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## Research article

# The Gini index brings asymmetric competition to light



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## ABSTRACT

Competition is known to be a key driver of plant population dynamics. However, understanding how different types of competitive processes interact with population structure in driving population dynamics remains challenging. Ecologists broadly distinguish between two types of competition: size-asymmetric competition (SAC), related to resource pre-emption, and size-symmetric competition (SSC), related to resource depletion. SAC and SSC are known to influence plant-size population structures differently. Usually, SAC increases size inequality and, in return, changes in size inequality reinforce the role of SAC. On the contrary, SSC generally triggers size structure homogeneity. Although numerous simulations and experimental studies have explored how SAC influences population size structure, there is still no clear way to estimate the reverse effect: how changes in the size structure of a population affects the role of SAC compared to SSC in plant growth. In this article, we propose a modelling approach to estimate how size structure influences the role SAC plays in growth in mono-specific forest stands. First, we show that the role of SAC can be assessed by an equation that involves the Gini index, a well-known size inequality index. We then apply our approach to national forest inventory data in France, focusing on two major species: European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.). This article discusses the conditions necessary to apply such a modelling approach and gives perspectives for further development in plant ecology.

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## Introduction

In plant ecology, competition from neighbouring individuals is a fundamental process which shapes population and community structures (Berger et al., 2008). Competition is mainly driven by resource depletion and resource pre-emption, two mechanisms that are related to plant size. Bigger plants can prospect a larger part of the surrounding soil and thus access higher amounts of soil resources, such as water and nutrients, than can smaller plants (Casper and Jackson, 1997). In addition, large plants can pre-empt essential resources (i.e. light, patchy soil resources) to the detriment of smaller individuals (Schwinning and Weiner, 1998). These phenomena have led ecologists to distinguish between two competition types: size-asymmetric competition (SAC) and size-symmetric competition (SSC) (Schwinning and Weiner, 1998; Weiner, 1990; Weiner and Damgaard, 2006). According to Weiner (1990), SAC occurs when “the larger individual has

a disproportionate effect or obtains a disproportionate share of the resources, for its relative size”. Conversely, SSC is obtained in “situations in which competitive effect or resource acquisition is proportional to some measure of size”. At the extremes of the scale, absolute symmetric competition (the exact same resource acquisition for all individuals) and absolute asymmetric competition (the largest individual is not impacted at all by smaller individuals) might be encountered in very specific conditions (Weiner, 1990).

The number of studies that have tried to estimate and/or model the SAC and SSC components of competition is rather limited. A common approach consists in assessing the importance of SAC from the non-linear relationship between size and growth, also called size-asymmetric growth (Damgaard et al., 2002; Nord-Larsen et al., 2006; Pretzsch and Biber, 2010). Although this approach can be easily implemented in the field (Metsaranta and Lieffers, 2008; Castagneri et al., 2012), Weiner and Damgaard (2006) warned that the quantitative relationship between SAC and size-asymmetric growth is not straightforward. Other studies have explored the effect of SSC and SAC on the structure and dynamics of populations with zone-of-influence models (Weiner et al., 2001; Weiner and Damgaard, 2006) or field-of-neighbourhood models (Bauer et al.,

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2004) for both herbaceous and forest species. However, parameterizing these models can be a daunting task, and this limits their applicability.

These previous studies have shown that SAC and SSC impact population structure and population dynamics differently (Damgaard and Weiner, 2000; Schwinning and Weiner, 1998) and that SAC at the individual level (Freckleton and Watkinson, 2001) can drive the size structure of plant populations by favouring certain individual plant sizes (Weiner, 1990; Weiner et al., 2001; Weiner and Damgaard, 2006). This is because SAC, by promoting dominant individuals, tends to trigger size inequality (Weiner, 1990) and in turn, changes in size inequality reinforce the importance of SAC: a kind of positive feedback loop. On the contrary, SSC generally triggers size structure homogeneity (Weiner, 1990) and can induce long-term oscillations in population dynamics due to synchrony in plant growth and mortality among individuals (Caplat et al., 2008). This means that the size structure of a given plant population is a key determinant of the average role of SAC in that population. Surprisingly, no studies have proposed clear ways to estimate how the size structure of a population affects the role of SAC relative to SSC, though a method would be particularly helpful to researchers investigating changes in competition type with population size structure. From a more static perspective, such a method would allow them to characterize populations according to the dominant type of competition that is at work.

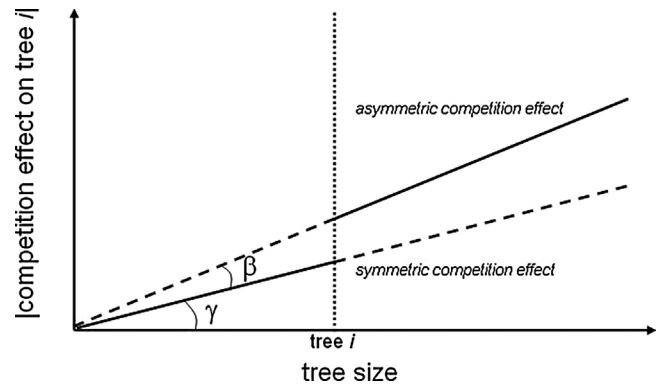
Size structure refers to the statistical distribution of a given individual plant size attribute in a population, for instance weight and height. It is generally characterized by the mean, the variance, the skewness and the kurtosis of the distribution (Hara, 1988). In regard to SAC, a key component of size structure lies in size hierarchy among individuals, also called size inequality (Weiner and Solbrig, 1984; Damgaard and Weiner, 2000). This is generally characterized by the Gini index or the coefficient of variation (Weiner and Solbrig, 1984; Hara, 1988; Knox et al., 1989; Damgaard and Weiner, 2000; Dudunam, 2011). In forest ecosystems, the Gini index has proven to be very efficient compared to other indices (e.g. Shannon index, stand variance index; see Staudhammer and LeMay, 2001; Lexerod and Eid, 2006; Valbuena et al., 2012) in discriminating stands with different types of diameter distribution.

In this article, we explore how forest size structure influences the relative role of SAC in the growth of mono-specific forest stands. We use a simple model of individual tree growth that includes both SAC and SSC at the tree level. We show that the relative importance of SAC for growth at the stand level is related to the Gini index of the size structure of the stand. We apply this approach to data from the French National Forest Inventory to analyze how size inequality controls the relative roles of SAC and SSC in the stand growth of two major species in Europe: European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.).

## Methods

### Modelling competition effect at tree level

We consider a mono-specific stand (or plot) composed of  $n$  trees with different diameters at breast height  $d_i$  (cm) arranged in ascending order ( $\forall i, d_{i+1} > d_i$ ). In forestry, several distance-dependent (i.e. which take into account the relative location of trees) and distance-independent (no information about the location of trees) competition indices have been proposed to assess the effect of competition on tree growth or tree mortality (see Biging and Dobbertin, 1992, 1995). Among these indices, distance-independent ones have proved to be particularly convenient since tree spatial data are scarce. A very simple yet efficient



**Fig. 1.** Schematic representation of the absolute value of the competition effect on tree  $i$  with the two competition indices retained in the study. A given tree  $i$  in the diameter hierarchy is influenced by smaller trees proportionally to their size (SSC: parameter  $\gamma$ ). In addition to SSC (dotted line), taller trees show a supplementary effect due to the pre-emption of essential resources (SAC: parameter  $\beta$ ). By changing the values of parameters  $\beta$  and  $\gamma$ , we can mimic all competition types except absolute SSC (same resource acquisition for all individuals irrespective of their size).  $\beta = 0$  ( $\gamma > 0$ ): SSC.  $\beta > 0$  ( $\gamma > 0$ ): SAC.  $\gamma = 0$  ( $\beta > 0$ ): absolute SAC (the largest tree is not impacted by smaller trees). In this article, we assume  $\gamma > 0$ ,  $\beta > 0$ . Both  $\beta$  and  $\gamma$  can depend on site conditions at the plot or stand level.

distance-independent index for a tree  $i$  in a given stand is the sum of the basal area  $g_k$  of the  $(n - 1)$  other competitive trees (Biging and Dobbertin, 1995; Monserud and Sterba, 1996; Contreras et al., 2011; Lederman, 2010), as follows:

$$BA_i = \sum_{k \neq i}^n g_k \quad (1)$$

where tree basal area is defined as  $g_k = \pi d_k^2 / 4$ , in  $m^2$ , and stand basal area as  $G = \sum_{k=1}^n g_k$ , in  $m^2$ . The index  $BA$  can be related to SSC and has been used to model tree growth in both theoretical and applied forest dynamics models (Coomes and Allen, 2007; Wykoff, 1990). In the real world, both SSC and SAC occur (e.g. Pretzsch and Biber, 2010). In order to take SAC into account, we can add a second index, namely the total basal area of the competitive trees that are bigger than the focal tree  $i$ :

$$BAL_i = \sum_{k=i+1}^n g_k \quad (2)$$

The index  $BAL$  can be related to absolute SAC, i.e. a tree of a given size is not impacted at all by smaller individuals. This formulation has been used to model tree growth in both theoretical and applied forest dynamics models (Coomes and Allen, 2007; Kohyama, 1993; Wykoff, 1990).

The resulting competitive effect on tree growth (or tree mortality) can then be modelled as the sum of the negative values of these two indices with two specific parameters:

$$\text{COMPETITION EFFECT}_i = -\beta BAL_i - \gamma BA_i \quad (3)$$

where  $\gamma$  corresponds to the sensitivity of the species to SSC ( $\gamma \geq 0$ : competitive trees have an effect proportional to their size) and  $\beta$  to the sensitivity of the species to SAC ( $\beta \geq 0$ : there is a disproportionate effect of larger trees due to the fact that they monopolize certain resources).

Our competition model, similar to the one proposed by Thomas and Weiner (1989), can easily be related to Weiner's (1990) definitions of SAC and SSC (see Fig. 1). Relative SSC is achieved when  $\beta = 0$ , and absolute SAC can be modelled when  $\gamma = 0$ . Only absolute SSC (equal resource acquisition for all individuals irrespective of their size) cannot be mimicked by our indices. However, it could

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