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# More species, more trees, more productivity: the role of the tree packing in forest diversity-productivity relationships

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## Résumé

Forests provide many vital ecosystem services that strongly depend on species diversity, as illustrated by the repeatedly observed relationships between tree species diversity and forest productivity. Yet, our understanding of the underlying processes of these relationships, especially species richness and ecosystem productivity, remains weak. In fact, the slow dynamics of forest ecosystems makes experimental tests difficult - although long-term experiment start bringing interesting results. This being said, the study of forest ecosystems beneficiates of a long history of modelling efforts, and such forest models represent key tools

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to explore the links among species composition, forest functioning and climate, complementing experimental and empirical approaches.

Regarding its causal mechanisms, the Diversity-Productivity relationship (DPR) is assumed to result mostly from complementarity between species at the tree level, while emerging community-level processes remain poorly explored. In this talk, we propose that the ‘tree packing effect’ (TPE), by which species diversity promotes productivity through tree-tree interactions but also by positively impacting maximum stand density, is an important determinant of DPR. We provide a proof of concept for the TPE through a dual approach, linking empirical observations and simulations. First, relying on national forest inventories, we fitted self-thinning lines of six European countries to examine whether these lines were influenced by plot species richness. This analysis showed that maximum stand density increased with tree species richness in Europe, in all but one country. This trend was stronger in extreme climates. Second, relying on an individual-based forest dynamics model, we ran a massive simulation-based experiment (including 7,024,815 simulations), to quantify DPRs for 1,015 sites in Europe, by controlling or not for the stand density. The simulations highlighted the generality of the TPE in Europe, by showing positive DPRs up to 10-times stronger than without TPE. This positive effect of diversity on forest productivity through tree packing is also stronger in extreme climates, especially in warm and dry conditions.

Our results highlight that the effect of diversity on forest functioning is partly mediated by changes in stand density. This mechanism has been long overlooked in biodiversity – ecosystem functioning studies, as it is for instance controlled in the majority of experiments aiming at depicting DPRs. Our finding opens key perspectives for forest management and climate change mitigation programs.

**Mots-Clés:** Forests, species richness, ecosystem functioning, modelling, overyielding, canopy packing, density