture has no effect on stand productivity: productivity of mixed  
615 stands is equivalent to the juxtaposition of pure stands. In the middle, mixture has a negative effect on stand  
616 productivity: productivity of mixed stands is lower than the productivity expected in juxtaposed pure stands. On  
617 the right, mixture has a positive effect on stand productivity: productivity of mixed stands is higher than the  
618 productivity expected in juxtaposed pure stands.

619

620 Figure 2. Comparison between the distance-dependent individual-based model and the stand model for oak (a)  
621 and pine (b) and for the 9 plots. Basal Area Increment = stand basal area increment predicted by the models over  
622 the 2000-2005 period. Individual model: distance-dependent individual-based model (equations 1 and 2). Stand  
623 model: stand model obtained by aggregation of the individual model (equation 7).

624

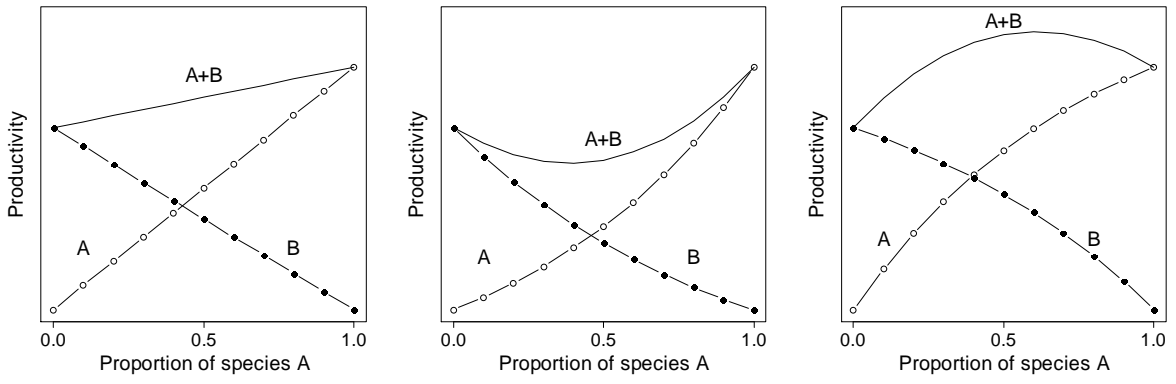
625 Figure 3. Stand productivity according to the mixing proportion for the 9 plots and for each species. The solid  
626 curve represents total stand productivity. The curve with black dots represents pine productivity. The curve with  
627 white dots represents oak productivity. The dashed vertical line represents the mixing proportion observed in the  
628 plot ( $x_{plot}$ ). The solid vertical line represents the optimum mixing proportion ( $x_{max}$ ).

629

630 Figure 4. Elasticities of  $x_{max}$  to the 10 parameters of the stand model for each plot. The bars show the absolute  
631 values of the elasticities, the sign of the elasticities being written on top of each bar.

632

633 **Figures**

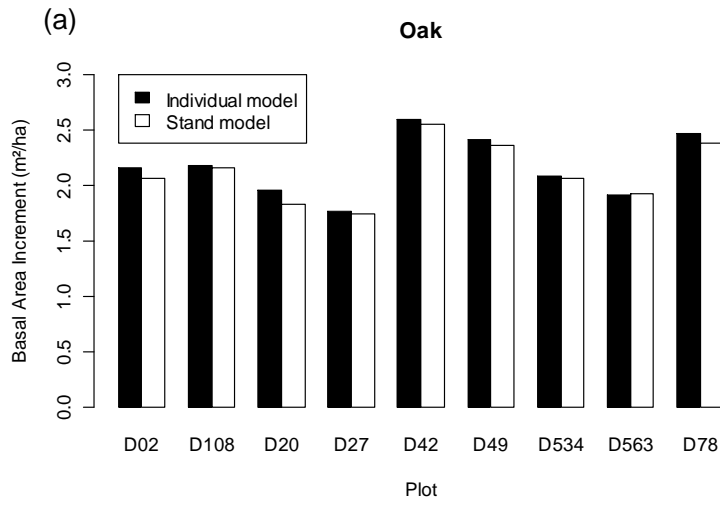


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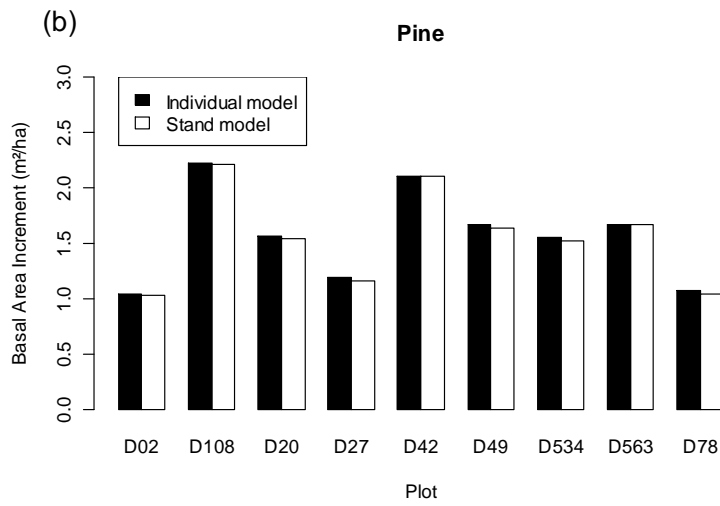
Figure 1

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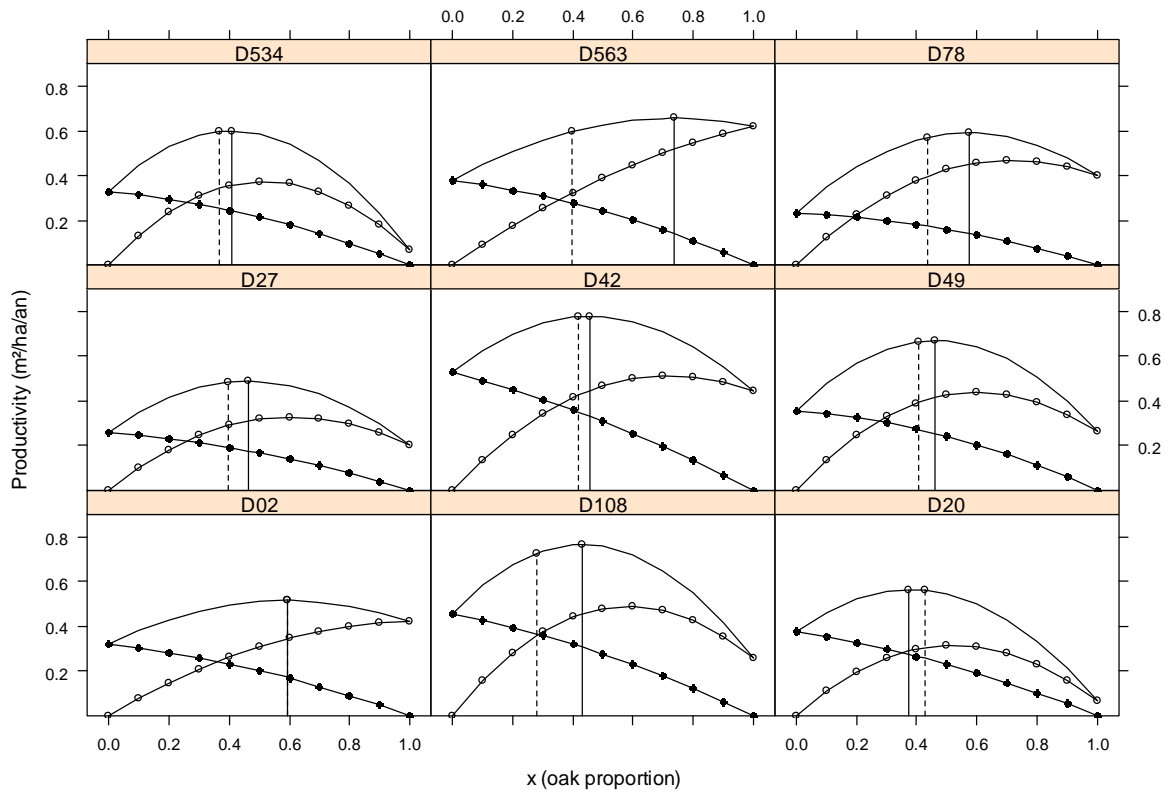
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Figure 2

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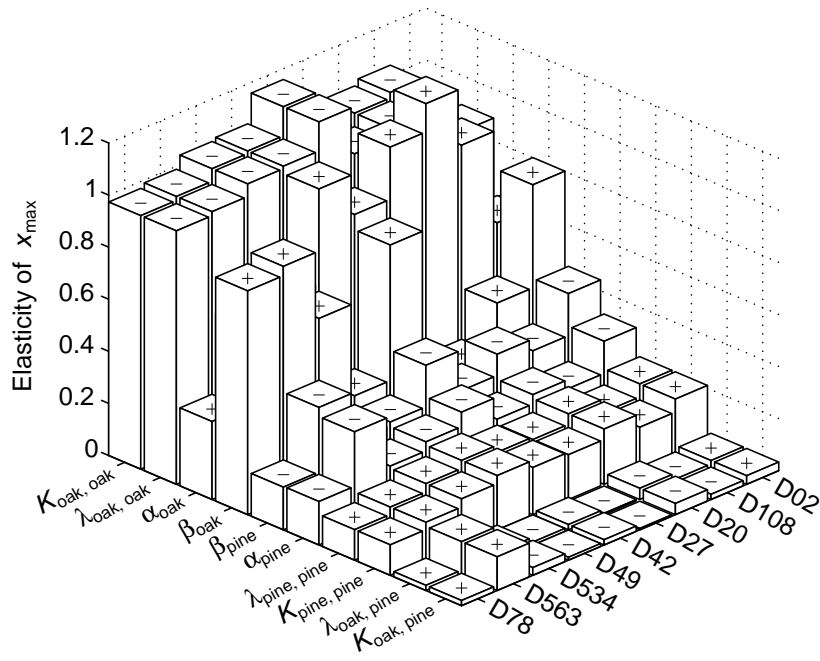
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Figure 3

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Figure 4

## 653 Appendix

### 654 Aggregating the distance-independent individual-based model

655 Given a distance-independent individual-based model:

$$656 \quad \Delta r_{i,j} = \gamma_j + \beta_j \text{girth}_{i,j} \quad (11)$$

657 where  $\Delta r_{i,j}$  is the radial increment of a tree  $i$  belonging to a species  $j$  between time  $t$  and  
658 time  $t+\Delta t$ ,  $\text{girth}_{i,j}$  is the girth at time  $t$  for a tree  $i$ . Starting from equation 11, we can develop a  
659 stand model for species  $j$  using an aggregation approach. The stand can be defined with three  
660 aggregated variables for each species: the number of trees  $N_j$ , the mean radius  $\bar{r}_j$  and the basal  
661 area  $G_j$ . The dynamic equations of these variables must be defined using equation 11. Since  
662 we assume that there is neither mortality nor recruitment between  $t$  and  $t+\Delta t$ , we have  
663  $\Delta N_j = 0$ . The mean radius is defined as follows:

$$664 \quad \bar{r}_j(t) = \frac{1}{N_j} \sum_{i=1}^{N_j} r_{i,j}$$

665 where  $\bar{r}_j(t)$  is the mean radius at time  $t$ . The mean radius increment can thus be written as  
666 a function of the individual radial increments:

$$667 \quad \Delta \bar{r}_j = \bar{r}_j(t + \Delta t) - \bar{r}_j(t) = \frac{1}{N_j} \sum_{i=1}^{N_j} r_{i,j}(t + \Delta t) - \frac{1}{N_j} \sum_{i=1}^{N_j} r_{i,j}(t) = \frac{1}{N_j} \sum_{i=1}^{N_j} \Delta r_{i,j}$$

668 It follows from equation 11 that:

$$669 \quad \sum_{i=1}^{N_j} \Delta r_{i,j} = \gamma_j N_j + 2\pi\beta_j N_j \bar{r}_j$$

670 And the mean radius increment is given by:

$$671 \quad \Delta \bar{r}_j = \gamma_j + 2\pi\beta_j \bar{r}_j$$

672 Similarly,  $\Delta G_j$  can be written as a function of the individual basal area increments ( $\Delta g_{i,j}$ ):

$$673 \quad \Delta G_j = G(t + \Delta t) - G(t) = \sum_{i=1}^{i=N_j} g_{i,j}(t + \Delta t) - \sum_{i=1}^{i=N_j} g_{i,j}(t) = \sum_{i=1}^{i=N_j} \Delta g_{i,j}$$

674 where  $g_{i,j}$  is the basal area of a tree  $i$  and  $\Delta g_{i,j} = g_{i,j}(t + \Delta t) - g_{i,j}(t)$ . Since  $g_{i,j}(t) = \pi(r_{i,j}(t))^2$

675 we can write  $g_{i,j}(t + \Delta t)$  as a function of  $r_{i,j}(t)$ ,  $r_{i,j}(t + \Delta t)$  and  $\Delta r_{i,j}$ :

$$676 \quad g_{i,j}(t + \Delta t) = \pi(r_{i,j}(t + \Delta t))^2 = \pi(r_{i,j}(t) + \Delta r_{i,j})^2 = \pi\left((r_{i,j}(t))^2 + 2r_{i,j}(t)\Delta r_{i,j} + (\Delta r_{i,j})^2\right)$$

677 Therefore:

$$678 \quad \Delta g_{i,j} = 2\pi r_{i,j}(t)\Delta r_{i,j} + \pi(\Delta r_{i,j})^2$$

679 It follows from equation 11 that:

$$680 \quad r_{i,j}(t)\Delta r_{i,j} = \gamma_j r_{i,j}(t) + \beta_j 2\pi(r_{i,j}(t))^2 = \gamma_j r_{i,j}(t) + \beta_j 2g_{i,j}(t)$$

681 and

$$682 \quad (\Delta r_{i,j})^2 = \gamma_j^2 + \gamma_j \beta_j 4\pi r_{i,j}(t) + \beta_j^2 4\pi^2 (r_{i,j}(t))^2 = \gamma_j^2 + \gamma_j \beta_j 4\pi r_{i,j}(t) + \beta_j^2 4\pi g_{i,j}(t)$$

683 We can now express the individual basal area increment as a function of  $r_{i,j}(t)$ ,  $g_{i,j}(t)$  and

684 the parameters of equation 11:

$$685 \quad \Delta g_{i,j} = \pi\gamma_j^2 + 2\pi\gamma_j(1 + 2\pi\beta_j)r_{i,j}(t) + 4\pi\beta_j(1 + \pi\beta_j)g_{i,j}(t)$$

686 Since  $\sum_{i=1}^{N_j} 1 = N_j$ ,  $\sum_{i=1}^{N_j} r_{i,j} = N_j \bar{r}_j(t)$  and  $\sum_{i=1}^{N_j} g_{i,j} = G_j(t)$ , we can sum the individual basal area

687 increments to obtain the stand basal area increment:

$$688 \quad \Delta G_j = \pi\gamma_j^2 N_j + 2\pi\gamma_j(1 + 2\pi\beta_j)N_j \bar{r}_j + 4\pi\beta_j(1 + \pi\beta_j)G_j$$

689 Therefore, the system of equations for the stand model is:

$$690 \quad \begin{cases} \Delta G_j = \pi\gamma_j^2 N_j + 2\pi\gamma_j(1 + 2\pi\beta_j)N_j \bar{r}_j + 4\pi\beta_j(1 + \pi\beta_j)G_j \\ \Delta \bar{r}_j = \gamma_j + 2\pi\beta_j \bar{r}_j \\ \Delta N_j = 0 \end{cases}$$

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695 **Optimum mixing proportion**

696 Since  $\Delta G'(x)$  is a polynomial equation of the second degree, its roots are:

697 
$$x_1 = \frac{-b - \sqrt{b^2 - 4ac}}{2a} \text{ and } x_2 = \frac{-b + \sqrt{b^2 - 4ac}}{2a}$$

698 The table below shows that for the nine plots,  $a$  is always positive so the function  $\Delta G'(x)$  is

699 convex. It is negative between  $x_1$  and  $x_2$  and positive for  $x < x_1$  et  $x > x_2$ .  $x_1$  is thus a maximum

700 for the function  $\Delta G(x)$ .

701 Coefficients and roots of  $\Delta G'(x)$  for the 9 plots.

Plot	$a$	$b$	$c$	$x_1$	$x_2$
D02	1493	-64785	37871	0.593	43
D108	14688	-168693	69966	0.431	11
D20	15403	-172769	62590	0.375	11
D27	6466	-83284	37311	0.465	12
D42	5225	-74980	33143	0.457	14
D49	13152	-185208	82799	0.462	14
D534	9357	-102027	40109	0.408	10
D563	268	-31239	22837	0.736	116
D78	5457	-95660	52986	0.573	17

702