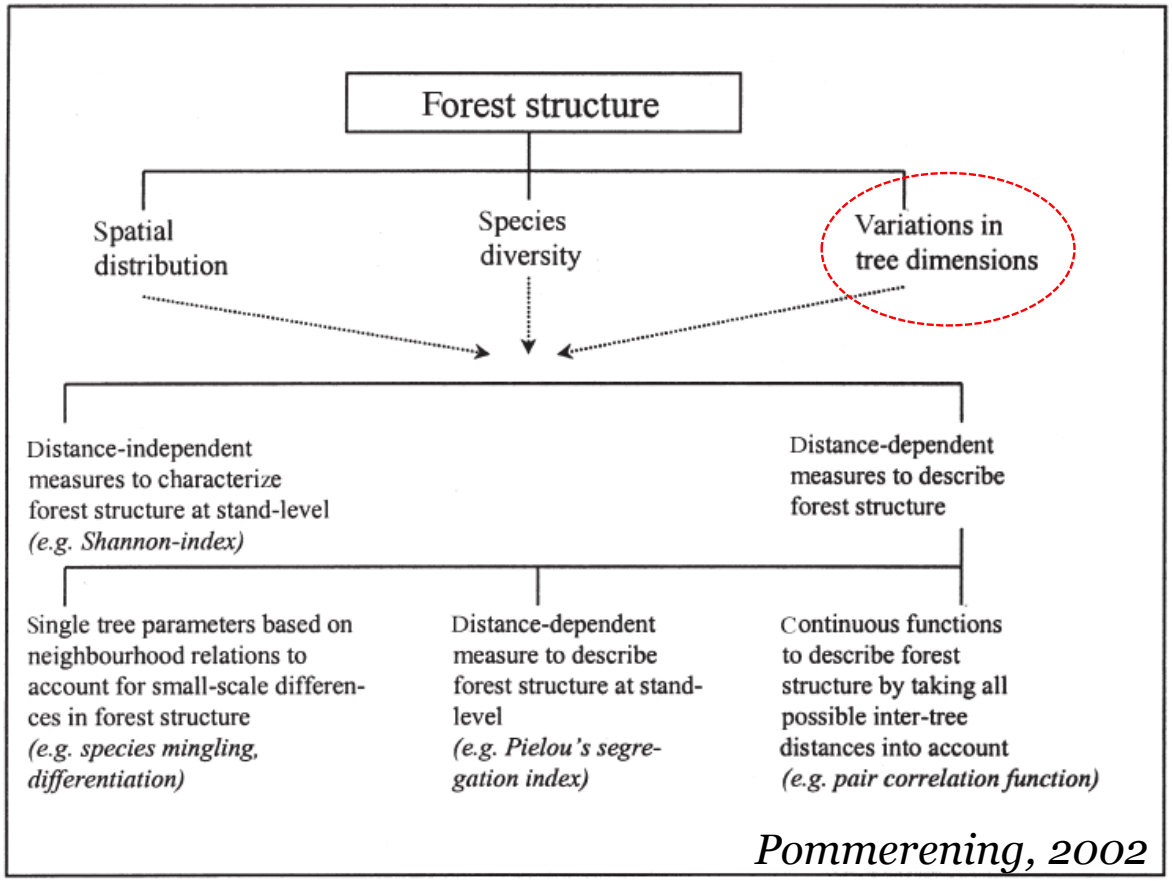
Tree size inequality and productivity in forests

Thomas Cordonnier & colleagues

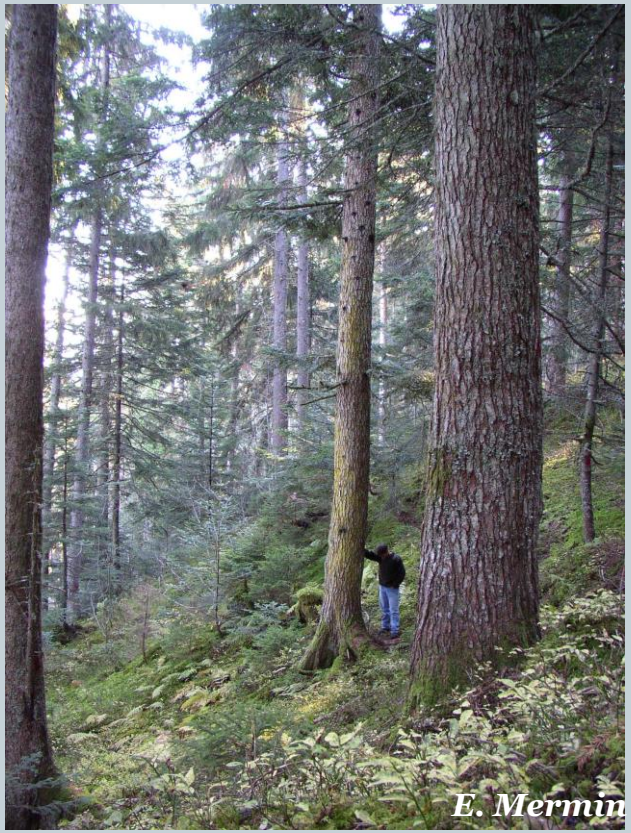
Irstea Grenoble, UR LESSEM, DYNAMICS group

Why focusing on tree size inequality?

- **It is an essential structural attribute of plant populations**

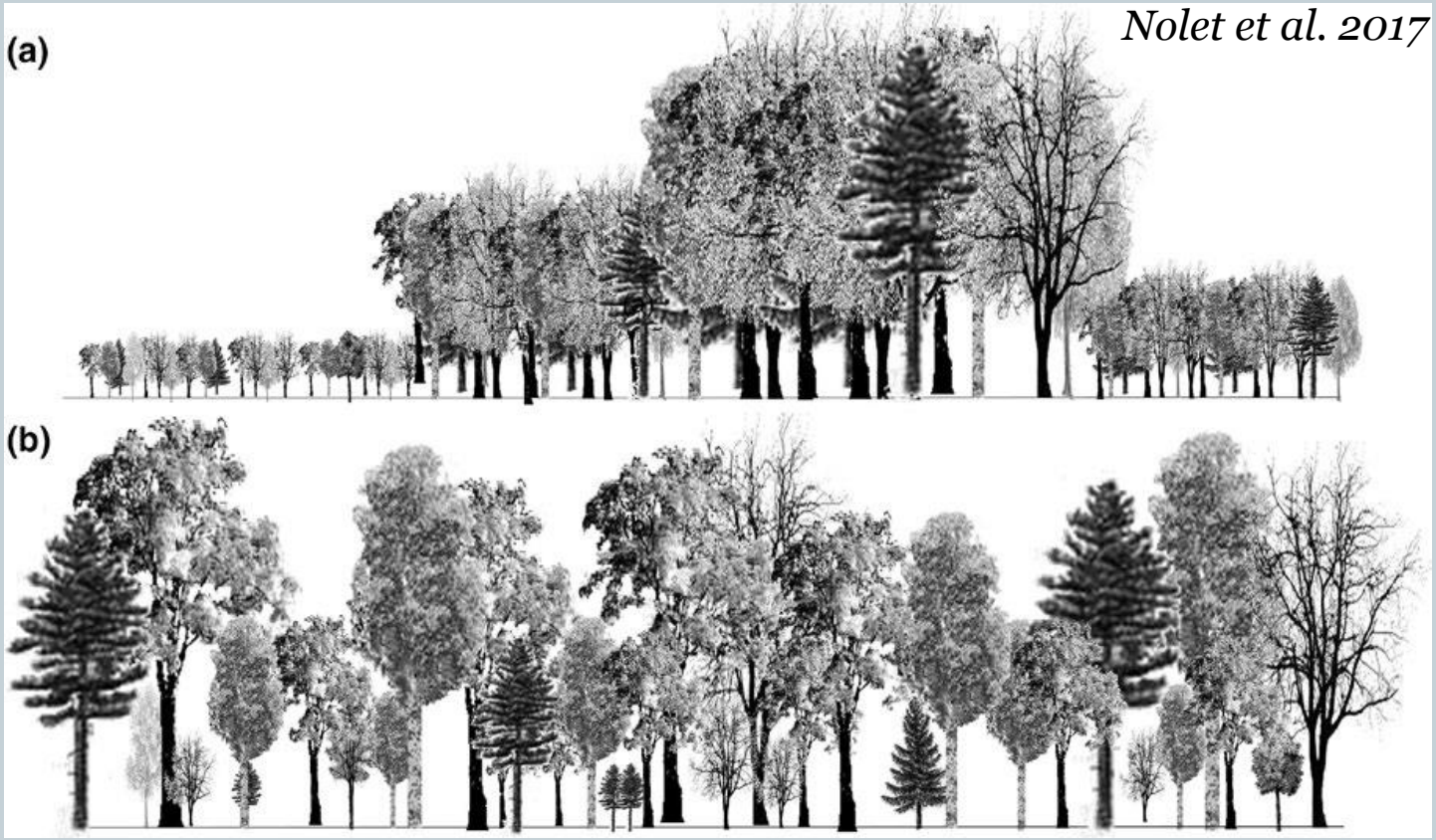


Pommerening, 2002



Why focusing on tree size inequality?

- **It is related to (and driven by) forest management systems**

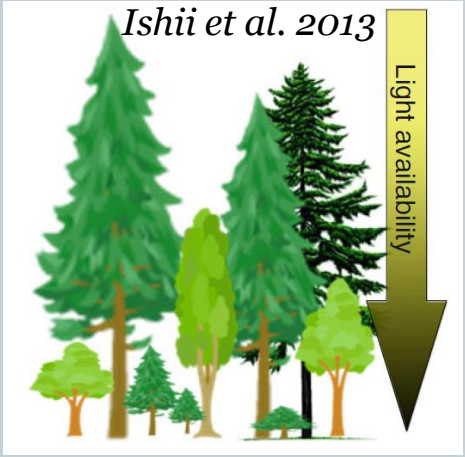


Why focusing on tree size inequality?

- **It directly impacts competition in plant populations**

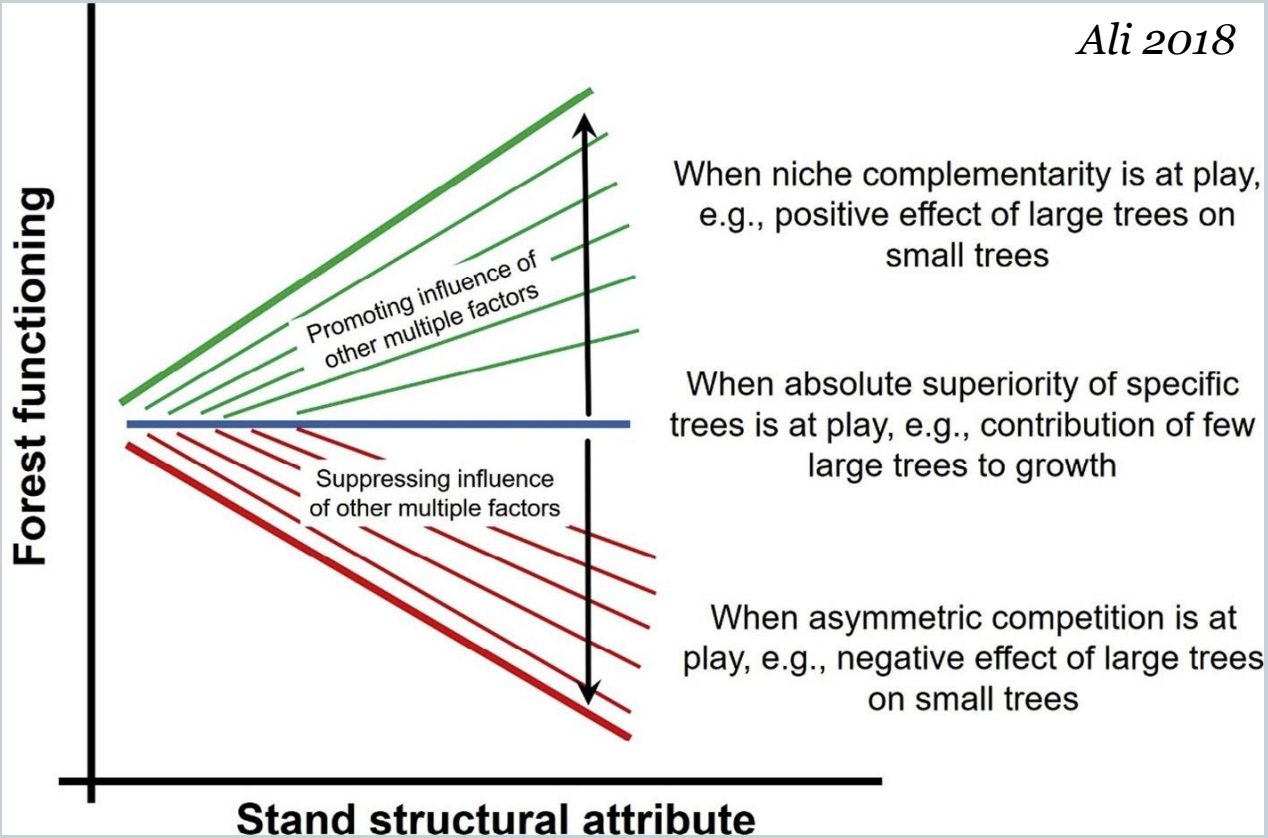
Asymmetric Competition in Plant Populations

Jacob Weiner



« For competition to be asymmetric, the larger individual must have a disproportionate effect or obtain a disproportionate share of the resources, for its relative size. »

Size inequality-productivity relationships



"[…] there is no ubiquitous relationship between stand structure and forest functioning […]"

A complementary effect

"A key concept for designing highly productive mixed-species stands is the need to combine species that ***differ in characteristics such as shade tolerance****"*

"[…] intolerant species […] can form an upper canopy stratum that transmits a substantial portion of light to shade tolerant species that form a lower stratum […]. ***Canopy stratification of this kind is an important aspect of complementary resource use****"*

Kelty 2006

Testing the complementary effect in mixed stands

- Mixed stands in France (NFI, >11 000 plots, 2006-2011)
- Basal area growth at the plot level
- Effect of species richness (R) and diversity of shade tolerances (FDIS)
- Effect of tree size inequality (GINI index of heights)
- Effect of the covariance between tree height and shade tolerance (COV)
  - Positive: shade tolerant species are dominant in height
  - Negative: shade intolerant species are dominant in height
- Control for stand basal area, quadratic mean diameter, species identities
- Control for the environment: Sum of daily temperatures exceeding 5.56°C and annual soil water budget.

Cordonnier et al. 2018

Hypotheses

- **Species richness : + (e.g. Vila et al. 2013)**
- **Tree size inequality : - (e.g. Bourdier et al. 2016)**
- **Height-shade tolerance covariance : - (e.g. Kelty 2006)**
- **Shade tolerance diversity : ?**

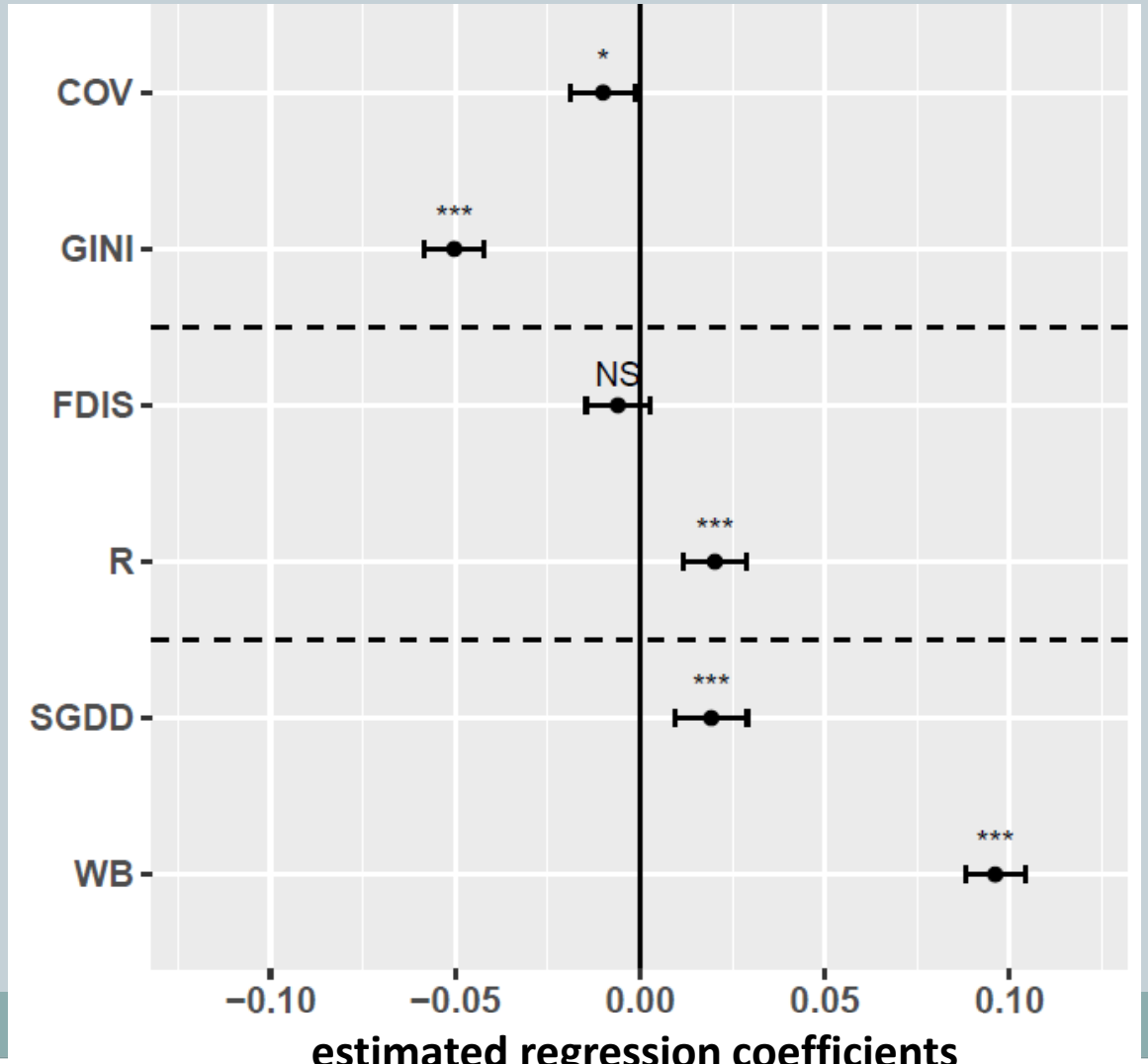
The model

$$\log(\mathrm{BAI}) = \log(\beta_0) + \alpha_1 \mathrm{WB} + \alpha_2 \mathrm{SGDD} + a_1 \log(\mathrm{BA}) + a_2 \mathrm{BA} + a_3 \mathrm{QMD} + b_1 \mathrm{R} + b_2 \mathrm{FDIS} + b_3 \mathrm{GINI} + b_4 \mathrm{COV} + \varepsilon$$

BAI:	Basal area increment ($m^2 ha^{-1} year^{-1}$)
WB:	Annual soil water budget (mm)
SGDD:	Sum of daily temperatures exceeding 5.56°C (°C)
BA:	Basal area ($m^2 ha^{-1}$)
QMD:	Quadratic mean diameter (m)
R:	Species richness (-)
FDIS:	Diversity in shade tolerance (-)
GINI:	Inequality of tree heights (-)
COV:	Covariance between tree heights and tree shade tolerances (m)
ε:	normal error

We have $\log(\beta_0) = \beta_1 \mathrm{SP}_1 + \beta_2 \mathrm{SP}_2 + \cdots + \beta_{20} \mathrm{SP}_{20}$ with SP_i the proportion of the species (or species group) *i*.

Results


COV
GINI
FDIS
R
SGDD
WB
*
***
NS
***
***
***
−0.10
−0.05
0.00
0.05
0.10
estimated regression coefficients

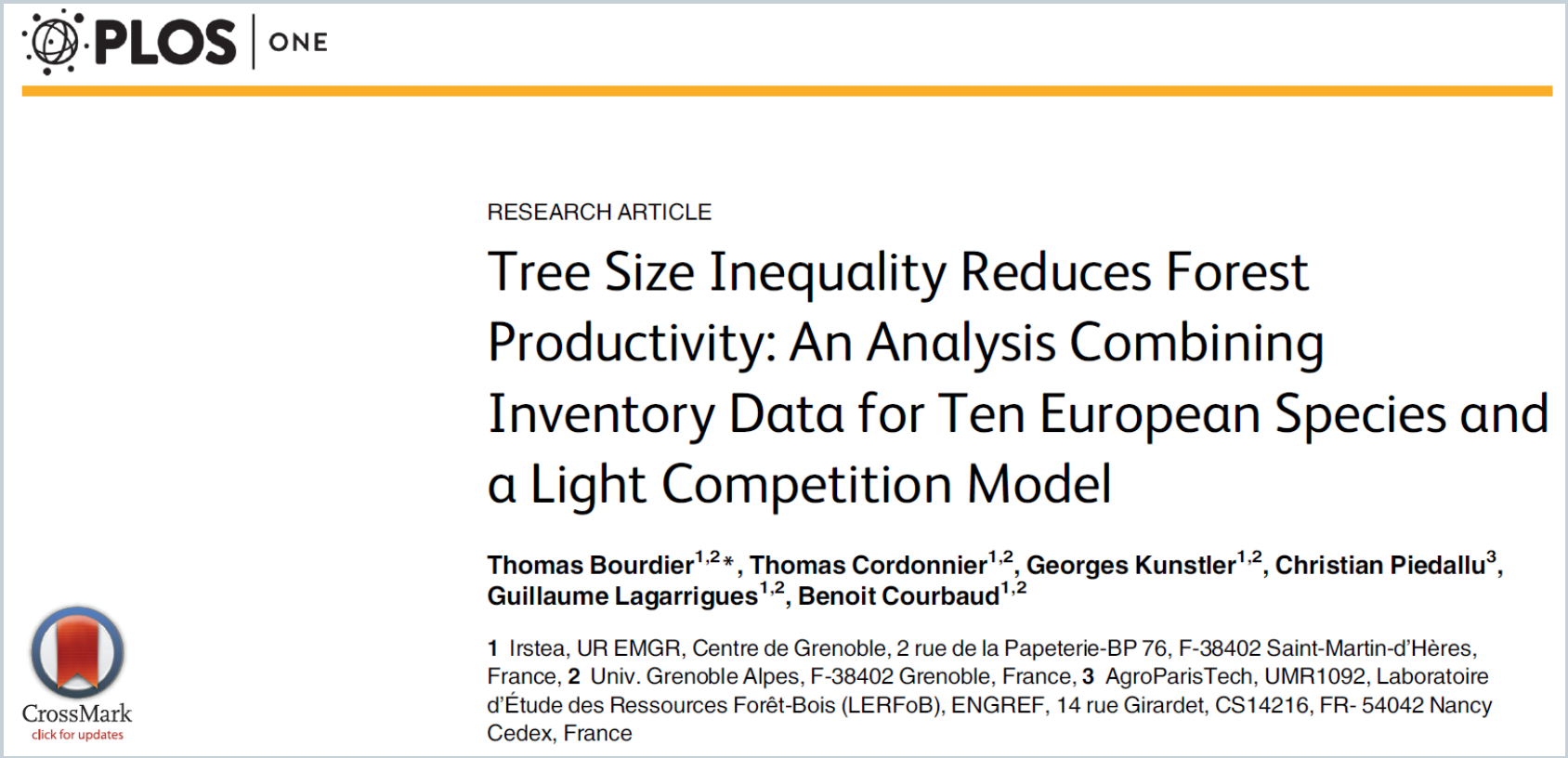
Synthesis

- Positive effect of species richness: coherent with the literature.
- Negative effect of size inequality *per se* (size-asymmetric competition).
- Negative (but low) effect of height-shade tolerance covariation (complementary effect).
- No effect of shade tolerance diversity: use other traits for functional diversity (?)

We need to better understand the relationships between species traits (species composition) and size structure, and their effects on forest functioning

The case of monospecific forest stands

- neutral and negative relationships



PLOS ONE

RESEARCH ARTICLE

Tree Size Inequality Reduces Forest Productivity: An Analysis Combining Inventory Data for Ten European Species and a Light Competition Model

Thomas Bourdier[1,2]*, Thomas Cordonnier[1,2], Georges Kunstler[1,2], Christian Piedallu[3], Guillaume Lagarrigues[1,2], Benoit Courbaud[1,2]

1 Irstea, UR EMGR, Centre de Grenoble, 2 rue de la Papeterie-BP 76, F-38402 Saint-Martin-d'Hères, France, **2** Univ. Grenoble Alpes, F-38402 Grenoble, France, **3** AgroParisTech, UMR1092, Laboratoire d'Étude des Ressources Forêt-Bois (LERFoB), ENGREF, 14 rue Girardet, CS14216, FR- 54042 Nancy Cedex, France

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Is asymmetric competition the main driver?

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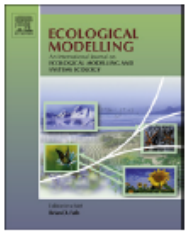


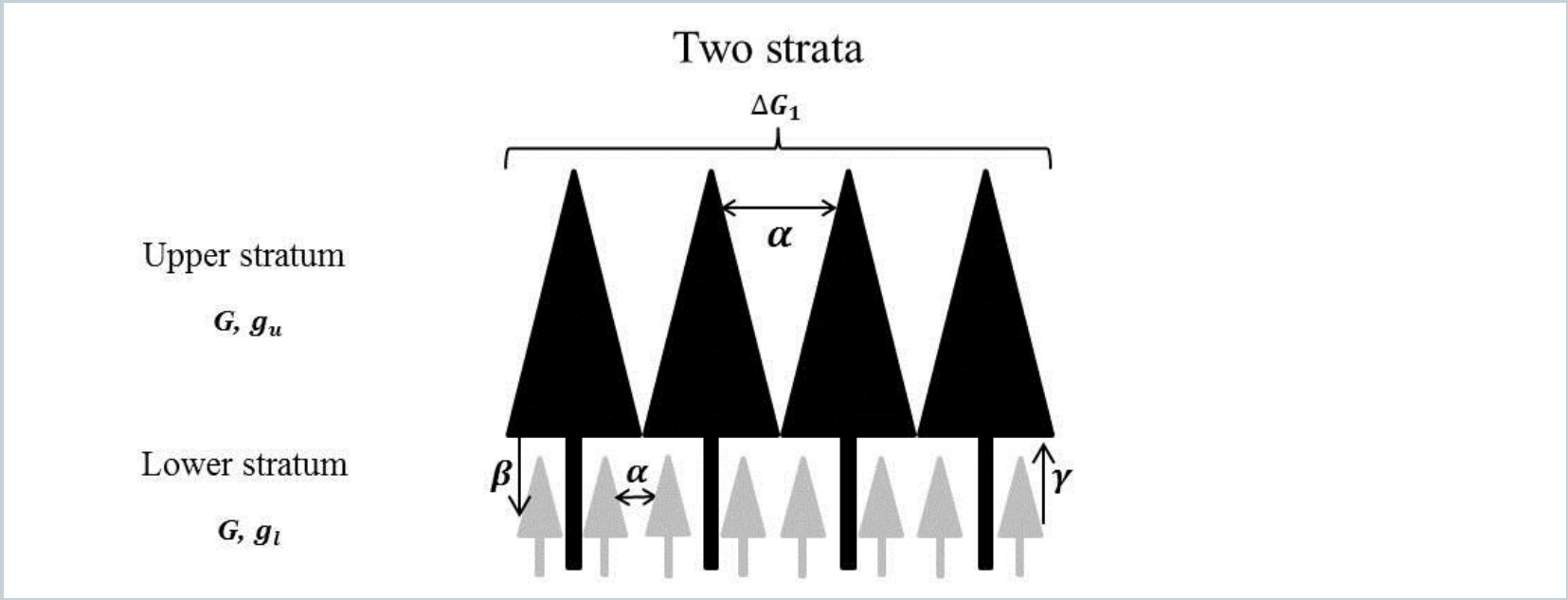
Modelling the effect of size-asymmetric competition on size inequality: Simple models with two plants

Camilla Ruø Rasmussen [a,*], Jacob Weiner [b]

[a] Department of Plant and Environmental Sciences, University of Copenhagen, Højbakkegaard Allé 13, DK-2630 Taastrup, Denmark
[b] Department of Plant and Environmental Sciences, University of Copenhagen,Thorvaldsensvej 40, DK-1871 Frederiksberg, Denmark

« Our results emphasize the need for explicit growth models, even very simple ones, for making inference about the effects of competition on plant growth and size inequality. »

A simple model

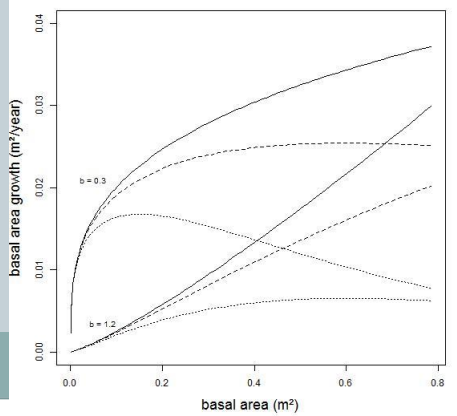


STAND GROWTH

$$\Delta G = \frac{G}{g_u}\Delta g_u + \frac{G}{g_l}\Delta g_l$$

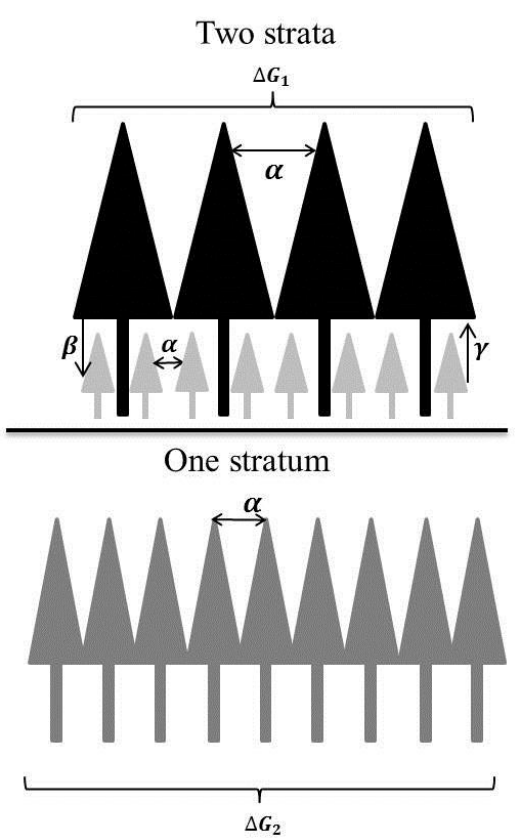
TREE GROWTH = POT * RED

$$\begin{cases} \Delta g_l = a{g_l}^b e^{-cg_l} * e^{-(\alpha+\beta)G} \\ \Delta g_u = a{g_u}^b e^{-cg_u} * e^{-(\alpha+\gamma)G} \end{cases}$$



A simple model

$$\frac{\Delta G_1}{\Delta G_2} > 1 \ ?$$



$$\beta' = \beta - \alpha$$
$$\gamma' = \alpha - \gamma$$

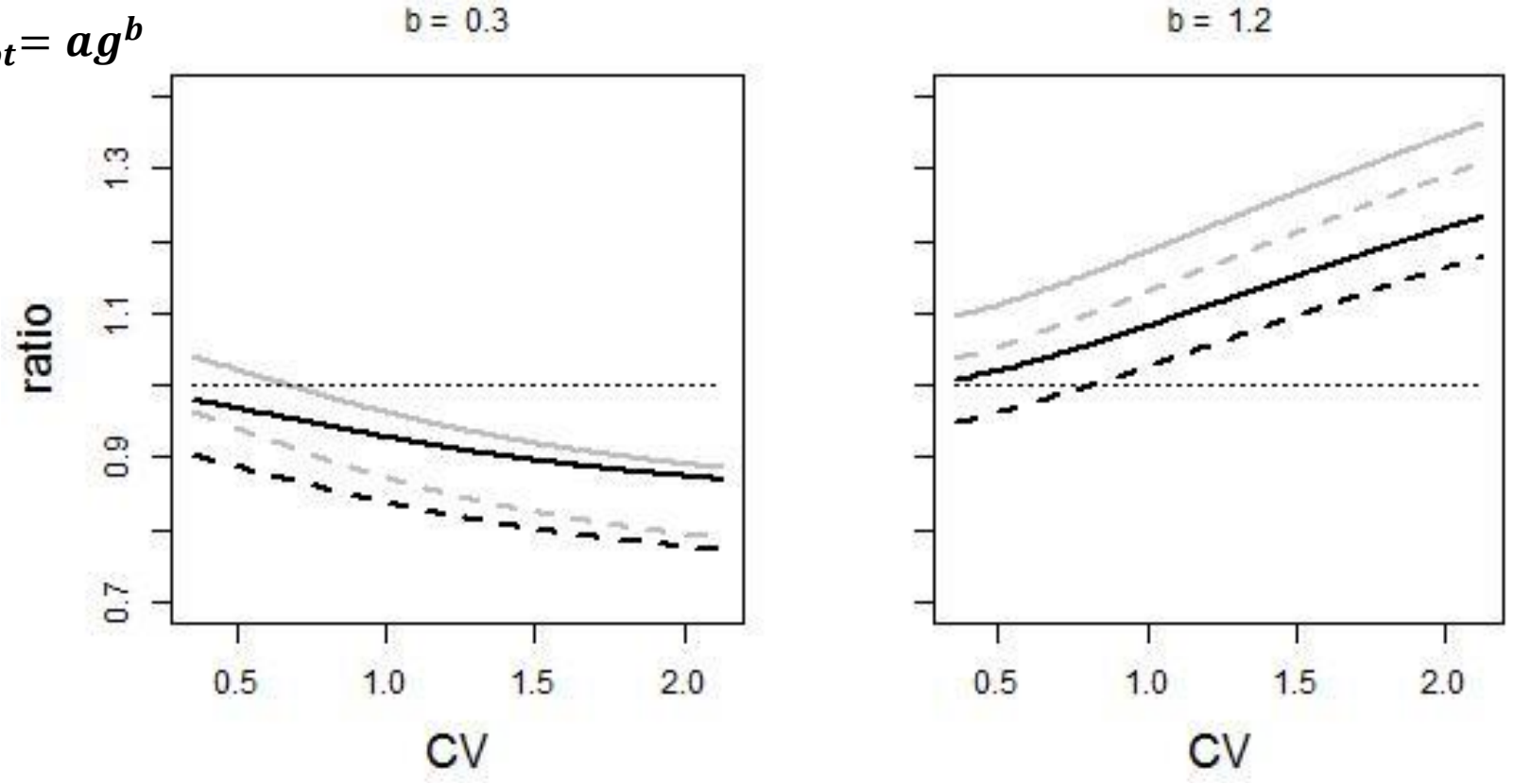
- β': **intensity** of size-asymmetric competition
- γ' : **type** of size-asymmetric competition
  - $\gamma' = 0$: relative size-asymmetric
  - $0 < \gamma' < \alpha$: partial size-asymmetric
  - $\gamma' = \alpha$: absolute size-asymmetric

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

Results: Case b>0, c=0

g=0.1m²; G=15m²ha^{-1}

$\Delta g_{pot} = a g^b$



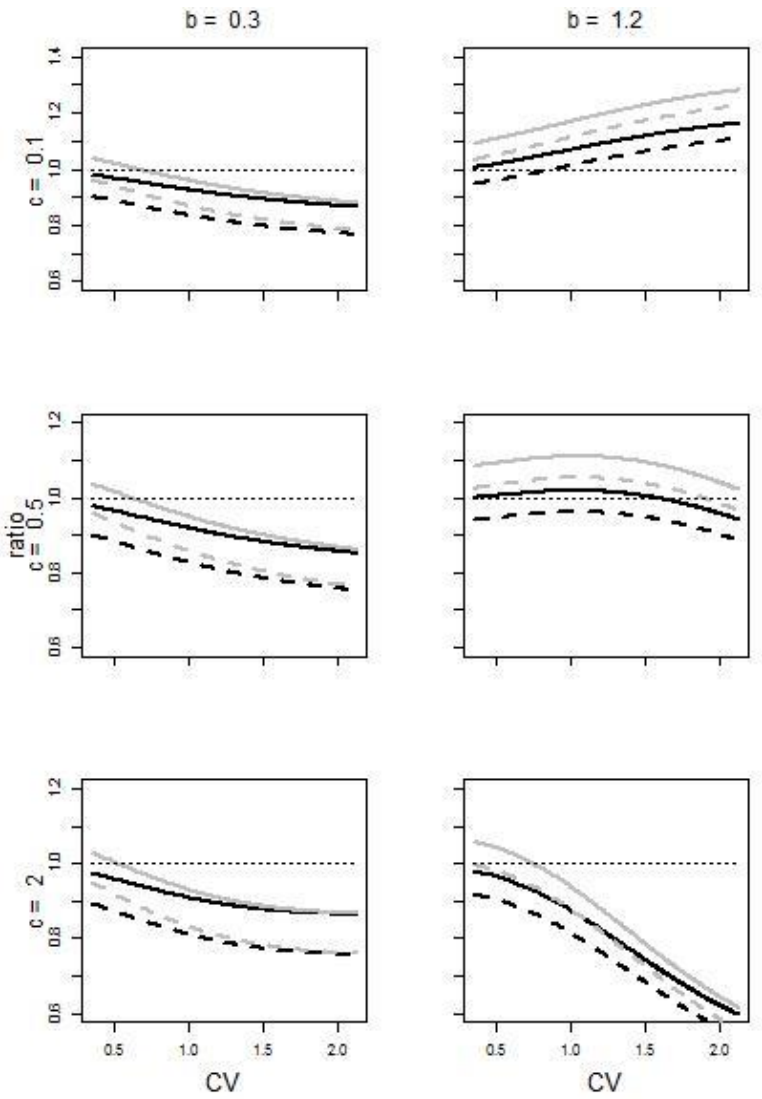
β′=0.001 γ′=0 γ′=0.01

β′=0.01

Results: Case b>0, c>0

g=0.1m²; G=15m²ha-1

$$\Delta g_{pot} = a g^b e^{-cg}$$



β′=0.001 γ′=0

β′=0.01 γ′=0.01

Synthesis

- Higher productivity of the two strata stand is favoured by low intensity of size-asymmetric competition
- Higher productivity of the two strata stand is favoured by absolute size-asymmetric competition
- Positive or negative relationships between size-inequality and productivity depends strongly on *b* (growth function)
- Non-monotonous relationships can emerge depending on the growth function (parameter $c>0$)
- Could explain why negative patterns are more frequent ($b<1$, $c>0$, β' is high)

Limits

- Static approach
- Too simple
  - increase the number of strata
  - relax the « equal basal area » hypothesis
  - relax the « perfect homogeneity » hypothesis
- Not mechanistic enough
- The results may be highly sensitive to the model structure

Conclusions

- We cannot infer processes from patterns (negative relationship ≠ size asymmetric competition effect)
- We need to test mechanisms that may cause positive or negative relationships (ex. phenotypic plasticity, Ishii et al. 2013)
- Going beyond patterns: We need to build predictions based on theoretical developments
- Forest dynamics models could be highly helpful

Thank you for your attention