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1 Asymmetric competition, ontogenetic growth and size inequality  
2 drive the difference in productivity between two-strata and  
3 one-stratum forest stands

4 Thomas Cordonnier<sup>a,\*</sup>, Charline Smadi<sup>b,c</sup>, Georges Kunstler<sup>a</sup>, Benoît Courbaud<sup>a</sup>

5 <sup>a</sup>*Univ. Grenoble Alpes, Irstea, LESSEM, 38000 Grenoble, France.*

6 <sup>b</sup>*Irstea, UR LISC, Laboratoire d'Ingénierie pour les Systèmes Complexes, 9 avenue Blaise Pascal-CS*  
7 *20085, 63178 Aubière, France.*

8 <sup>c</sup>*Complex Systems Institute of Paris Ile-de-France, 113 rue Nationale, Paris, France.*

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9 **Abstract**

Size inequality has been considered a key feature of plant population structure with impacts on ecosystem functions. In forest ecosystems, studies examining the relationship between tree size inequality and stand productivity have produced mixed outcomes. These studies found positive, neutral or negative relationships and discussed how this could be influenced by competition for light between trees (e.g. light interception efficiency), but far less attention has been paid to the role played by tree ontogenetic growth. In this article, we present a simple mathematical model that predicts the basal area growth of a two-strata stand as a function of tree basal areas and asymmetric competition. Comparing the growth of this stand to the growth of a spatially homogeneous one-stratum stand and a spatially heterogeneous one-stratum stand, we show that higher growth of the two-strata stand is achieved for concave shape, increasing functions of ontogenetic growth and for low intensities of absolute size-asymmetric competition. We also demonstrate that the difference in growth between the two-strata stand and the one-stratum stands depends on tree size inequality, mean tree basal area and total basal area in the two-strata stand. We finally found that the relationships between tree size inequality and productivity can vary from positive to negative and even non-

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\*Corresponding author

*Email addresses:* [thomas.cordonnier@irstea.fr](mailto:thomas.cordonnier@irstea.fr) (Thomas Cordonnier),  
[charline.smadi@irstea.fr](mailto:charline.smadi@irstea.fr) (Charline Smadi), [georges.kunstler@irstea.fr](mailto:georges.kunstler@irstea.fr) (Georges Kunstler),  
[benoit.courbaud@irstea.fr](mailto:benoit.courbaud@irstea.fr) (Benoît Courbaud)

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monotonous. However, we highlight that negative relationships may be more frequent. As a conclusion, our results indicate that ontogenetic growth can have a major impact on the form and the magnitude of the size inequality-productivity relationship.

10 *Keywords:* forest structure, tree basal area increment, theoretical model, competition,  
11 stand productivity

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## 12 **1. Introduction**

13 Understanding how structural complexity influences ecosystems' dynamics and func-  
14 tioning is a central ecological question because human activities tend to homogenise  
15 natural systems (e.g. Messier et al., 2015). With the biodiversity crisis, this topic has  
16 been mainly explored from the point of view of species diversity loss (Cardinale et al.,  
17 2012) but other aspects of structural complexity can also be crucial. For instance in  
18 forests, size inequality (i.e. a measure of size differentiation or size hierarchy between  
19 trees in a stand) has been considered a key component of structural complexity with  
20 impacts on forest dynamics (Courbaud et al., 2015), ecosystem processes (Forrester and  
21 Bausch, 2016) and associated biodiversity (McElhinny et al., 2005). Because of this,  
22 several forest management systems such as gap-based management (Kern et al., 2017)  
23 or nature-based management (Brang et al., 2014) have been developed with the goal of  
24 fostering size inequality. Since productivity is an essential feature of forest functioning  
25 and a major driver of forest management planning (Villa et al., 2013; Bontemps and  
26 Bouriaud, 2014), the effect of size inequality on productivity (in basal area, volume or  
27 biomass) has received increased interest in the last few decades.

28 Studies examining the relationship between size inequality and productivity (stand  
29 growth in terms of basal area, volume or biomass) have produced contradictory results.  
30 On the one hand some studies using field observations, experiments or individual-based  
31 models reported negative or neutral relationships between size inequality (measured  
32 with various indices such as the Gini index, the coefficient of variation or the Shannon

33 entropy index) and stand productivity (Liang et al., 2007; Bourdier et al., 2016; Ryan  
34 et al., 2010; Long and Shaw, 2010; Soares et al., 2016; Bohn and Huth, 2017). On the  
35 other hand, other studies found positive relationships in mixed stands (Danescu et al.,  
36 2016; Silva Pedro et al., 2017). A striking example of these contradictions is the recent  
37 study of Zeller et al. (2018) based on national forest inventory plots, which showed  
38 a negative size inequality effect in Germany but a positive effect in the USA. Such  
39 contradictory results can be explained by the fact that studies present several major  
40 differences concerning the ecological context considered, the surface of the plots, the  
41 temporal scale, the size inequality index selected and the factors controlled for stand  
42 structure. Moreover, correlations between size inequality and other stand attributes,  
43 such as stand development stage, density and species richness, can be difficult to control  
44 in observational studies. If we want to progress on this question and make sense of these  
45 contradictory results we need to build theoretical predictions about the variables and  
46 mechanisms influencing the effects of size inequality on productivity.

47 Competition is one of the key processes influencing productivity in plant populations  
48 and communities (Connell, 1983). Size inequality has been related to size-asymmetric  
49 competition (Damgaard and Weiner, 2000; Cordonnier and Kunstler, 2015), a type of  
50 competitive interaction where large plants have a disproportionate competitive advan-  
51 tage over small plants (Weiner, 1990). Competition for light is presented as a classic  
52 mechanism leading to size-asymmetric competition (Schwinning and Weiner, 1998). Dis-  
53 cussions on the effect of size inequality on productivity have thus focused on mechanisms  
54 related to competition for light (e.g. Bourdier et al., 2016; Binkley et al., 2010). In ad-  
55 dition to competition, ontogenetic growth, i.e. the change of growth with tree age or  
56 tree size (West et al., 2001), might be crucial but has received far less attention. For  
57 instance, a recent study on plants has stressed the need to control for the ontogenetic  
58 growth function in order to avoid misinterpretations about the effect of asymmetric com-  
59 petition on the evolution of population size inequality (Rasmussen and Weiner, 2017).

60 In forest ecosystems, absolute tree growth generally increases with size (Stephenson et  
61 al., 2014), but other forms (e.g. skewed unimodal) have been reported (e.g. Wykoff,  
62 1990). These ontogenetic changes in growth are likely to influence the effect of size  
63 inequality on productivity depending on the shape of the ontogenetic growth function  
64 and the mean size of the stand. Because of the lack of theoretical developments we  
65 have no expectations about the relative role of competition and the ontogenetic ef-  
66 fect on size inequality-productivity relationships. Although highly useful to investigate  
67 size-inequality relationships through a dynamic perspective, the few existing simulation  
68 studies (Silva Pedro et al., 2017; Bohn and Huth, 2017; Bourdier et al., 2016) use complex  
69 individual-based models in which disentangling the effects of competition and ontogeny  
70 is difficult.

71 In this article, we present a simple mathematical model that predicts the basal  
72 area growth of a two-strata stand. This model takes into account the competition  
73 between trees of the same stratum and between trees of different strata to represent  
74 different intensities of size-asymmetric competition of the upper stratum and types of  
75 size-asymmetric competition of the lower stratum: absolute (trees in the lower stratum  
76 have no influence on trees in the upper stratum), partial (trees in the lower stratum have  
77 less influence on trees in the upper stratum than on trees in the lower stratum) and rel-  
78 ative (trees in the lower stratum have the same influence on all trees). In addition, the  
79 model explores various shapes of the ontogenetic growth function, while controlling for  
80 the mean tree basal area and the stand basal area. Using this model, we compared the  
81 basal area growth of a two-strata stand with a spatially homogeneous one-stratum stand.  
82 We also compared the basal area growth of the two-strata stand to the growth of a spa-  
83 tially heterogeneous one-stratum stand, which allowed us to remove the direct effect of  
84 ontogenetic growth on the size inequality-productivity relationship. Our objective was  
85 twofold: first to analyse the conditions that lead to higher productivity of the two-strata  
86 stand compared to one-stratum stands and second to identify parameter combinations

87 leading to different relationships between size inequality and productivity. Our main  
 88 hypothesis was that both ontogenetic growth and size-asymmetric competition have a  
 89 major influence on the qualitative and quantitative behaviours of our system.

## 90 2. The model

### 91 2.1. Stand with two strata (2-strata)

92 Let us consider a stand with two main strata ( $u$ : upper,  $l$ : lower). In a given stratum  
 93 all trees share the same size, here individual basal area ( $g_u$ : upper,  $g_l$ : lower; in  $m^2$ ). We  
 94 chose basal area as most empirical studies used this variable to deal with size growth at  
 95 the individual scale. The following formulation can also work with other metrics such as  
 96 tree diameter, tree volume or tree biomass. Here we need to specify how stand basal area  
 97 or tree density is distributed between the two strata. Based on the frequent observation  
 98 of J-shaped size distributions in natural forests, we consider the specific case where each  
 99 stratum has the same basal area per hectare  $G$  ( $G > 0$ ;  $m^2ha^{-1}$ ) and thus different  
 100 number of trees per hectare ( $N_u$  and  $N_l$ ). We then define the annual basal area growth  
 101  $\Delta g_l$  ( $m^2ha^{-1}year^{-1}$ ) of a tree in the lower stratum as follows:

$$\Delta g_l = ag_l^b e^{-c g_l} * e^{-\alpha(N_l-1)g_l} * e^{-\beta G} \approx ag_l^b e^{-c g_l} * e^{-(\alpha+\beta)G},$$

102 where  $a, b, c, \lambda, \beta$  are positive parameters. The first term,  $ag_l^b e^{-c g_l}$ , defines the ontoge-  
 103 netic effect on basal area growth of a tree without competition. This term depends on  
 104 the size of the tree, here its basal area. The selected function defines a wide range of  
 105 diameter growth patterns (positive concave, positive convex, skewed unimodal; Fig. 1)  
 106 and has been used in several forest modelling studies (e.g. Wykoff, 1990; Pokharel and  
 107 Dech, 2012; Cordonnier and Kunstler, 2015). The second term represents the reduction  
 108 of growth due to the competition by trees of the same stratum ( $e^{-\alpha G}$ ) and by trees of  
 109 the upper stratum ( $e^{-\beta G}$ ), respectively. The approximation  $e^{\alpha g_l} \approx 1$  is applied because

110  $\alpha g_l$  is assumed to be small. In forest modelling studies, it is usually assumed that  $\beta \geq \alpha$ ,  
 111 i.e. that a dominant tree has a higher effect than a dominated tree on a dominated tree.  
 112 This is related to the intensity of size-asymmetric competition. Here, we also assume  
 113 that  $\beta$  does not change with tree size inequality between the two strata. However,  $\beta$   
 114 should converge towards  $\alpha$  when the relative tree size difference between the two strata  
 115 tends to 1 (Fig. 2). To avoid misinterpretations, we will consider theoretical stands with  
 116 substantial relative tree size difference between the two strata (limiting our analysis to  
 117  $g_u/g_l \geq 2$ ).

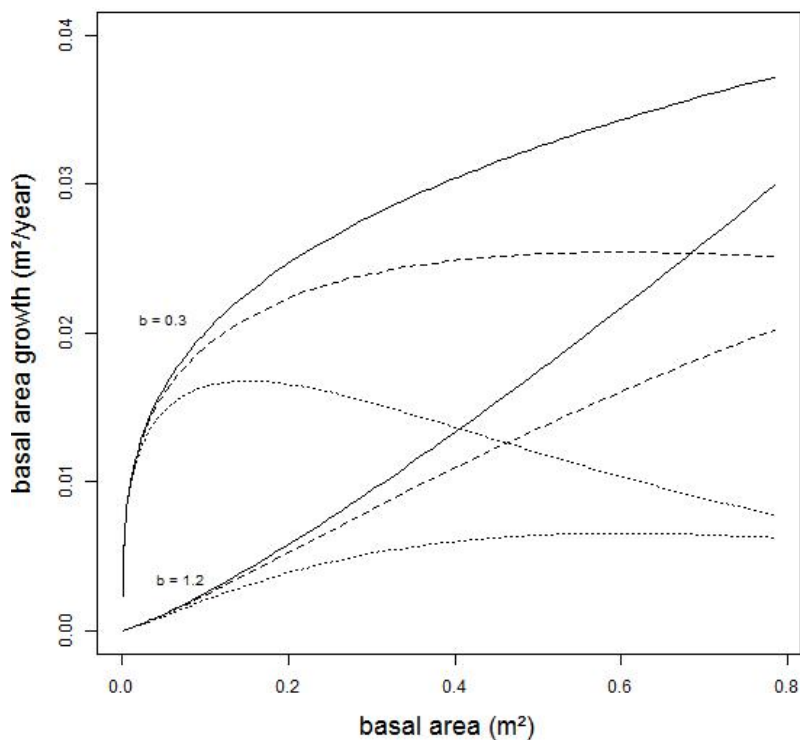


Figure 1: Basal area growth as a function of tree basal area for different values of parameters for the growth function  $\Delta g = ag^b e^{-cg}$ . Solid line:  $c = 0$ , dashed line:  $c = 0.5$ , dotted line:  $c = 2$ .

118 Following the same reasoning, we can define the basal area growth of a tree belonging  
 119 to the upper stratum:

$$\Delta g_u = a g_u^b e^{-c g_u} * e^{-(\alpha+\gamma)G},$$

120 with  $0 \leq \gamma \leq \alpha$ , which means that a tree belonging to the lower stratum has an equal  
 121 or lower effect on a tree in the upper stratum than on a tree in the same stratum. The  
 122 term  $e^{-\gamma G}$  represents the competitive effect of the lower stratum on trees in the upper  
 123 stratum. This is related to the type of size-asymmetric competition. We assume here  
 124 that the intra-stratum competition effect of a tree (parameter  $\alpha$ ) is the same for the two  
 125 strata. Summing all trees and the two strata, we obtain the total basal area growth of  
 126 the stand ( $m^2 ha^{-1} year^{-1}$ ):

$$\Delta G_1 = G \left( \frac{\Delta g_l}{g_l} + \frac{\Delta g_u}{g_u} \right) = G \left[ g_l^{b-1} e^{-c g_l} e^{-(\alpha+\beta)G} + g_u^{b-1} e^{-c g_u} e^{-(\alpha+\gamma)G} \right].$$

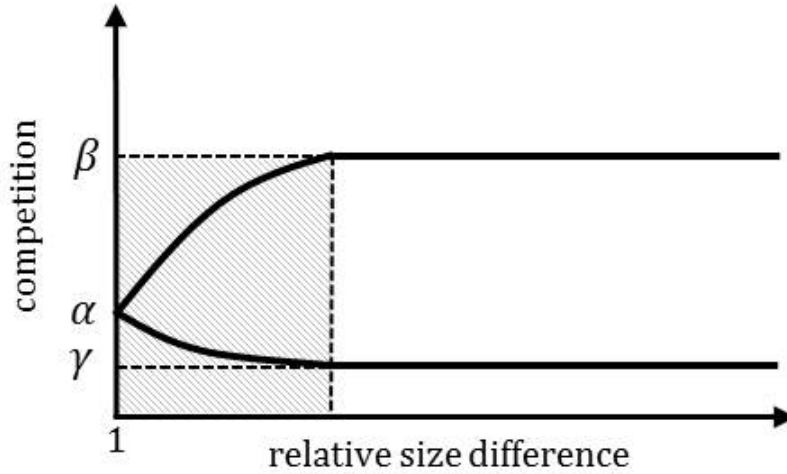


Figure 2: Theoretical relationships between competition parameters and the relative size difference between the two strata. Our model for the 2-strata stand, which assumes constant values for competition parameters, cannot be interpreted for low relative size differences.



127 *2.2. One-stratum (1-stratum) stands*

128 Let us now define a stand with only one spatially homogeneous stratum. This stand  
 129 has the same basal area  $2G$  and the same mean tree basal area  $g$  as the 2-strata stand  
 130 (Fig. 3). The mean tree basal area  $g$  of the trees thus equals:

$$g = \frac{2g_l g_u}{g_l + g_u}.$$

131 For this spatially homogeneous 1-stratum stand, the basal area growth is defined as:

$$\Delta G_2 = 2G \frac{\Delta g}{g} = 2G g^{b-1} e^{-cg} e^{-\alpha 2G}.$$

132 We also define a stand characterised by two spatially segregated strata of half an  
 133 hectare each and with basal area per hectare  $2G$  (Fig. 3): the first stratum contains trees  
 134 with size  $g_l$  and the other stratum trees with size  $g_u$ . For this spatially heterogeneous  
 135 1-stratum stand, the basal area growth equals:

$$\Delta G_3 = \frac{1}{2} 2G \left( \frac{\Delta g_l}{g_l} + \frac{\Delta g_u}{g_u} \right) = G [a g_l^{b-1} e^{-c g_l} e^{-\alpha 2G} + a g_u^{b-1} e^{-c g_u} e^{-\alpha 2G}].$$

136 These two stands reflect two different situations. For the first stand, we compare a  
 137 2-strata stand with a perfectly homogeneous 1-stratum stand with trees of intermediate  
 138 size, which is usually what people investigate when they analyse the effect of tree size  
 139 inequality on productivity. For the second stand, we compare a 2-strata stand with  
 140 equivalent but spatially segregated strata. This spatially heterogeneous 1-stratum stand  
 141 and the 2-strata stand have the same size inequality. By comparing the results obtained  
 142 for these two 1-stratum stands we can assess the direct effect of the ontogenetic growth  
 143 on the 2-strata stand productivity.

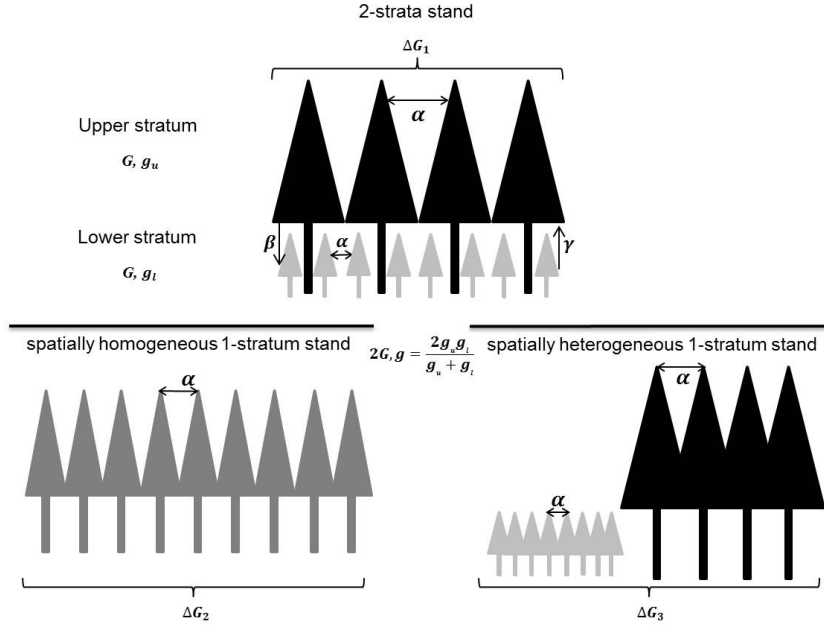


Figure 3: Comparison of the basal area growth of the 2-strata stand with two 1-stratum stands: a spatially homogeneous 1-stratum stand and a spatially heterogeneous 1-stratum stand. The 2-strata stand and the two 1-stratum stands have the same total basal area per hectare  $2G$  and the same quadratic mean diameter  $g$ , two key parameters of productivity (stocking and development stage). Parameters  $\alpha, \beta, \gamma$  characterise competitive interactions between trees of the same stratum or between trees of the two strata.  $\beta' = \beta - \alpha$  represents the intensity of size-asymmetric competition of the upper stratum.  $\gamma' = \alpha - \gamma$  represents the type of size-asymmetric competition of the lower stratum.  $\gamma' = \alpha$ : absolute size-asymmetric competition;  $0 < \gamma' < \alpha$ : partial size-asymmetric competition;  $\gamma' = 0$ : relative size-asymmetric competition.

### 144 2.3. Comparing the 2-strata stand with 1-stratum stands

145 The objective is now to compare the basal area growth of the 2-strata stand with  
 146 the two 1-stratum stands. One way consists in calculating the ratio of their basal area  
 147 growths (which are assumed to be strictly positive), which gives respectively:

$$\frac{\Delta G_1}{\Delta G_2} = \frac{1}{2} \left[ \left( \frac{g_l}{g} \right)^{b-1} e^{-c(g_l-g)} e^{-(\beta-\alpha)G} + \left( \frac{g_u}{g} \right)^{b-1} e^{-c(g_u-g)} e^{-(\gamma-\alpha)G} \right],$$

$$\frac{\Delta G_1}{\Delta G_3} = \frac{g_l^{b-1} e^{-c g_l} e^{-(\beta-\alpha)G} + g_u^{b-1} e^{-c g_u} e^{-(\gamma-\alpha)G}}{g_l^{b-1} e^{-c g_l} + g_u^{b-1} e^{-c g_u}}.$$

148 When these ratios are strictly greater than 1, the 2-strata stand has higher growth  
 149 than the 1-stratum stands, which leads to the following inequalities:

$$\frac{1}{2} \left[ \left( \frac{g_l}{g} \right)^{b-1} e^{-c(g_l-g)} e^{-\beta'G} + \left( \frac{g_u}{g} \right)^{b-1} e^{-c(g_u-g)} e^{\gamma'G} \right] > 1, \quad (1)$$

$$\frac{g_l^{b-1} e^{-c g_l} e^{-\beta'G} + g_u^{b-1} e^{-c g_u} e^{\gamma'G}}{g_l^{b-1} e^{-c g_l} + g_u^{b-1} e^{-c g_u}} > 1, \quad (2)$$

150 with  $\beta' = \beta - \alpha$  ( $\beta' > 0$ ) and  $\gamma' = \alpha - \gamma$  ( $0 \leq \gamma' \leq \alpha$ ).

151 The parameter  $\beta'$  represents the intensity of size-asymmetric competition of the  
 152 upper stratum. Higher values of  $\beta'$  lead to a greater detrimental effect of dominant  
 153 trees on dominated trees. The parameter  $\gamma'$  represents the type of size-asymmetric  
 154 competition of the lower stratum. When  $\gamma' = \alpha$ , we obtain “absolute size-asymmetric  
 155 competition” (Rasmussen and Weiner, 2017) (also called perfect one-sided competition  
 156 (Kohyama, 1993)). In this case, trees in the lower stratum have no effect on trees in  
 157 the upper stratum. When  $0 < \gamma' < \alpha$ , we obtain “partial size-asymmetric competition”  
 158 (Rasmussen and Weiner, 2017). Here, trees in the lower stratum have less effect on  
 159 dominant trees than on trees in the same stratum. We call the specific case  $\gamma' = 0$   
 160 “relative size-asymmetric competition”. This corresponds to the classic hypothesis that  
 161 a dominated tree has the same competitive effect ( $e^{-\alpha g_l}$ ) on all trees in the stand. It  
 162 is important to note that contrary to the definitions of the type of size-asymmetric  
 163 competition used in previous publications (see Rasmussen and Weiner, 2017) here we  
 164 distinguish between the size-asymmetric competition of the upper and lower strata.

165 In the next sections we investigate under which conditions inequalities (1) and (2) are  
 166 achieved. For each 1-stratum stand, we first study the specific case of size-independent  
 167 growth ( $b = c = 0$ ). Then we analyse the case of positive size-dependent growth ( $b > 0$   
 168 and  $c = 0$ ). Finally, we address the general case ( $c > 0$  and  $b > 0$ ). To represent the  
 169 relative difference in tree sizes between the two strata, we define  $x$  as the ratio of their

170 basal areas:

$$x := \frac{g_u}{g_l}.$$

171 Throughout the article, we will consider  $x \geq 2$  (see explanation above). To charac-  
172 terize size inequality, we use the coefficient of variation of tree basal areas (e.g. Danescu  
173 et al., 2016) in the 2-strata stand. We have:

$$CV = \frac{x - 1}{2\sqrt{x}}.$$

174 For numerical applications, we extracted from the literature values obtained for  $b$  and  
175  $c$  (Pokharel and Dech, 2012; Cordonnier and Kunstler, 2015; Wykoff, 1990; Monserud  
176 and Sterba, 1996; Schröder et al., 2002). We will thus consider  $0.3 \leq b \leq 1.2$  and  
177  $0 \leq c \leq 4$ . For competition parameters we chose arbitrary but realistic values of  $\beta'$  and  
178  $\gamma'$ :  $0.001 \leq \beta' \leq 0.01, 0 \leq \gamma' \leq 0.01$ . In numerical examples we also provide  $CV$  with a  
179 minimum value of 0.35 ( $x = 2$ ).

### 180 3. Results

#### 181 3.1. Size-independent growth ( $b = c = 0$ )

We assume here that basal area growth is independent of tree basal area. In this case the inequalities (1) and (2) are equivalent and become:

$$\frac{g}{g_l} e^{-\beta'G} + \frac{g}{g_u} e^{\gamma'G} > 2.$$

182 As  $\frac{g}{g_l} = \frac{2x}{1+x}$  and  $\frac{g}{g_u} = \frac{2}{1+x}$ , we obtain the following inequality:

$$x \left( e^{-\beta'G} - 1 \right) + e^{\gamma'G} > 1.$$

183 For the sake of readability, let us define the function  $f$  as follows:

$$f(x) = x \left( e^{-\beta'G} - 1 \right) + e^{\gamma'G} - 1.$$

184 We have  $f'(x) < 0$  and  $\lim_{x \rightarrow +\infty} f(x) = -\infty$  ( $f$  is a linear function of  $x$ ). The value  
 185 of the function  $f$  at the minimum value of  $x$  considered (2) is given by:

$$f(2) = 2e^{-\beta'G} + e^{\gamma'G} - 3, \quad (3)$$

186 which is positive when:

$$\gamma' > \frac{\ln(3 - 2e^{-\beta'G})}{G} = \gamma'_0. \quad (4)$$

187 We thus obtain two cases:

- 188 • if  $\gamma' > \gamma'_0$ ,  $f$  is positive and then negative. It crosses 0 at  $x = x_0 = \frac{e^{\gamma'G} - 1}{1 - e^{-\beta'G}}$ ;
- 189 • if  $\gamma' < \gamma'_0$ ,  $f$  is negative and the 2-strata stand is always less productive than the  
 190 1-stratum stands.

191 When  $\gamma' = 0$  (relative size-asymmetric competition) the 2-strata stand cannot have  
 192 higher productivity than the 1-stratum stands. Inequality (4) also leads to the conclusion  
 193 that  $\alpha$  and  $\gamma'$  must be high enough to allow for higher productivity of the 2-strata  
 194 stand. In other words, a higher intensity of size-asymmetric competition ( $\beta'$ ) must be  
 195 compensated by a higher value of intra-stratum competition ( $\alpha$ ) and a reduction of  
 196 the effect of the lower stratum on the upper stratum (higher value of  $\gamma'$ ; highest value  
 197 obtained for absolute size-asymmetric competition). The equations for  $\gamma'_0$  and  $x_0$  also  
 198 indicate that higher values of  $G$  are beneficial to the 2-strata stand ( $\lim_{G \rightarrow +\infty} \gamma'_0 = 0$ ,  
 199  $\lim_{G \rightarrow 0} \gamma'_0 = \beta'$ ,  $x_0$  is an increasing function of  $G$ ). Fig. 4 gives numerical examples.  
 200 Note that we are representing the variation of the growth ratio as a function of  $CV$  and

201 not  $x$  as  $CV$  is the variable the most frequently used in field studies (this will be the  
 202 case for all figures.)

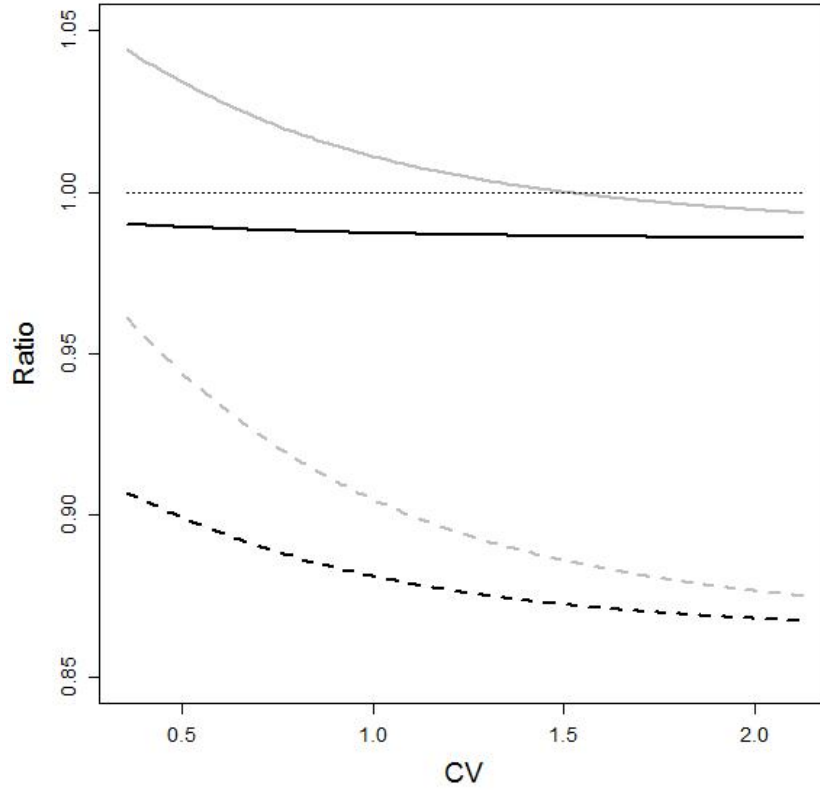


Figure 4: Growth ratio between the 2-strata stand and 1-stratum stands for the size-independent growth model ( $b = c = 0$ ) as a function of the coefficient of variation  $CV$ . Black:  $\gamma' = 0$ , grey:  $\gamma' = 0.01$ , solid line:  $\beta' = 0.001$ , dashed line:  $\beta' = 0.01$ .  $G = 15$ .

203 *3.2. Positive size-growth relationship ( $b > 0, c = 0$ )*

204 *3.2.1. Spatially homogeneous 1-stratum stand*

205 In this case, basal area growth increases monotonically with size and inequality (1)

206 becomes:

$$\left(\frac{g_l}{g}\right)^{b-1} e^{-\beta'G} + \left(\frac{g_u}{g}\right)^{b-1} e^{\gamma'G} > 2. \quad (5)$$

This inequality can be written:

$$g(x) = (2x)^{1-b}e^{-\beta'G} + 2^{1-b}e^{\gamma'G} - 2(1+x)^{1-b} > 0.$$

207 For  $b < 1$  we have  $\lim_{x \rightarrow +\infty} g(x) = -\infty$  and for  $b > 1$  we have  $\lim_{x \rightarrow +\infty} g(x) =$   
 208  $2^{1-b}e^{\gamma'G}$ . We can derive  $g$ :

$$g'(x) = 2^{1-b}(b-1)x^{-b} \left( \left( \frac{2x}{1+x} \right)^b - e^{-\beta'G} \right),$$

209 whose sign depends on  $b-1$ . If  $b > 1$ ,  $g'(x)$  is positive for all  $x$  and  $g$  is an increasing  
 210 function of  $x$ . If  $b < 1$ ,  $g'(x)$  is negative and the function  $g$  is a decreasing function  
 211 of  $x$ . For the value of  $g(2)$ , we obtain equation (3) multiplied by  $2^{1-b}$ . The inequality  
 212 determining if  $g(2)$  is greater than 0 is the same as inequality (4).

213 We thus have four cases (Fig. 5):

- 214 •  $b < 1$  and  $\gamma' < \gamma'_0$ :  $g$  is a decreasing function of  $x$  and is always negative. The  
 215 2-strata stand has a lower productivity than the spatially homogeneous 1-stratum  
 216 stand.
- 217 •  $b < 1$  and  $\gamma' > \gamma'_0$ :  $g$  is a decreasing function of  $x$ , first positive and then negative.  
 218 There exists a  $x_1$  so that  $g(x_1)=0$ .
- 219 •  $b > 1$  and  $\gamma' > \gamma'_0$ :  $g$  is an increasing function of  $x$  and is always positive. The 2-  
 220 strata stand is always more productive than the spatially homogeneous 1-stratum  
 221 stand.
- 222 •  $b > 1$  and  $\gamma' < \gamma'_0$ :  $g$  is an increasing function of  $x$ , first negative then positive.  
 223 There exists a  $x_1$  so that  $g(x_1) = 0$ .

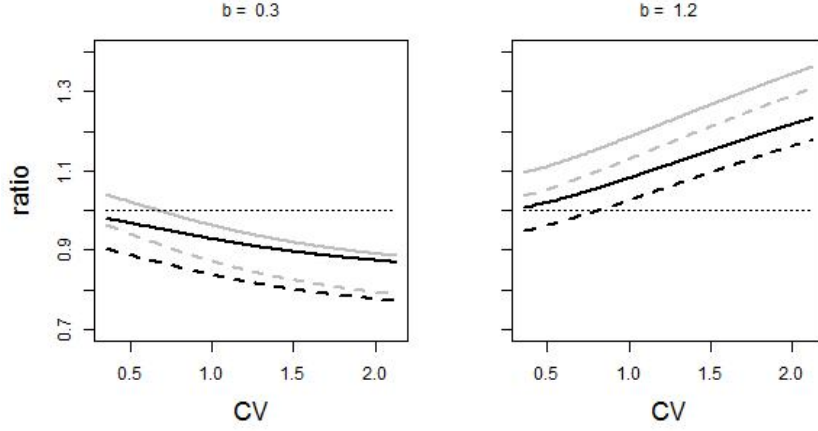


Figure 5: Growth ratio between the 2-strata stand and the spatially homogeneous 1-stratum stand as a function of the coefficient of variation  $CV$  for  $b > 0$  and  $c = 0$ . Black:  $\gamma' = 0$ , grey:  $\gamma' = 0.01$ , solid line:  $\beta' = 0.001$ , dashed line:  $\beta' = 0.01$ .  $G = 15$ ,  $g = 0.1$ .

### 224 3.2.2. Spatially heterogeneous 1-stratum stand

225 As for the spatially homogeneous 1-stratum stand we obtain four different cases  
 226 that are represented on Fig. 6. The main difference is that the magnitude of the  
 227 effect of the  $CV$  on the growth ratio is much smaller for the spatially heterogeneous  
 228 1-stratum stand than for the spatially homogeneous 1-stratum stand (Fig. 6 vs Fig 5).  
 229 The mathematical derivation of the four cases is very close to the one of the spatially  
 230 homogeneous 1-stratum stand.

Inequality (2) becomes:

$$\frac{g_l^{b-1}e^{-\beta'G} + g_u^{b-1}e^{\gamma'G}}{g_l^{b-1} + g_u^{b-1}}.$$

This can be written:

$$h(x) = e^{-\beta'G} - 1 + x^{b-1} (e^{\gamma'G} - 1) > 0.$$

We have:

$$h'(x) = (b-1)x^{b-2} (e^{\gamma'G} - 1),$$



231 whose sign depends on  $b - 1$ . We also obtain equation (3) and inequality (4) for  $h(2)$   
 232 and  $\gamma'$  respectively.

233 We thus obtain four cases (Fig. 6):

- 234 •  $b < 1$  and  $\gamma' < \gamma'_0$ :  $h$  is negative and is a decreasing function of  $x$ . The 2-strata  
 235 stand has a lower productivity than the spatially heterogeneous 1-stratum stand.
- 236 •  $b < 1$  and  $\gamma' > \gamma'_0$ :  $h$  is a decreasing function of  $x$  and crosses 0 at  $x =$   
 237  $\left(\frac{1-e^{-\beta'G}}{e^{\gamma'G}-1}\right)^{\frac{1}{b-1}} = x_0^{\frac{1}{1-b}}$ .
- 238 •  $b > 1$  and  $\gamma' > \gamma'_0$ :  $h$  is positive and is an increasing function of  $x$ . The 2-strata  
 239 stand is always more productive than the spatially heterogeneous 1-stratum stand.
- 240 •  $b > 1$  and  $\gamma' < \gamma'_0$ :  $h$  is an increasing function of  $x$  and crosses  $x$  at  $x = x_0^{\frac{1}{1-b}}$ .

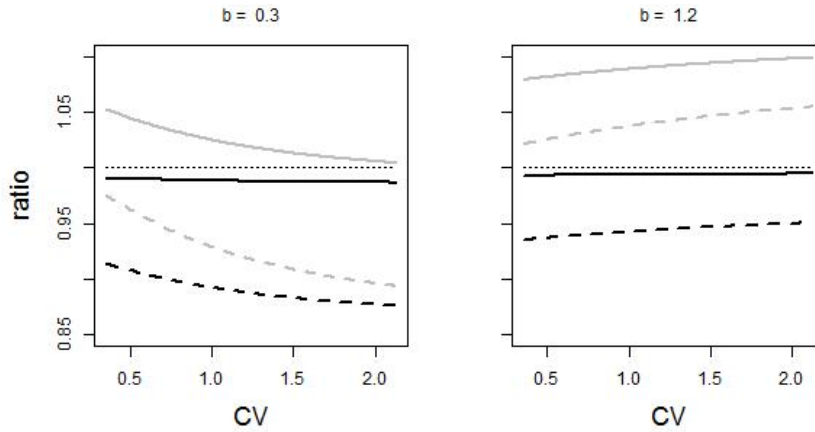


Figure 6: Growth ratio between the 2-strata stand and the spatially heterogeneous 1-stratum stand as a function of the coefficient of variation  $CV$  for  $b > 0$  and  $c = 0$ . Black:  $\gamma' = 0$ , grey:  $\gamma' = 0.01$ , solid line:  $\beta' = 0.001$ , dashed line:  $\beta' = 0.01$ .  $G = 15$ ,  $g = 0.1$ .

### 241 3.3. General case ( $b > 0$ , $c > 0$ )

#### 242 3.3.1. Spatially homogeneous 1-stratum stand

243 This case cannot be addressed analytically. In Fig. 7, we provide examples of  
 244 relationships between the size inequality and the growth ratio between the two stands

245 for different values of  $c$ ,  $b$ ,  $\gamma'$  and  $\beta'$ . Compared to the previous cases, we can observe  
 246 non-monotonous relationships when  $b > 1$ .

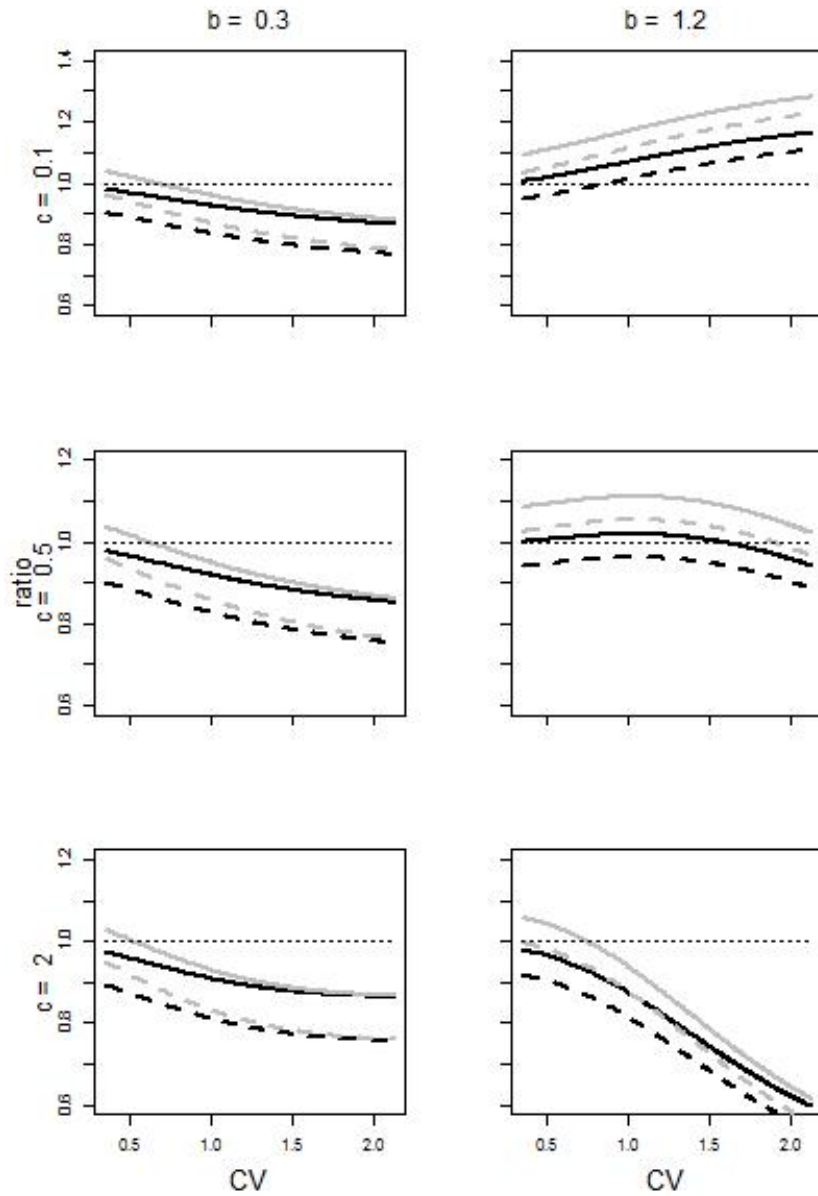


Figure 7: Growth ratio between the 2-strata stand and the spatially homogeneous 1-stratum stand as a function of the coefficient of variation  $CV$  for  $b > 0$  and  $c > 0$ . Black:  $\gamma' = 0$ , grey:  $\gamma' = 0.01$ , solid line:  $\beta' = 0.001$ , dashed line:  $\beta' = 0.01$ .  $G = 15$ ,  $g = 0.1$ .

247 *3.3.2. Spatially heterogeneous 1-stratum stand*

248 Because this case removes the direct effect of ontogeny we can address the determi-  
 249 nant of the growth ratio analytically (see below). We found the same kind of relationships  
 250 but the magnitude of the effect of  $CV$  was much smaller than in the spatially homoge-  
 251 neous 1-stratum stand (Fig. 8 vs. Fig. 7). The analytic derivation is similar to the one  
 252 of the positive size-growth model ( $b > 0, c = 0$ ). We obtain the following inequality:

$$\frac{e^{-\beta'G} + x^{b-1}e^{-cg_l(x-1)}e^{\gamma'G}}{1 + x^{b-1}e^{-cg_l(x-1)}} > 1,$$

253 which is equivalent to:

$$k(x) = e^{-\beta'G} - 1 + x^{b-1}e^{-cg_l(x-1)}(e^{\gamma'G} - 1) > 0.$$

254 We have:

$$k'(x) = (e^{\gamma'G} - 1)x^{b-2}e^{-cg_l(x-1)}((b-1) - cg_lx),$$

255 whose sign depends on  $l(x) = (b-1) - cg_lx$ . We define:

$$x_l = \frac{b-1}{cg_l}.$$

256 If  $b < 1$ ,  $l(x) < 0$  then  $k$  is a decreasing function of  $x$ . If  $b > 1$ : for  $1 < x < x_l$ ,  
 257  $k$  is an increasing function of  $x$  and for  $x > x_l > 1$ ,  $k$  is a decreasing function of  $x$ .  
 258 We also obtain equation (3) and inequality (4) for  $k(2)$  and  $\gamma'$  respectively. We have  
 259  $\lim_{x \rightarrow +\infty} f(x) = e^{-\beta'G} - 1 < 0$ .

260 We have thus the following cases (Fig. 8):

261 •  $b < 1$  or ( $b > 1$  and  $x_l < 1$ ),  $k$  is a decreasing function of  $x$ .

262 -  $\gamma' < \gamma'_0$ :  $k$  is always negative and the 2-strata stand has a lower productivity

- 263 than the spatially heterogeneous 1-stratum stand.
- 264 -  $\gamma' > \gamma'_0$ :  $k$  is positive and then negative. There exists a  $x_2$  so that  $f(x_2) = 0$ .
- 265 •  $b > 1$  and  $x_l > 1$ :  $k$  increases then decreases.
- 266 -  $\gamma' < \gamma'_0$  and  $k(x_l) > 0$ :  $k$  is negative, then positive and then negative again. It  
 267 crosses 0 twice.
- 268 -  $\gamma' < \gamma'_0$  and  $k(x_l) < 0$ :  $k$  is always negative and the 2-strata stand has a lower  
 269 productivity than the spatially heterogeneous 1-stratum stand.
- 270 -  $\gamma' > \gamma'_0$ :  $k$  is positive and then negative. There exists a  $x_2$  so that  $f(x_2) = 0$ .

### 271 3.3.3. *Effects of basal area and mean tree basal area on the growth ratio*

272 We investigated the effects of the basal area  $G$  ( $mha^{-1}$ ) and the mean tree basal area  
 273  $g$  ( $m$ ) on the growth ratio in the case of the spatially homogeneous 1-stratum stand. We  
 274 especially looked at whether a change in  $G$  or  $g$  increases or decreases the range of  $CV$   
 275 where the growth ratio is greater than 1. To do that we analysed the effect of  $G$  and  $g$   
 276 on the value of  $CV$  at which the growth ratio equals 1 ( $CV_1$ ). When the growth ratio is  
 277 a an increasing (decreasing) function of  $CV$ , an increase in  $CV_1$  decreases (increases) the  
 278 range of  $CV$  with a growth ratio greater than 1 (favourable to the 2-strata stand). Fig.  
 279 9 shows that when the size inequality-productivity relationship is negative (e.g.  $b = 0.3$ )  
 280 an increase in basal area increases the range of  $CV$  favourable to the 2-strata stand. For  
 281 the mean tree basal area, we found a negative effect on the range of  $CV$  favourable to  
 282 the 2-strata stand (Fig. 10).

## 283 4. Discussion

284 With our simple model, we have shown that the 2-strata stand can be either more  
 285 productive or less productive than the 1-stratum stands depending on the ontogenetic

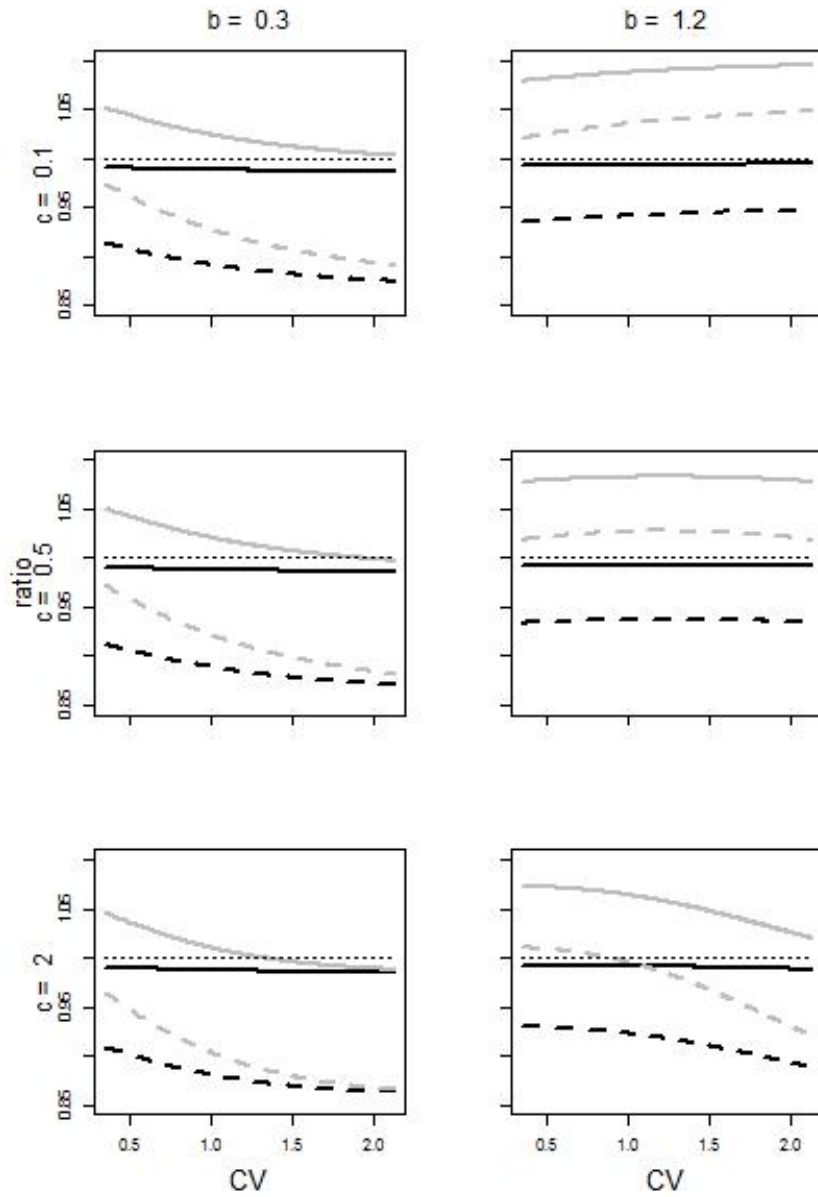


Figure 8: Growth ratio between the 2-strata stand and the spatially heterogeneous 1-stratum stand as a function of the coefficient of variation  $CV$  for  $b > 0$  and  $c > 0$ . Black:  $\gamma' = 0$ , grey:  $\gamma' = 0.01$ , solid line:  $\beta' = 0.001$ , dashed line:  $\beta' = 0.01$ .  $G = 15$ ,  $g = 0.1$ .

286 and competitive effects and the characteristic of the stand. We have also shown that,  
 287 contrary to the classical hypothesis of a competition effect, the main driver of the effect  
 288 of size inequality on productivity is the shape of the ontogenetic growth function. These

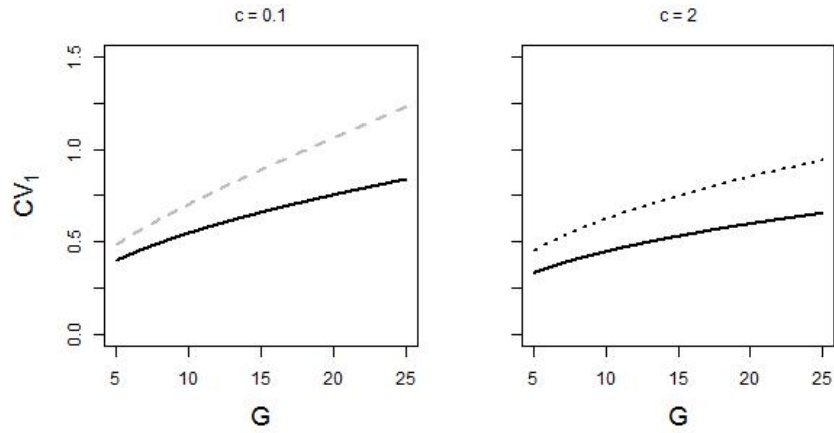


Figure 9: Coefficient of variation  $CV_1$  when the growth ratio equals 1 as a function of the basal area  $G$  ( $m^2 ha^{-1}$ ) (spatially homogeneous 1-stratum stand;  $b > 0$  and  $c > 0$ ). Black: negative relationship between size inequality and productivity ratio. Grey: positive relationship between size inequality and productivity ratio. Solid line:  $\beta' = 0.001$ ,  $\gamma' = 0.01$ ,  $b = 0.3$ . Dashed line:  $\beta' = 0.01$ ,  $\gamma' = 0$ ,  $b = 1.2$ . Dotted line:  $\beta' = 0.001$ ,  $\gamma' = 0.01$ ,  $b = 1.2$ .  $g = 0.1$ .

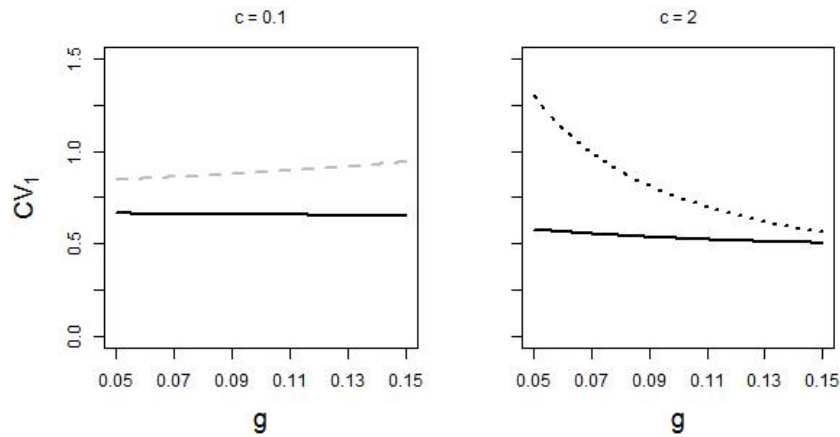


Figure 10: Coefficient of variation  $CV_1$  when the growth ratio equals 1 as a function of the mean tree basal area  $g$  ( $m^2$ ) (spatially homogeneous 1-stratum stand;  $b > 0$  and  $c > 0$ ). Black: negative relationship between size inequality and productivity ratio. Grey: relationship between size inequality and productivity ratio. Solid line:  $\beta' = 0.001$ ,  $\gamma' = 0.01$ ,  $b = 0.3$ . Dashed line:  $\beta' = 0.01$ ,  $\gamma' = 0$ ,  $b = 1.2$ . Dotted line:  $\beta' = 0.001$ ,  $\gamma' = 0.01$ ,  $b = 1.2$ .  $G = 15$ .

289 results help to better understand the diversity of patterns reported in the literature  
 290 concerning the size inequality-productivity relationship.

#### 291 4.1. *Ontogenetic effects*

292 Our results show that the ontogenetic growth function has a huge impact on the  
293 conclusions drawn on higher or lower productivity of 2-strata stands. For instance, we  
294 found that depending on the values of  $b$ , one can find higher productivity ( $b > 1$ ) or  
295 lower productivity of the 2-strata stands ( $b < 1$ ) for the same values of competition  
296 parameters. In the literature,  $b$  has been shown to take values ranging roughly from 0.3  
297 (Wykoff, 1990; Monserud and Sterba, 1996; Schröder et al., 2002) to 1.2 (Pokharel and  
298 Dech, 2012), depending on the species. Although less frequent, values above 1 have been  
299 reported in different parts of the world: in North America (Pokharel and Dech, 2012;  
300 Wykoff, 1990) and in Europe (Cordonnier and Kunstler, 2015). The parameter  $c$ , which  
301 was significant for most species in empirical studies (see Monserud and Sterba (1996)  
302 for some exceptions but in this case the parameter  $b$  is inferior to 1), had a negative  
303 effect. Moreover, the effect of total basal area on the 2-strata stand depends also on  
304 the ontogenetic growth function (parameter  $b$ ). This indicates that one cannot conclude  
305 on the effects of tree interactions based on size inequality-productivity patterns without  
306 controlling for species ontogenetic growth. This also indicates that conditions to obtain  
307 more productive 2-strata stands should be quite limited ( $b$  usually inferior to 1 and  $c > 0$   
308 when  $b > 1$ ).

#### 309 4.2. *Competition effects*

310 For competition parameters, the higher productivity of the 2-strata stand appears  
311 easier to achieve when the intensity of size-asymmetric competition ( $\beta'$ ) is low and  
312 the type of size-asymmetric competition tends towards absolute size-asymmetric com-  
313 petition ( $\gamma'$  close to  $\alpha$ ). This corresponds to the case where inter-strata competition  
314 (represented by  $\beta' - \gamma'$ ) is reduced compared to intra-stratum competition ( $\alpha$ ). Abso-  
315 lute size-asymmetric competition (also called perfect one-sided competition) has been  
316 considered in theoretical modelling studies either to simplify analytical results or to fo-

317 cus on competition for light (e.g. Kohyama and Takada, 2012). The results reported  
318 herein indicate that this choice can have a major influence on conclusions about stand  
319 productivity in size-structured forest ecosystems. Other ecological studies assumed rel-  
320 ative size-asymmetric competition ( $\gamma' = 0$ , Kunstler et al. (2011)). In the present study,  
321 this appears to be detrimental to the 2-strata stands because it increases inter-strata  
322 competition. Our study shows that modelling choices on competition types can lead to  
323 different conclusions on the relative advantage of 1-stratum or 2-strata stands as regards  
324 current productivity.

#### 325 4.3. *Species characteristics and site effects*

326 The intensity of asymmetric competition (here  $\beta'$ ) has been reported to be usually  
327 high in forest ecosystems (Cordonnier and Kunstler, 2015; Pretzsch and Biber, 2010;  
328 Onoda et al., 2016). Actually, in plant communities, both competition for light and  
329 competition for soil resources (usually considered as size-symmetric competition) occur  
330 at the same time (Schwinning and Weiner, 1998) with intensities varying depending  
331 on species characteristics and the ecological situations considered. Using plots in New  
332 Zealand forests and controlling for basal area, Coomes and Allen (2007) showed that  
333 competition for light was high at low elevation, decreased with elevation and became  
334 comparable to competition for soil resources (that does not vary with elevation) at high  
335 elevation. This pattern has also been highlighted by Pretzsch and Biber (2010) who  
336 found higher size-asymmetric competition on fertile sites for three common species in  
337 Europe. Regarding our modelling framework, this would potentially lead to a higher  
338 occurrence of more productive 2-strata stands compared to 1-stratum stands in low  
339 productive sites. However, a recent study (Sun et al., 2018) found more pronounced  
340 negative effects of size inequality in low quality sites in *Sassafras tzumu* plantations  
341 in central China. According to our results, this pattern could be explained by a joint  
342 change in the intensity of size asymmetric competition ( $\beta'$ ) and the type of competition



343 ( $\gamma'$ ) with site quality. This points out the need to better quantify the effect of ecological  
344 conditions on size-symmetric and size-asymmetric competitions and its consequence for  
345 size-productivity relationships.

346 Our results also indicate that 2-strata stands with species that are highly sensitive to  
347 light competition (e.g. *Quercus robur*, *Pinus sylvestris*, *Pinus contorta*) should be less  
348 productive than 1-stratum stands. This result has been found for *Eucalyptus* species  
349 (Soares et al., 2016). However, Bourdier et al. (2016) found no impact of species shade  
350 tolerance on the effect of size inequality on stand productivity. This result could come  
351 from positive co-variations between canopy light interception and shade tolerance (Can-  
352 ham et al., 1994; Messier et al., 1998), which here would lead to comparable values of  
353 parameter  $\beta'$  among species.

354 We found that for  $b < 1$  the total basal area should have a positive effect on the  
355 range of size-inequality values favourable to the 2-strata stand. For the mean tree basal  
356 area, we found a negative effect. These results confirm the need to control for these  
357 two key variables (stand density and mean tree size) when one wants to compare the  
358 productivity of stands having different size structures.

#### 359 4.4. The size inequality-productivity relationship

360 The effect of size inequality measured here by the coefficient of variation of tree  
361 sizes in the 2-strata stand has contrasting effects on productivity depending on growth  
362 and competition parameters. This result is of major importance because it could partly  
363 explain why some studies highlight negative relationships between tree size diversity and  
364 productivity (e.g. Bourdier et al., 2016; Soares et al., 2016; Sun et al., 2018) while others  
365 emphasise positive ones (e.g. Danescu et al., 2016), although positive ones have only  
366 been found in mixed forests (once the species richness effect controlled). In the present  
367 study, size inequality is usually detrimental to productivity except when  $b > 1$  and  $c$  is  
368 low. We also found cases where the relationship between size inequality and productivity

369 is non-monotonous (e.g. Fig. 7 and 8). These patterns indicate that attention must be  
370 paid to covering large gradients of size diversity, which is not necessarily easy to achieve  
371 in field studies. The patterns obtained for the two 1-stratum stands were very similar,  
372 indicating that the direct effect of ontogenetic growth does not really impact the size-  
373 inequality-productivity relationship qualitatively. However, for the same competition  
374 and growth parameters, variations of the growth ratio were much higher for the spatially  
375 homogeneous 1-stratum stand than for the spatially heterogeneous 1-stratum stand.  
376 This result highlights a major quantitative effect of ontogenetic growth on the size  
377 inequality-productivity relationship.

#### 378 *4.5. Model limitations*

379 Our conclusions must be taken with caution given our simplistic approach and some  
380 important simplifications made. For instance, parameter  $\gamma'$  might depend on size in-  
381 equality  $x$  (we expect  $\gamma'$  to increase with  $x$ ; Fig. 1) because trees with a substantial  
382 difference in size might interact differently for resource acquisition than trees with sim-  
383 ilar sizes. This phenomenon could emerge in simulations with models having detailed  
384 algorithms on competition for light (Courbaud et al., 2015). According to our results,  
385 this would lead to more positive relationships between size inequality and productivity,  
386 a result that has been obtained in some, but not all, simulation studies (Silva Pedro et  
387 al., 2017). In addition, these results do not capture canopy plasticity and thus potential  
388 packing effects induced by this plasticity (Ishii et al., 2013). This phenomenon can be  
389 translated into a lower increase of  $\beta'$  with  $x$ , which here again is favourable to more  
390 productive 2-strata stands.

391 Our model is static and does not deal with long-term effects of stand stratification  
392 on productivity. Nevertheless, it has the potential to be used to study the temporal  
393 size inequality-productivity relationship because the ratio between the relative growth  
394 rates of the two strata determines the change of  $CV$  with time. However, to accurately

395 represent the long-term change in the  $CV$ , this would require modelling mortality and  
396 recruitment rates. Finally, the extension of our model to stands having more than two  
397 strata is not straightforward.

398 Despite these limitations, our model can provide interesting insights on the expected  
399 effects of species, local conditions and stand structures on the size inequality-productivity  
400 relationship and thus contribute to discussions on forest management system options in  
401 different ecological conditions.

#### 402 4.6. *The stand structure effect*

403 Our approach relies on evaluating the productivity of a 2-strata stand with varying  
404 levels of size inequality. Once the basal area  $G$ , the mean tree basal area  $g$  and the size  
405 inequality  $CV$  are specified, several stand structures can still be defined, which requires  
406 to build on another assumption. Here we assumed that basal area  $G$  is the same in the  
407 two strata, which results in lower number of trees in the upper stratum than in the lower  
408 stratum. This is a reasonable approximation, based on the wide spread observation of  
409 J shaped size distributions in natural forests ecosystems. As shown in Fig. 4, this  
410 leads to a negative effect of size inequality on the growth ratio even without ontogenetic  
411 growth. This "stand structure effect" *per se* could explain why we conclude on a higher  
412 prevalence of negative relationships between size inequality and productivity. However,  
413 other assumptions regarding stand structure are also possible. As a consequence, we  
414 investigated another specific case where the number of trees is the same in the two strata  
415 (equal size distribution). Although the main conclusions still hold, we found some slight  
416 differences (not shown). For  $b < 1$  but close to 1, we can obtain positive relationships  
417 between size inequality and productivity for a combination of low values of  $\gamma'$  and high  
418 values of  $\beta'$  and  $g$ . We can also observe negative relationships for  $b > 1$  ( $b$  close to 1)  
419 when  $\gamma'$ ,  $\beta'$  and  $g$  are high. These results indicate that our conclusions appear quite  
420 robust to the way we distribute the number of trees or the basal area between the two

421 strata. It however also shows that the choice is not totally neutral and can induce some  
422 differences for size inequality-productivity patterns, which requires further analyses.

#### 423 *4.7. Conclusions*

424 The strength of our 2-strata model is to show that even with a simple representa-  
425 tion of growth and competition we found a wide range of patterns of size inequality-  
426 productivity relationships. Overall, our results indicate that negative size inequality-  
427 productivity relationships in monospecific stands may be the rule and that positive  
428 relationships may emerge when size-asymmetric competition is weak, size-asymmetric  
429 competition is quasi-absolute and growth-size relationship is concave-shaped. We hope  
430 this will motivate researchers to develop mechanistic approaches to better identify con-  
431 ditions that lead to higher productivity of highly size-structured stands.

432

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