Received: 26 March 2024 | Accepted: 7 October 2024

DOI: 10.1111/1365-2745.14460

BRITISH ECOLOGICAL SOCIETY Journal of Ecology

RESEARCH ARTICLE

More species, more trees: The role of tree packing in promoting forest productivity

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Funding information
French Ministry of Ecology and Sustainable Development, Grant/Award Number: DISTIMACC/ECOFOR-2014-23; SUMFOREST Era Net, Grant/Award Number: REFORM/PCIN2017-026; Agence Nationale de la Recherche, Grant/Award Number: BIOPROFOR/ANR-11-PDOC-030-01, DIPTICC/ANR-16-CE32-0003 and FISSA/ANR-21-CE32-0010-01; European Union's Seventh Programme, Grant/Award Number: FP7/2007–2013

Handling Editor: Tommaso Jucker

Abstract

1. Forests provide many ecosystem services that strongly depend on species diversity, as illustrated by the repeatedly observed diversity–productivity relationships (DPRs). These forest DPRs are assumed to result mostly from complementarity between species at the tree level whilst emerging community-level processes remain poorly explored.
2. In this study, we propose that the 'tree packing effect' (TPE), where species diversity promotes productivity by positively impacting maximum stand density, is an important determinant of DPRs. We tested the two components of TPE: (i) whether maximum stand density increases with species richness and (ii) whether this higher stand density allowed by species richness promotes forest productivity.
3. First, relying on national forest inventories of six European countries (NFIs, totaling 2,367,776 trees), we fitted self-thinning lines to examine whether these lines were influenced by plot species richness. We showed that maximum stand density increases with tree species richness in Europe, in all but one country. This trend was notably stronger in extreme climates.
4. Second, we ran a large simulation-based experiment (including 7,024,815 simulations) with an individual-based forest dynamics model able to control for stand-density effects, to quantify DPRs for more than 1000 sites in Europe. Relying on an original method to quantify DPRs at the site level, we compared the strength of DPRs simulated with and without control for stand density. We found positive DPRs up to 10-times stronger when TPE is at play than when stand density is controlled. This positive effect of diversity on forest productivity through tree packing is also stronger in extreme climates, especially in warm and dry conditions.
5. *Synthesis*. Highlighting the generality of the TPE in European forests, our results reveal that the effect of diversity on forest functioning is partly mediated by

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diversity-driven changes in stand density. This mechanism has been long overlooked in biodiversity—ecosystem functioning studies, but our findings strongly call for its reconsideration, especially in natural forests. It also opens key perspectives for management and climate change mitigation programmes.

KEYWORDS
biodiversity, canopy packing, complementarity, ecosystem functioning, forest dynamics model, forests, stand density, tree packing

1 | INTRODUCTION

Despite having supplied humanity for millennia with many important goods and services (Brockerhoff et al., 2017; FAO and UNEP, 2020), forests have only recently received large international attention regarding their role in mitigating both climate change and the biodiversity crisis (FAO and UNEP, 2020; Griscom et al., 2017; Pachauri & Meyer, 2014). Many studies have shown that tree species diversity can foster forest productivity and carbon sequestration, resulting in positive diversity–productivity relationships (DPRs) (Brockerhoff et al., 2017; Hooper et al., 2012; Liang et al., 2016). This result is now well-established in the literature and has been corroborated by many methodological approaches relating biodiversity and ecosystem functioning (BEF), including studies relying on forest inventories (Aussenac et al., 2021; Liang et al., 2016; Paquette & Messier, 2011; Ratcliffe et al., 2016; Toigo et al., 2015) or empirical observations (Jucker et al., 2014; Pretzsch et al., 2015), experiments (Sapijanskas et al., 2014; Toïgo et al., 2022; Williams et al., 2017), and simulations with process-based models (Bohn & Huth, 2017; Maréchaux & Chave, 2017; Morin et al., 2011).

DPRs have been assumed to result mostly from species complementarity in resources uptake and use-efficiency (Barry et al., 2019), thus primarily depending on niche partitioning between species. In the case of forests, niche partitioning can occur through root spatial stratification (Cabal et al., 2024), but most evidence concerns light uptake as forest dynamics are generally strongly driven by light availability (Pacala et al., 1996; Rüger et al., 2020), leading to a size-asymmetric competition (Cordonnier et al., 2019; Schwinning & Weiner, 1998). Niche partitioning may lead to a more efficient use of canopy volume in multispecific forests than in monospecific ones and to an increased light interception at the ecosystem level (Guillemot et al., 2020; Rissanen et al., 2019; Williams et al., 2021). This 'canopy packing' effect has thus been proposed as a key mechanism explaining the positive effect of species diversity on forest productivity (Morin et al., 2011), and has been evidenced in both temperate (Jucker et al., 2015; Pretzsch, 2014; Williams et al., 2017) and tropical forests (Sapijanskas et al., 2014).

The optimization of canopy packing in multispecific stands is usually explained by two complementary processes: neighbourhood-driven plasticity in crown shape and volume (Guillemot et al., 2020; Jucker et al., 2015; Pretzsch, 2014), and a stronger vertical stratification of tree crowns in the canopy (Morin et al., 2011). Although crown plasticity has received more attention (Guillemot et al., 2020; Jucker et al., 2015; Pretzsch, 2014; Williams et al., 2017), evidence has been provided for both processes, either in observational data (Jucker et al., 2015) or tree diversity experiments (Williams et al., 2021).

Yet, crown plasticity and vertical stratification mostly depend on direct interactions between individual trees. More generally, the hypotheses used to explain BEF patterns in forests are usually based on tree–tree interactions (Trogisch et al., 2021), thus at local scale. This focus may have overshadowed the possible role of complementarity processes on patterns occurring at a larger scale, that is, the scale of the tree community level. This scale, defined as the collection of individual trees within a given area, typically between 10^3 and 10^4 m^2, is often referred to as the stand in the forestry literature. Here, we hypothesize that a more efficient use of resources due to niche partitioning between species may increase the carrying capacity at the stand scale. In other words, species diversity may raise the maximum stand density, with more trees coexisting in multispecific forests than in monospecific ones. In this hypothesis, we therefore assume that diversity effects on tree–tree interactions at the local scale have also consequences at the stand scale by influencing the number of trees in the community. So far, such a pattern has only been indirectly suggested, for specific mixtures (Pretzsch & Biber, 2016). In addition, we make a step further by hypothesizing that the larger number of trees, resulting from the increased species diversity, may in turn increase stand productivity. This effect, that we call the 'tree packing effect' (*TPE*, Figure 1), is thus a consequence of species complementarity for resource use on spatial coexistence and ecosystem productivity.

There are several indirect clues in favour of this TPE hypothesis. First, stand density has been known to affect forest productivity for a long time (Forrester, 2014; Reineke, 1933). Second, stand density is usually controlled for in tree diversity experiments (Schnabel et al., 2019; Toïgo et al., 2022; Williams et al., 2017) and in semi-experimental field samplings (Jucker et al., 2015; Pretzsch et al., 2015) that aim at disentangling the effect of species richness on ecosystem functioning through tree–tree interactions. In the same vein, in observational studies, stand density (or proxys for it) has often been considered as a covariate to be controlled to isolate putative effects of tree diversity on productivity, rather than a response variable driving DPRs (Chisholm et al., 2013; Paquette & Messier, 2011; Ratcliffe et al., 2016; Vila et al., 2013). Therefore, the

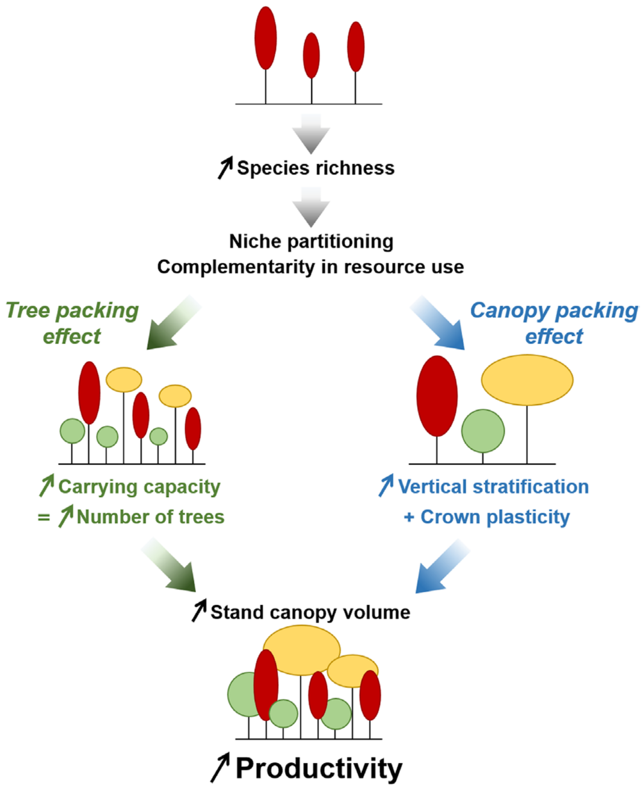

FIGURE 1 Theoretical scheme representing the effect of canopy packing (blue path) and tree packing (green path) effects on stand canopy volume and productivity in response to increasing tree species diversity. Processes involved in the canopy packing effect are rather related to tree–tree interactions and do not affect the number of trees per area, but more the individual allometry and functioning of neighbouring trees. Processes involved in the tree packing effect act at the community level, that is, the total number of trees changes at the stand level.

importance of diversity effects on stand density in driving positive DPRs remains largely unexplored (Chisholm & Dutta Gupta, 2023). Yet, if the TPE is confirmed, it implies that a key effect of diversity on forest productivity has been overlooked in BEF-studies.

The TPE thus relies on two components: (i) on average, species richness increases maximum stand density and (ii) this higher stand density enabled by increased species richness promotes forest productivity. To the best of our knowledge, these two components have never been clearly connected and thus tested. Regarding the first one, the positive effect of species richness on stand density has been suggested or indirectly mentioned in several studies (Pretzsch & Biber, 2016; Tatsumi & Loreau, 2023), but has not yet been generally quantified, especially for a large range of tree species and environmental conditions.

The state-of-the-art for the second component of the TPE is also very incomplete. To the best of our knowledge, although former studies have provided some insights about the role of stand density (or proxys for it) on forest functioning in mixed forests (e.g. Brunner & Forrester, 2020; Paquette & Messier, 2011; Ratcliffe et al., 2016), the links between species diversity, stand density, and forest productivity have not yet been clearly and generally depicted. Furthermore, testing for this second component is not straightforward, as higher stand density may be associated with smaller average tree size and/or younger age, possibly leading to a decrease in biomass production per tree. Moreover, understanding the links between tree species diversity, stand density and forest productivity is challenging because they are impacted by many factors, such as climate, soils, stand age, or past management.

Here, we test for the existence of the TPE across a wide range of forest ecosystems and environmental conditions in Europe. Considering the two components of the TPE, we tested (i) whether diverse forests have a larger maximum stand density than monospecific ones, and (ii) whether this can result in a positive effect of species richness on forest productivity. We tested these two components using two separate but complementary analyses, relying respectively on an observational dataset and a process-based simulation experiment.

To test for the first component of the TPE, we analysed the effect of species richness on the maximum stand density in forest plots (N_{max} [number of trees.ha^{-1}]), defined as the maximum number of trees a plot can sustain at a given developmental stage, which is a well-known rule in forest ecosystems, also called the self-thinning boundary (Forrester et al., 2021; Reineke, 1933). We did so by analysing national forest inventories data from six European countries (Ratcliffe et al., 2016), thus sampling a large diversity of tree species assemblages and environmental conditions.

To test for the second component of the TPE, we used a simulation experiment to explore whether TPE can be involved in shaping DPRs in European forests. Former studies that quantified DPRs in large observational datasets (Liang et al., 2016; Paquette & Messier, 2011; Ratcliffe et al., 2016) did not focus on the link between species richness and stand density and its implications for forest productivity. In fact, evaluating the interactive effects of species richness and stand density on productivity in observational data cannot be done properly because disentangling these effects requires comparing forests with similar tree species composition, in the same environmental conditions but with contrasting stand densities, which is impossible in practice. This is especially the case when focusing on a wide range of species and community composition. Therefore, we tested the significance and strength of the second component of TPE using a validated forest dynamics model in which stand density can be controlled. Relying on functional and demographic processes, such models consider biotic interactions (especially competition for light) and abiotic drivers such as climate (Bohn & Huth, 2017; Morin et al., 2011), and can provide robust predictions of ecosystem composition, structure, and functioning (Maréchaux et al., 2021). Their simulations have been already used to help disentangle the mechanisms behind DPRs especially how climate conditions may modulate these relationships (Bohn & Huth, 2017; Maréchaux & Chave, 2017; Morin et al., 2011, 2018). We thus used the individual-based forest model ForCEEPS (Morin et al., 2021) to test for the effect of maximum stand density (N_{max}) on DPRs, by simulating forest stands with various species richness levels across the whole range of environmental conditions in Europe, with or without controlling for stand density.

2 | MATERIALS AND METHODS

2.1 | Testing the effect of diversity on tree packing

2.1.1 | Rationale

Demonstrating that stand density increases with increasing species richness (TPE first component) is not straightforward because a higher stand density is usually associated with smaller average tree size and/or younger trees. Therefore, we tested whether maximum stand density increases with species diversity for a given average tree size. To do so, we assessed self-thinning boundary lines (Reineke, 1933) that quantify the maximum number of trees that a stand can hold, for a given developmental stage, before the appearance of mortality from competition. This line is classically species-specific, as it was originally designed for monospecific even-aged stands.

2.1.2 | Data

NFI data

Forest inventory data came from the FunDivEUROPE inventory Platform (Ratcliffe et al., 2017; www.fundiveurope.eu), and consisted of harmonized data from National Forest Inventories (NFIs) of six European countries (Spain, Germany, France, Sweden, Finland, and Walloon region of Belgium; Table A). Using NFI data brings major advantages: as NFI are systematic over the countries, their data maximize the types of species assemblages, structure, and management conditions that are sampled, especially in comparison with experimental data. The large geographical extent of the sampling across Europe also maximizes the ranges of climate and edaphic conditions in the data. The sampled plots have a relatively small size (Table A), which ensures that each plot encompasses a single habitat. The dataset includes DBH data for 2,367,776 trees with a minimum threshold of 7.5 cm in diameter, from 190,335 forest plots (Table S2).

Climate data

Climate data were extracted from the CHELSA database (Karger et al., 2017) that provides high-resolution (~1 × 1 km) climate data for the whole Earth land surface areas. CHELSA provides time-series of historical climate at a monthly time step covering the period going from 1979 to 2013. We used annual average temperature and annual sum of precipitation data at a 10-min scale to characterize the climate in Europe. For each site, we averaged times series of temperature and precipitation over the 34 years. Then, using Martonne aridity index (de Martonne, 1926), we calculated a mean aridity index identified as *MAI* (for mean Martonne aridity index). Note that high values of *MAI* correspond to low hydric stress.

2.1.3 | Statistical analyses

The maximum number of trees $N_{\max}$ given by the self-thinning rule is:

$$\ln(N_{\max}) = a + b \times \ln(D_g) \tag{1}$$

where D_g is the mean quadratic diameter of the stand, a good proxy for the development stage. When D_g is close to 7.5 cm (i.e. the minimum threshold considered in NFIs), the estimation of $N_{\max}$ can be biased due to trees that are not counted below the threshold of 7.5 cm in DBH. To avoid this, we kept only plots with a D_g over 10 cm, as done in former studies (Condés et al., 2017).

For each country, we estimated tree packing by fitting a 95th quantile regression between log-transformed values of stem number (N) and mean quadratic diameter (D_g), also considering other co-variables. Quantile regression has many applications in ecology, linking for instance rate functions to their limiting factors (Cade & Noon, 2003), but also determining self-thinning boundaries in plants (Cade & Guo, 2000) and more specifically in forests (Aussenac et al., 2021; Condés et al., 2017; Toïgo et al., 2018). We expected that stand density would depend on tree species richness and that this relationship would vary between countries because of changes in tree species identities and climate conditions. In this study, we focused on species richness as a main proxy for species diversity. Yet, it is worth mentioning that other facets of diversity may be impactful on DPRs, such as species evenness (Hordijk et al., 2023). We also added a 'country' effect in the statistical model to take into account differences in sampling design (Table A). We thus included a three-way interaction between D_g (log-transformed), species richness, and country. In addition, a four-way interaction between D_g (log-transformed), species richness, mean annual temperature (*MAT*) and *MAI* was added to take into account the fact that climate conditions may influence the effect of $D_g.SR$ on N. We centered the values of species richness ($\mu_{SR} = 2.1$), *MAT* ($\mu_{MAT} = 10.3°\mathrm{C}$) and *MAI* ($\mu_{MAI} = 40.6$) to facilitate the interpretation of the interactions.

The model is summarized below:

$$\begin{aligned} \ln(N) \sim \ln(D_g) \times (SR - \mu_{SR}) \times \text{country} + \ln(D_g) \times (SR - \mu_{SR}) \\ \times (MAI - \mu_{MAI}) \times (MAT - \mu_{MAT}) \end{aligned} \tag{2}$$

where N is the number of stems in the stand; D_g is the mean quadratic diameter; *SR* is the species richness; *MAI* is the mean Martonne aridity index and *MAT* is the mean annual temperature. We performed these analyses with R version 4.1.2 (R-Core-Team, 2020) and package *quantreg* (Koenker, 2022). Fixed effects were tested using a *t*-test. We checked that the variables were not too collinear relying on the variation inflation factor (VIF; Dormann et al., 2013). We also calculated the check score (fit estimator for quantile regression Koenker & Bassett, 1978), with a value of 0.056.

In addition to the main analysis, we had to ensure that our analyses were not strongly influenced by management because most forests in Europe are managed. We thus tested whether stand density increased with species richness in an independent dataset for forests in France, in which management history is known, and with managed and unmanaged forests in French Reserve plots. This is further shown and discussed in Appendix C.

2.2 | Testing the effect of tree packing on stand productivity

The workflow of this simulation experiment is summarized in Figure A.

2.2.1 | Description of the ForCEEPS model

We used the model ForCEEPS to simulate DPRs and test for an effect of maximum stand density (N_{max}) on DPRs (TPE second component). ForCEEPS is an individual-based model that relies on a limited set of essential assumptions, with low parameter requirements. Following the standard approach of gap models (Botkin et al., 1972; Bugmann, 2001), the establishment, growth, and mortality of trees in multiple forest patches are simulated whilst considering abiotic and biotic constraints. Vertical stratification can occur in the model due to differences in shade tolerance between species. Crown plasticity can also partly occur (i.e. only in the vertical dimension of the canopy) in response to light exposition of the tree, with the crown length decreasing with increasing shading. Properties simulated at the patch scale can be aggregated to derive forest properties at a larger spatial extent. ForCEEPS was developed for simulations over a wide range of environmental conditions and was calibrated for the most widespread tree species in Europe (Morin et al., 2021), and has already been used to simulate DPRs Europe (García-Valdés et al., 2020). Here we focused on the 22 most dominant species (see Table S5). ForCEEPS was implemented in the Capsis platform (Dufour-Kowalski et al., 2012), a detailed model description is available in previous work (Morin et al., 2021) and in Appendix A. However, as we aimed at running the model across sites in Europe, we checked the model's ability to predict potential species composition and stand growth at the continental scale using 148 sites across Europe (described in Appendix B).

In this study, we took advantage of the ability of ForCEEPS to control for stand density, to run simulations without any a priori constraints on stand density and simulations with a forced value for stand density. In the first mode (natural regeneration), the number of coexisting trees varies as the simulation progresses, but is limited by competition between trees. The number of trees in the stand is thus not a priori controlled and reaches small or large values depending on species composition and environmental conditions. The second mode mimics plantations at a given controlled stand density (Morin et al., 2020), in which dead trees are replaced by newly planted seedlings. In this mode, the realized stand density is thus forced to a specific value (i.e. 500 or 1500 trees.ha^{-1} in this study). Note that the realized value can be lower in some instances if the local site conditions do not support such a number of trees to coexist in a stand (e.g. the new seedlings die just after being planted because of drought or shade)—as shown in Figure S6.

A key point to mention is that in the model, the outcome of intra and interspecific competition for light is directly driven by light availability at the tree level and environmental conditions. The simulated realized species richness, stand density, and productivity are driven by these factors, and not through pre-defined competition indices. If the simulations are run long enough, there is no reason that species-rich tree communities should contain a priori more trees than communities with fewer species. Processes that allow more trees to coexist and for those trees to be more productive in species-richer communities thus emerge from the simulations—as already shown for DPRs in not-controlled stand densities (Morin et al., 2011).

2.2.2 | Simulation design

Number of simulations

We selected 1015 sites across Europe, through a random sampling in the continental climatic space (see Appendix D for details). In each site, we considered three scenarios of stand density: not-controlled stand density (i.e. no control on N_{max}), and two forced densities in which N_{max} is forced to 500 and 1500 trees.ha^{-1} (representing low and high-stand density values for most European forests, respectively; Ratcliffe et al., 2016). In each site, we simulated DPRs for each stand-density scenario—see Morin et al. (2011, 2014, 2018) for previous DPR simulations using a similar model.

These simulations differed in their potential species pools, ranging from 1 to 22 species. Simulating all possible species combinations would represent more than 4 million combinations per site and stand density scenario. Therefore, we first chose to run simulations for the potential species richness levels of $SR = \{1, 2, 3, 5, 8, 11, 14, 17, 20, 21, 22\}$, as previous studies have shown that simulating all potential species richness levels (i.e. number of species at the beginning of the simulation) did not significantly improve the estimation of DPRs (Morin et al., 2011, 2018). Second, to further reduce simulation time, we limited the simulation runs for each richness level tested to 300. More precisely, for the potential species richness levels of $SR = \{1, 2, 20, 21, 22\}$ we were able to simulate all possible combinations: for $SR = 22$, we ran one simulation with all species; for $SR = 1$ and $SR = 21$, we ran simulations corresponding to the 22 possible combinations; for $SR = 2$ and $SR = 20$, we also ran simulations corresponding to the 231 possible combinations. For the levels $SR = \{5, 8, 11, 14, 17\}$, we ran 300 simulations for each level, randomly drawn from all possible combinations of species, respectively. This random choice was the same for all sites and modalities, to allow non-biased comparison of tree communities. Therefore, for each site and stand-density scenario, we reach 2307 simulations ($22 + 231 + 5 \times 300 + 231 + 22 + 1$). In total, we ran 7,024,815 simulations (Figure S6). The total number of trees simulated under this scheme (including those that died) exceeded 400 billion.

Simulations runs and outputs

Simulations of 3-ha-forests (30 patches of 0.1 ha) started from bare ground and were run for 2000 years with stable climate conditions so that the simulated forest could reach the pseudo-equilibrium (as gap dynamics still randomly occurs due to the nature of cyclical succession on each patch) in terms of species composition, standing biomass and stand density—a classic simulation method with such tools (Morin et al., 2011, 2018). Consistent with the observation-based analysis with NFI data, we used historical conditions between 1979 and 2013 from the CHELSA database to build 2000-year time-series, by repeating the 34 years randomly.

As the realized species richness was stable in the last 1000 years of simulation (pseudo-equilibrium state), we defined the final species richness (realized *SR*) as the species richness at the end of the simulation and we considered a species to be present if its biomass represented more than 1% of total above-ground biomass. We used mean site basal area gross increment [*BAI*] as a classic proxy for productivity (Morin et al., 2011, 2021; Ratcliffe et al., 2016; Schnabel et al., 2019).

Productivity was obtained by averaging the yearly productivity of 10 years at a 100-year distance (1100, 1200, …, 2000) to minimize temporal autocorrelation (Morin et al., 2011). A visual representation of the outputs for each stand-density scenario is shown in Figure S6. We also output the simulated final leaf area index (*LAI*), the species relative abundances calculated from the basal area, and the mean number of trees per hectare.

2.2.3 | Analyses

Depicting DPRs with a new method

To properly depict the effect of species richness (realized *SR*) on stand productivity amongst the three stand-density scenarios, we analysed the outputs from the simulations with an original two-step approach. The aim of this approach was to capture the effect of *SR* on productivity with a single parameter β corresponding to the productivity benefit (if positive) or disadvantage (if negative) of having an infinite number of species compared with monocultures (e.g. $\beta = 0.2$ means that having an infinity of species would represent a 20% productivity increase compared with monocultures; see example in Figure S7). To do so, we first developed a mixed-effect model (Zuur et al., 2009) using data from all the simulations, with stand-density scenario nested within the site included as a random effect. Second, we analysed these random effects to evaluate the link between the stand-density scenario and the *SR* effect on productivity.

For each stand-density scenario at a given site, we modelled the productivity (in terms of *BAI*) as a function of *SR* with an exponential increase or decrease up to an asymptotic value when *SR* tends toward infinity, as described by Equation 3:

$$BAI = \alpha \times \left(1 + \beta \times \left(1 - \exp^{\ln\left(\frac{1}{2}\right) \times \frac{(SR-1)}{(\gamma-1)}}\right)\right) \tag{3}$$

This allowed us to estimate the parameter β (see above), whilst α is the value of productivity for monocultures (i.e. when $SR = 1$) and γ the value of *SR* for which the change in *BAI* is half of the one when *SR* tends to infinity. The method is illustrated in Figure S7.

Considering that model convergence of Equation 3 was not possible due to the large number of levels and the very large number of simulations, we had to fit the model with the following procedure and simplifications. First, we fitted Equation 3 with a random site effect on parameters α and β, but only a fixed effect for the stand-density scenario variable. This simplification implies that the variability of α and β between the three stand-density scenarios is ignored in this first step. From this first model fit, we obtained a value for parameter γ that we will consider as constant for the next steps of the procedure (we checked that the results are not sensitive to this parameter). Once γ was fixed, we were then able to transform Equation 3 into a linear form. We defined the transformed variable *X* as:

$$X = 1 - \exp^{\ln\left(\frac{1}{2}\right) \times \frac{(SR-1)}{(\gamma-1)}} \tag{4}$$

Then, we transformed Equation 3 into

$$BAI = \alpha \times (1 + \beta \times X)$$

and then

$$BAI = \alpha + \beta' \times X \tag{5}$$

with the new parameter $\beta' = \alpha \times \beta$.

In this new formulation, α remains the productivity value for a monoculture and β' is the absolute increase or decrease when *SR* tends toward infinity. To come back to the relative value of increase or decrease, we can calculate $\beta = \beta' / \alpha$. A drawback of this calculation is that it can provide very large values of β for very unproductive stands where α is close to zero. The convergence of Eq5 was then possible including nested stand-density scenario within site random effects on both parameters α and β'. Finally, we analysed these random effects to evaluate the differences amongst the three stand-density scenarios. Analyses were done with the package *nlme* in R, version 3.6 (Pinheiro et al., 2020). See Appendix D for more details.

Moreover, to check the consistency of the DPRs depicted with this original method, we also analysed them under a classic framework (Loreau, 1998), in which the mixture effect is calculated as the comparison between the productivity of the mixture versus the productivity of the monoculture (see Appendix D).

Structural equation model analyses

We used data from the simulations without control on stand density to assess the relative importance of tree packing and canopy packing for driving forest productivity as both effects are at play. We built a structural equation model (SEM) to determine the functional paths driving forest productivity, considering all drivers (climate, soil conditions, initial species richness and composition) and main stand properties (realized species richness, realized stand density, LAI, community-weighted mean (CWM) in shade tolerance, BAI).

More precisely, the SEM allowed us to assess the relative strength of paths linking species richness to productivity, that is, through the TPE or canopy packing effect (CPE). Forest productivity simulated in the model is strongly linked to the stand LAI. As tree packing and canopy packing are both expected to increase LAI at the plot level, we thus considered the relative role of the number of trees per ha and the CWM of shade tolerance (see Morin et al., 2011) in driving LAI as good proxys for TPE and CPE, respectively. In addition, we also considered the direct effects of the number of trees per ha and CWM of shade tolerance on forest productivity to account for residual effects apart from those on LAI. To account for the differences in climate conditions across sites, we created a latent variable *'Abiotic'* that depended on *MAT*, *MAI*, and SWHC (although the latter was not significant in the selected model). Given the very large dataset used here, Bentler's comparative fit index (CFI) was used because it standardizes for sample size (Bentler, 1990), with a model being relevant if CFI >0.90 (and with SRMR <0.80). Sites in which no forests were simulated (i.e. SR = 0 and BAI = 0) were removed. The SEM analysis was carried out in R through the *lavaan* package (Rosseel, 2012).

3 | RESULTS

3.1 | Species richness effects on maximum stand density (TPE first component)

Consistent with our hypothesis, we found that the average number of trees per area increased with species richness for in all regional datasets (Figure S5a), except Wallonia – the smallest dataset with only 0.65% of the plots. Then, we found that $N_{\max}$ (maximum stand density derived from self-thinning lines) increased with species richness in all regional datasets, again except Wallonia (Figure 2), with variable strength between regions (Figure 3a–c). In addition, we found that this positive effect was stronger in harsh environments (cold/wet and warm/dry), whilst it became negligible in milder conditions (between 7.5 and 10°C, Figure 3d–f). These results were qualitatively consistent whatever the mean quadratic tree diameter (D_g, Figure 3 and Table S3). Yet, it is noticeable that smaller effects were observed in the cold/wet conditions in the large quadratic diameter classes because there were fewer observations in such conditions (Figure 3g,h). The fact that the addition of a species had the largest effect on N_{max} at the extremes of the climate space was not due to increasingly poor model performance in those extreme climate conditions (Figure S4), although there is a slight pattern in the coldest locations for the smallest trees.

Moreover, using a 5738 additional dataset made of unmanaged plots in France (Appendix C), we found a significant and positive relationship between species richness and stand density (Figure S5b,c, Table S4), which is consistent with the patterns observed with NFI data mixing managed and unmanaged plots (Figure 2 and Figure S5a). This also shows that our results are not biased by possible differences in management intensity between monospecific and mixed stands, thus reinforcing the generality of our conclusions.

3.2 | Species richness effects on forest productivity as a consequence of increased stand density (TPE second component)

Regarding the simulation experiment to depict DPRs and test for the possible role of TPE on forest productivity, we found that β (ie.

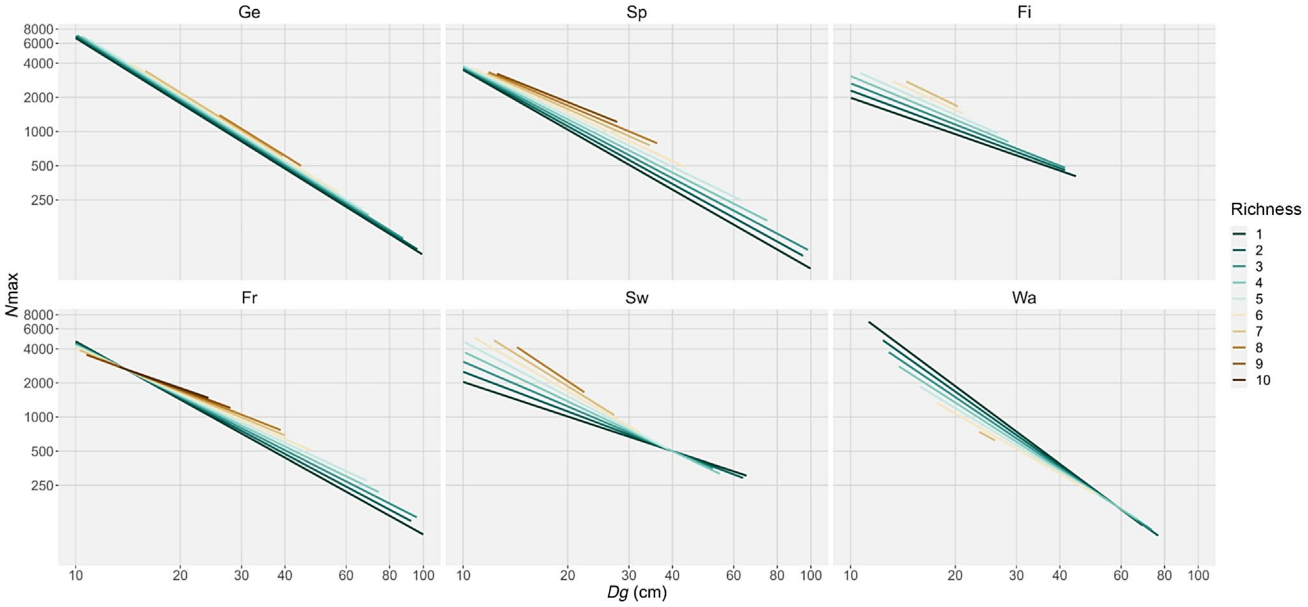

FIGURE 2 Self-thinning boundary lines of forest stands for each species richness and each country. Predicted value of the maximal number of trees per hectare ($N_{\max}$) according to mean quadratic diameter (D_g) (log–log graphical representation) and species richness per country at a mean value of mean Martonne aridity index and mean annual temperature (observed in each country). The lines span the range of D_g for each species richness level in each country (the maximum value corresponds to the 99.9% quantile). *Ge*: Germany (47,274 plots); *Sp*: Spain (59,549 plots); *Fi*: Finland (2330 plots); *Fr*: France (69,145 plots); *Sw*: Sweden (10,802 plots); *Wa*: Wallonia (1235 plots).

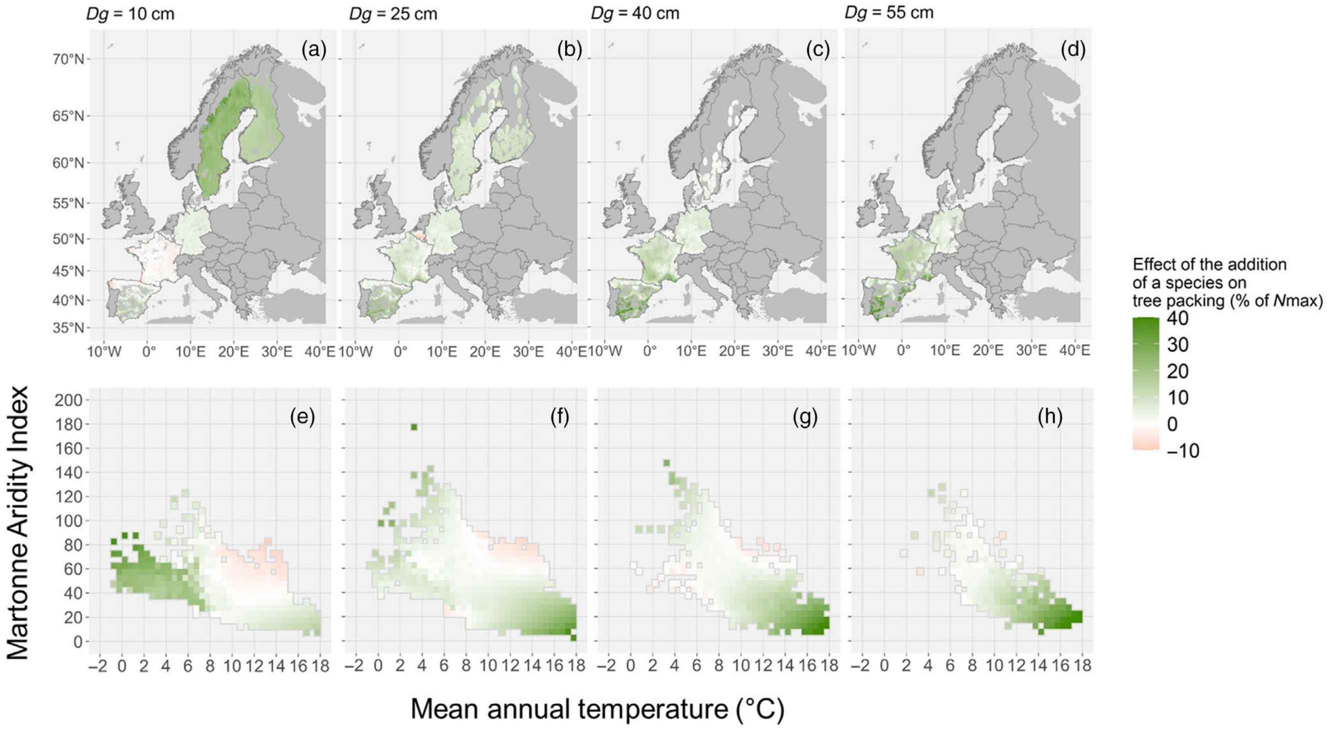

FIGURE 3 Predicted effect of the addition of one species on tree packing (as percentage of maximal tree number N_{max}) in geographical space (top panel—a–d) or climatic space (mean Martonne aridity index vs. Mean Annual Temperature, low panel—e–h), for four quadratic mean diameters (D_g = 10, 25, 40, 55 cm). Values are linearly interpolated in the geographical space. In the climatic space, predicted values are averaged by mean Martonne aridity index classes of five points and by temperature classes of 0.5°C. High values of the mean Martonne aridity index correspond to low hydric stress.

the parameter capturing the effect of SR on productivity) was much stronger for simulations with not-controlled stand density (with a mean realized stand density of 976.95 trees.ha^{-1}, Figure S6) than for simulations with density forced at 500 trees.ha^{-1} and 1500 trees.ha^{-1} (Figure 4). The median of β was slightly negative for 500 trees.ha^{-1} (−7.2%), slightly positive for 1500 trees.ha^{-1} (9.0%), and strongly positive for not-controlled stand density (97.9%) (Figure S7 and Table S6). Consistently, given the large number of sites, the absolute benefit β' was significantly different from zero for all three types of stand density levels: slightly negative (−0.015 m^2.ha^{-1}.year^{-1}) for 500 trees.ha^{-1}, slightly positive (0.018 m^2.ha^{-1}.year^{-1}) for 1500 trees.ha^{-1}, and positive with a higher magnitude (0.224 m^2.ha^{-1}.year^{-1}) for not-controlled stand density. Fixed effects were highly significant; and regarding the structure of the random effects, the variance was balanced between the different levels of the nested effects and the residuals. Furthermore, the results from the classic framework (Loreau, 1998) produced consistent results with those of the original method developed here (Appendix D and Figure S8). These findings thus highlight a TPE resulting in up to 10-times stronger diversity effect on stand productivity when the stand density is not controlled.

Moreover, β values were stronger in cold/wet or warm/dry environments, whilst lower and negative values were found in less extreme environmental conditions (Figure 5). This is consistent with our inventory-based results about the interactive effect of species richness and climate on maximum stand density (Figure 3). This pattern is also stronger in the simulations with a not-controlled stand density (Figure 5c,f).

Furthermore, our simulations with controlled stand density allow an estimation of the canopy packing alone, because in these simulations the effect of species richness on productivity only depends on changes in species composition in a given number of trees (i.e. change in tree–tree interactions). On average, a positive β value (i.e. positive canopy packing) was observed for a majority of sites at 1500 trees.ha^{-1}, but not at 500 trees.ha^{-1} (Figure 4). The absence of a diversity effect on productivity in simulations with the smallest controlled density can be explained by the weak interactions between trees at low density. In addition, we found that predicted stand basal area also increases with tree species richness in sites with the highest β values (Figure S9).

3.3 | Assessing the relative role of canopy packing and tree packing on productivity

The SEM returned a strong fit (CFI = 0.923 and SRMR = 0.062), especially regarding the very large number of observations (n = 2,217,571). It showed that increased species richness led to increased productivity through canopy packing and tree packing, as they both led to an increased LAI, as expected (Figure 6), but also through residual direct effects on productivity. Furthermore, the path linking mean shade tolerance and stand density also showed that canopy packing and TPE are related in the simulations, as observed in nature. However,

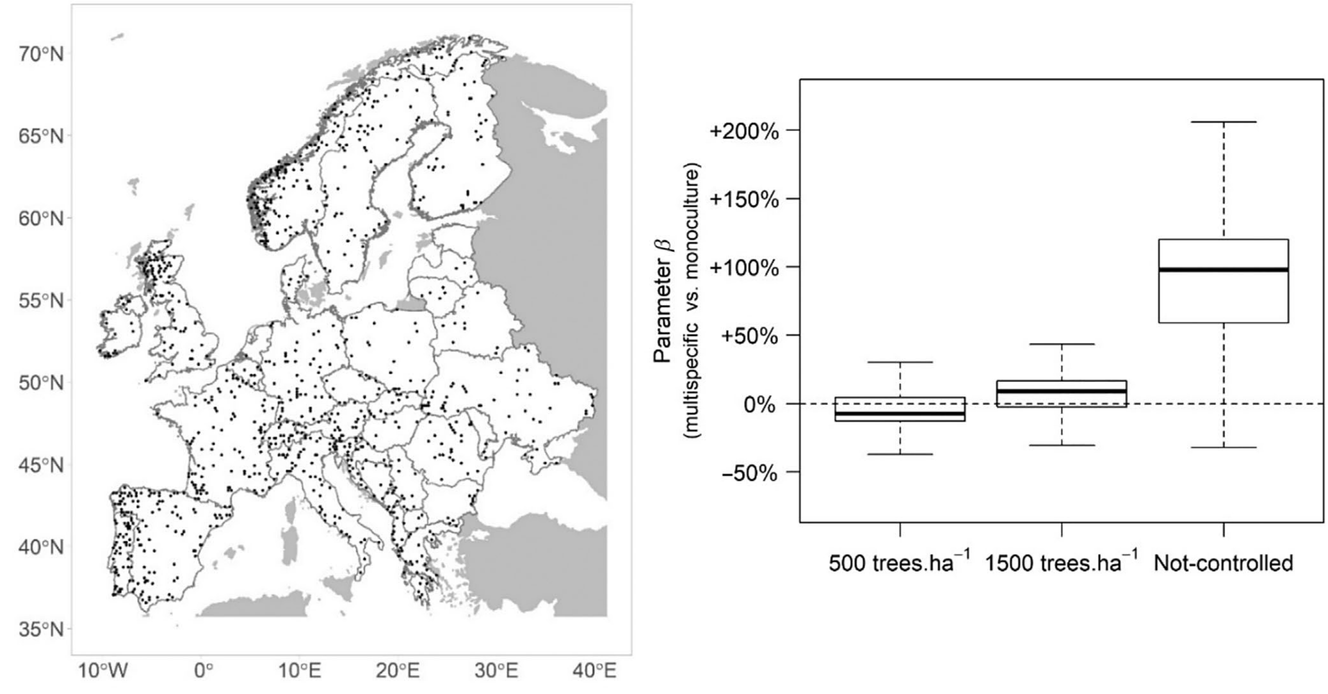

FIGURE 4 *Left panel*: Selected sites ($n = 1015$) for the simulation experiment in geographical space. *Right panel*: Comparison of the values of stand productivity benefit β for an infinite number of species relative to the productivity in a monoculture, between the three stand-density scenarios. Each stand-density scenario gathers data for the 1015 sites.

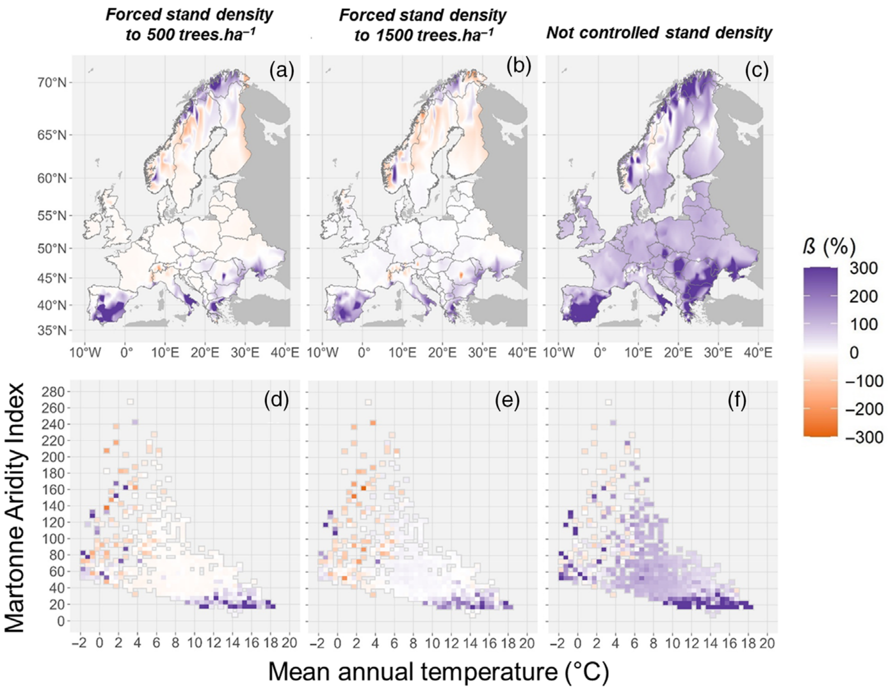

FIGURE 5 Values of stand productivity benefit β for an infinite number of species relative to the productivity in a monoculture. β values are shown for the 1015 locations in Europe in geographical space (top panel - a, b, c) or in climatic space (mean Martonne aridity index vs. mean annual temperature, low panel - d, e, f); for the three stand-density scenarios (500 trees.ha^{-1} - a, d; 1500 trees.ha^{-1} - b, e; not controlled density - c, f). Values are linearly interpolated in the geographical space. In the climatic space, values are averaged by mean Martonne aridity index classes of five points and by temperature classes of 0.5°C. High values of the mean Martonne aridity index correspond to low hydric stress.

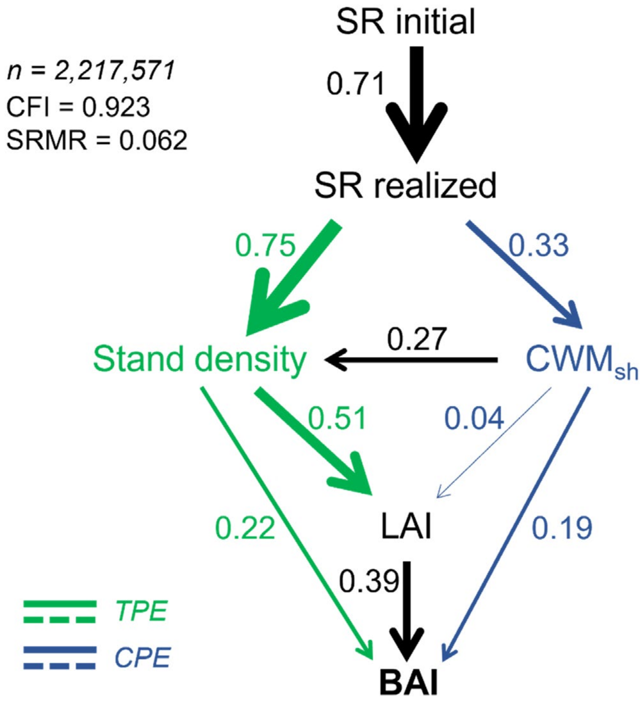

FIGURE 6 Representation of the SEM tested with not-controlled stand-density data. Arrows represent causal paths. Solid and dashed arrows correspond to positive and negative respectively. All paths shown are significant, and the thickness of the arrows is proportional to the strength of the related effect (Table S8). For the sake of clarity, environmental variables and paths are not represented, but their effects are shown in Table S8. Error paths are not presented. *Green arrows*: Paths of the TPE; *blue arrows*: Paths of the CPE (canopy packing effect). *SR*, Species richness; *CWMsh*, Community-weighted mean of shade tolerance of species in the community; *LAI*, Stand leaf area index; *BAI*, Stand basal area increment; *SR initial* (i.e. potential species pool); *SR realized* (i.e. actual species richness at pseudo-equilibrium), *Stand density* was log-transformed.

the strength of the TPE, relating species richness, stand density and LAI to stand productivity, was about two magnitudes stronger than the strength of canopy packing ($0.75 \times 0.51 \times 0.39 = 0.149$ vs. $0.33 \times 0.04 \times 0.39 = 0.005$ respectively, Figure 6 and Table S8). This analysis further highlights the central role of TPE in driving DPRs in forests, and more generally in forest dynamics.

4 | DISCUSSION

4.1 | Tree packing effect mediates DPRs in forests

In this study, we presented evidence for the role of the TPE on the productivity of mixed forests. We first showed that diverse forests in Europe tend to have a larger maximum stand density than monospecific ones, supporting the first component of the TPE. Second, our simulation-based experiment validated the second component of TPE as it suggested that the effect of species richness on maximum stand density can be key in driving DPRs in tree communities. Overall, we thus provide a proof of concept for an often overlooked effect of tree species diversity on forest productivity through an increased maximum stand density, emerging from both tree- and community-level processes. Our results highlight that species complementarity in resource use and response to environmental conditions not only allows more trees to coexist in a stand but also increases stand productivity. This is consistent with the positive effect of stand density or basal area on forest productivity commonly found in observation-based studies (Liang et al., 2016; Paquette & Messier, 2011; Ratcliffe et al., 2016). However, our findings represent a step further by clearly highlighting the interdependence amongst species diversity, stand density, and forest productivity.

In addition, we also found that tree species richness may also increase the maximum stand basal area in some sites (Figure S9), which may extend the scope of our results on forest carbon storage and its associated ecosystem services. The ability of species-rich stands to harbour more trees than species-poor stands, and therefore, to be more productive and to possibly accumulate more standing biomass, should be considered as a key asset of multispecific forests regarding ecosystem services and climate change mitigation.

The role of tree packing has probably been overshadowed in BEF-studies because of the supposed zero-sum game on productivity between stands with large density and small trees versus stands with small density and big trees. Our results clearly show that it is not the case. The magnitude of TPE strongly exceeds the effects usually found in BEF-studies, which may challenge their design, either through experimental, observational, or modelling approaches. In fact, most BEF-experiments were designed to explore the importance of tree–tree interactions for DPRs, resulting in great advances (Guillemot et al., 2020; Sapijanskas et al., 2014; Schnabel et al., 2019; Trogisch et al., 2021). Also echoing recent experimental findings highlighting the limited attention to the role of stand density in BEF-studies (Chisholm & Dutta Gupta, 2023; Tatsumi & Loreau, 2023), our study suggests that future experiments should broaden their scope and explore the effect of the interaction between species richness and stand density on ecosystem functioning. This would provide a better understanding of the biological and ecological mechanisms underlying the TPE in different contexts, and more generally of the effects of diversity on ecosystems.

4.2 | Linking species coexistence and ecosystem functioning through diversity effects

Our findings also highlight the importance of species coexistence in ecosystem structure and functioning. First, demonstrating that multispecific communities include, on average, more trees than monospecific communities whilst growing in the same conditions, our results from both observations and simulations thus bring support to former theoretical hypotheses (Hurtt & Pacala, 1995). Second, by showing that complementarity between species could increase the maximum number of coexisting trees in a stand and thus stimulate forest productivity, our study highlights how coexistence processes could be related to BEF patterns (Godoy et al., 2020) in forest ecosystems whilst this link is still difficult to disentangle (Loreau & Hector, 2019; Turnbull et al., 2013).

4.3 | Complementarity between canopy packing and tree packing

We acknowledge that the distinction between canopy packing and tree packing is a necessary simplification in our study (Figure 1). However, they represent the two main effects emerging from above-ground complementarity processes between tree species and thus driving DPRs in forests. Explaining their differences and relative impacts on stand productivity is thus key to better understand these DPRs. The SEM analysis clearly shows the complementarity of both processes. Furthermore, we also evidenced the importance of canopy packing when stand density is controlled (Figure 4). This finding is consistent with recent findings from experimental plantations on the importance of canopy packing in driving DPRs (Duarte et al., 2021; Guillemot et al., 2020; Schnabel et al., 2019).

4.4 | Alternative hypotheses relating species richness, stand density, and productivity

The main hypothesis behind the TPE is that stand density increases with tree species richness. Yet, the direction of the link between diversity and productivity has been debated for several decades (Loreau et al., 2001; Waide et al., 1999). For instance, the 'more-individuals hypothesis' (MIH Storch et al., 2018), proposes that when environmental conditions allow more individual trees to co-exist, there is a greater chance of finding more species in a stand. It is similar to a 'sampling effect' in which a stand with more trees has more chances to include more species, at least in the outcome. Yet, evidence for the MIH from empirical studies is mixed (Storch et al., 2018), and the possible link between MIH and DPRs remains unclear so far. Nevertheless, as it may represent an alternative explanation for our observation-based result, we explored whether MIH or sampling effects could be at play in our results. Regarding the observation-based results, there is no easy way to test a causal direction in the link between species richness and stand density with NFI data, because they are both sampled simultaneously in random plots. However, if the number of trees in a stand influences its realized species richness, this effect should decrease over time because of environmental filtering and interspecific competition (Abbas et al., 2019; Ulrich et al., 2017). The link between species richness and stand density should thus fade in the most mature and undisturbed stands. Yet, our results from French Reserves plots show that stand density and species richness remain linked, even in old stands (Figure S5b,c), which indirectly supports our hypothesis rather than the MIH/sampling effect. Also, in our simulation-based results, the final species richness did not depend on the number of trees in the simulations (Table S7). Finally, we tested an alternative SEM, in which stand density drives realized species richness (Figure S10), and this model was inconsistent with data (CFI=0.784, Table S9). This further shows that MIH or sampling effects are not involved in our simulation-based results.

4.5 | Methodological aspects

This study illustrates how combining results from observation data with those from a simulation experiment can be complementary, echoing recent calls to better mix these two kinds of approaches (Grainger et al., 2022). Analysing data from national forest inventories has allowed us to test whether species diversity can impact stand density (the first component of TPE), whilst we relied on the long-recognized relevance of forest dynamics models (Bugmann & Seidl, 2022) to explore the consequences on forest functioning (the second component of TPE). As stated in the introduction, we needed the simulation approach to be able to properly disentangle the relationships between species richness, stand density and productivity. Yet, it was crucial to ensure that species richness positively impacts stand density in observed data to anchor our TPE hypothesis on solid grounds.

Regarding the relevance and limits of using the ForCEEPS model for this study, we may remind that the model depends on key ecological hypotheses and processes to represent biotic and abiotic constraints on forest dynamics, but it does not embed all the complexity of ecological processes occurring in forest ecosystems. Choosing between the generality and precision of models' predictions is a classic trade-off in ecology (Levins, 1966) and this study does not pretend to perfectly reflect all facets of forest functioning. This is the reason why we present this study as a proof of concept. However, the ForCEEPS model filled key requirements to be used in this study: it includes many species, it can simulate forest dynamics along strong climatic gradients without re-parameterization, and canopy packing and tree packing were not implemented a priori from specific mechanisms. Nevertheless, exploring the TPE with more complex models is certainly a perspective for future work in order to further depict its biological and ecological determinants.

4.6 | Perspectives

This study calls for the development of further research on the TPE. It is noteworthy that the TPE is predicted to be stronger in harsher climate conditions, that is, cold/wet and warm/dry climates, corresponding to expected conditions for many European forests under climate change for the latter case, which is consistent with a former study relating DPRs and climatic effects across Europe (Jucker et al., 2016). This finding is consistent with the stress gradient hypothesis stating that interspecific interactions become less negative with increasing environmental stress (Bertness & Callaway, 1994), also confirming trends from empirical (Aussenac et al., 2021;

Paquette & Messier, 2011; Toigo et al., 2015) and simulations-based (Morin et al., 2011, 2018) studies.

Finally, as the advantages of promoting multispecific forests to mitigate climate change impacts are increasingly documented (Anderegg et al., 2018; Brockerhoff et al., 2017; Pardos et al., 2021; Sebald et al., 2021; Thom et al., 2019), our finding has important implications for forest management and conservation. First, TPE can only emerge from tree interactions through intimate species mixing in the same stand, and not from a collection of monospecific stands. Second, whilst many European forest stands are monospecific, even-aged, and density-controlled, we show new advantages of promoting species-rich forests as a relevant management option. Increasing forest productivity through TPE has direct consequences on key ecosystem services, such as stimulating carbon sequestration in forests, but may also have consequences on others, such as those related to stand structure and provision of habitats for biodiversity.

AUTHOR CONTRIBUTIONS

Xavier Morin and Lorenz Fahse had the original idea for this study; Xavier Morin, Maude Toigo, and Patrick Vallet designed the study; Xavier Morin, Maude Toigo, Raúl García-Valdés, and Patrick Vallet developed the study methodology; Xavier Morin and François de Coligny developed and validated the ForCEEPS model; Sophia Ratcliffe, Maxime Cailleret, and Miguel A. Zavala help in providing ICP and NFI data; Eugénie Cateau provided RNF data; Maude Toigo, Joannès Guillemot, Raúl García-Valdés and Maxime Cailleret processed ICP Forests data and NFI data; Maude Toigo, Xavier Morin, and Patrick Vallet analysed NFI data; Xavier Morin, Maude Toigo, Joannès Guillemot, Louise Riotte-Lambert, and Patrick Vallet analysed model simulations; Xavier Morin, Maude Toigo, Joannès Guillemot, and Patrick Vallet wrote the first draft; all co-authors contributed to writing, reviewing and editing the final draft. Our study brings together authors from a number of different countries. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectivesAUTHOR: Please check whether the graphical abstract text has been set correctly. they represent were considered from the onset. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

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ACKNOWLEDGEMENTS

We thank the FunDivEUROPE project [funded by the European Union's Seventh Programme (FP7/2007–2013) under grant agreement no. 265171] for providing NFI data. We thank the MITECO (Spain, Ministerio para la Transición Ecológica y el Reto Demográfico) for granting access to Spanish Forest Inventory Data, the Johann Heinrich von Thünen-Institut for access to the German National Forest Inventories, the Finnish Forest Research Institute (METLA) for making permanent sample plot data from the Finnish NFI available, the Swedish University of Agricultural Sciences for making the Swedish NFI data available, the Institut National Géographique et Forestière (IGN) for providing French National Forest Inventory data, and Hugues Lecomte, from the Walloon Forest Inventory, for access to the Walloon NFI data. We also thank data providers: Paloma Ruiz Benito, Jonas Dahlgren, Gerald Kändler, Aleksi Lehtonen, and Christian Wirth. Model validation was based on data that were collected by partners of the official UNECE ICP Forests Network (http://icp-forests.net/contributors). Part of the data was co-financed by the European Commission (Data achieved at 28 of May 2019). This study was funded by the projects BIOPROFOR (ANR-11-PDOC-030-01), DISTIMACC (ECOFOR-2014-23, French Ministry of Ecology and Sustainable Development, French Ministry of Agriculture and Forest), DIPTICC (ANR-16-CE32-0003), REFORM (ERA-Net SUMFOREST, PCIN2017-026), and FISSA (ANR-21-CE32-0010-01).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14460.

DATA AVAILABILITY STATEMENT

Dataset of processed simulation outputs for conducting the analysis presented is available in ZENODO: https://doi.org/10.5281/zenodo.6320862 (Morin et al., 2022a). ICP Forests data used for model validation are available at https://zenodo.org/records/13952979 (Morin, 2024) (note that raw ICP Forests data are available at http://icp-forests.net/page/data-requests upon request). RNF data used in the study are available at https://zenodo.org/doi/10.5281/zenodo.11064978 (Cateau et al., 2024). National inventory data from FunDivEUROPE are available at the following links: Data are available from Spanish National Forest Inventory (https://www.miteco.gob.es/es/biodiversidad/

servicios/banco-datos-naturaleza/informacion-disponible/ifn3_bbdd_descargas_htm.html, https://www.miteco.gob.es/en/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn2_descargas.aspx, and https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ifn3_bbdd_descargas_htm.html), the French National Forest Inventory (https://inventaire-forestier.ign.fr/spip.php?article532) and the German National Forest Inventory (https://bwi.info/Download/de/BWI-Basisdaten/ACCESS2003/). The Swedish and Finnish data are not public on the NFI websites, but data with blurred geographic coordinates https://doi.org/10.5061/dryad.wm37pvmkw. Contact persons for the Swedish and Finnish NFI are Jonas Dahlgren (jonas.dahlgren@slu.se) and Aleksi Lehtonen (aleksi.lehtonen@luke.fi), respectively. The codes for conducting the data integration and analyses are available in ZENODO: https://doi.org/10.5281/zenodo.6425394 (Morin et al., 2022b). The ForCEEPS model is available from the Capsis platform (https://capsis.cirad.fr), and the version used in this study (including archived source code at the time of publication) is available in ZENODO with the identifier: https://doi.org/10.5281/zenodo.6303305 (Morin & de Coligny, 2022).

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REFERENCES

Abbas, S., Nichol, J. E., Zhang, J., & Fischer, G. A. (2019). The accumulation of species and recovery of species composition along a 70 year succession in a tropical secondary forest. *Ecological Indicators*, *106*, 105524. https://doi.org/10.1016/j.ecolind.2019.105524

Anderegg, W. R. L., Konings, A. G., Trugman, A. T., Yu, K., Bowling, D. R., Gabbitas, R., Karp, D. S., Pacala, S., Sperry, J. S., Sulman, B. N., & Zenes, N. (2018). Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature*, *561*(7724), 538–541. https://doi.org/10.1038/s41586-018-0539-7

Aussenac, R., Pérot, T., Fortin, M., de Coligny, F., Monnet, J.-M., & Vallet, P. (2021). The Salem simulator version 2.0: A tool for predicting the productivity of pure and mixed forest stands and simulating management operations. *Open Research Europe*, *1*, 61. https://doi.org/10.12688/OPENRESEUROPE.13671.2

Barry, K. E., Mommer, L., van Ruijven, J., Wirth, C., Wright, A. J., Bai, Y., Connolly, J., De Deyn, G. B., de Kroon, H., Isbell, F., Milcu, A., Roscher, C., Scherer-Lorenzen, M., Schmid, B., & Weigelt, A. (2019). The future of complementarity: Disentangling causes from consequences. *Trends in Ecology & Evolution*, *34*(2), 167–180. https://doi.org/10.1016/j.tree.2018.10.013

Bentler, P. M. (1990). Comparative fit indexes in structural models. *Psychological Bulletin*, *107*, 238–246.

Bertness, M. D., & Callaway, R. M. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, *9*, 191–193.

Bohn, F. J., & Huth, A. (2017). The importance of forest structure to biodiversity–productivity relationships. *Royal Society Open Science*, *4*(1), 4160521. http://rsos.royalsocietypublishing.org/content/4/1/160521

Botkin, D., Janak, J., & Wallis, J. (1972). Some ecological consequences of a computer model of forest growth. *The Journal of Ecology*, *60*, 849–872.

Brockerhoff, E. G., Barbaro, L., Castagneyrol, B., Forrester, D. I., Gardiner, B., González-Olabarria, J. R., Lyver, P. O., Meurisse, N., Oxbrough, A., Taki, H., Thompson, I. D., van der Plas, F., & Jactel, H. (2017). Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and Conservation*, *26*(13), 3005–3035. https://doi.org/10.1007/S10531-017-1453-2

Brunner, A., & Forrester, D. I. (2020). Tree species mixture effects on stem growth vary with stand density—An analysis based on individual tree responses. *Forest Ecology and Management*, *473*, 118334. https://doi.org/10.1016/J.FORECO.2020.118334

Bugmann, H. (2001). A review of forest gap models. *Climatic Change*, *51*(3–4), 259–305.

Bugmann, H., & Seidl, R. (2022). The evolution, complexity and diversity of models of long-term forest dynamics. *Journal of Ecology*, *110*(10), 2288–2307. https://doi.org/10.1111/1365-2745.13989

Cabal, C., Valladares, F., & Pacala, S. W. (2024). Root foraging strategies and niche segregation of three mediterranean shrub species. *Oikos*, e10724. https://doi.org/10.1111/OIK.10724

Cade, B. S., & Guo, Q. (2000). Estimating effects of constraints on plant performance with regression quantiles. *Oikos*, *91*(2), 245–254. https://doi.org/10.1034/J.1600-0706.2000.910205.X

Cade, B. S., & Noon, B. R. (2003). A gentle introduction to quantile regression for ecologists. *Frontiers in Ecology and the Environment*, *1*(8), 412–420. https://doi.org/10.1890/1540-9295(2003)001

Cateau, E., Debaive, N., Drapier, N., Chantreau, F., Gilg, O., Laroche, F., Morin, X., Demets, V., Pimenta, R., Thompson, L., & Paillet, Y. (2024). Data from: Tree inventory data from permanent plots in French forest reserves [data set]. Ecology (1.0, p. e4324). *Zenodo*. https://doi.org/10.5281/zenodo.11064978

Chisholm, R. A., & Dutta Gupta, T. (2023). A critical assessment of the biodiversity–productivity relationship in forests and implications for conservation. *Oecologia*, *201*, 887–900.

Chisholm, R. A., Muller-Landau, H. C., Abdul Rahman, K., Bebber, D. P., Bin, Y., Bohlman, S. A., Bourg, N. A., Brinks, J., Bunyavejchewin, S., Butt, N., Cao, H., Cao, M., Cárdenas, D., Chang, L. W., Chiang, J. M., Chuyong, G., Condit, R., Dattaraja, H. S., Davies, S., … Zimmerman, J. K. (2013). Scale-dependent relationships between tree species richness and ecosystem function in forests. *Journal of Ecology*, *101*(5), 1214–1224. https://doi.org/10.1111/1365-2745.12132

Condés, S., Vallet, P., Bielak, K., Bravo-Oviedo, A., Coll, L., Ducey, M. J., Pach, M., Pretzsch, H., Sterba, H., Vayreda, J., & del Río, M. (2017). Climate influences on the maximum size-density relationship in Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) stands. *Forest Ecology and Management*, *385*, 295–307. https://doi.org/10.1016/J.FORECO.2016.10.059

Cordonnier, T., Smadi, C., Kunstler, G., & Courbaud, B. (2019). Asymmetric competition, ontogenetic growth and size inequality drive the difference in productivity between two-strata and one-stratum forest stands. *Theoretical Population Biology*, *130*, 83–93. https://doi.org/10.1016/J.TPB.2019.07.001

de Martonne, E. (1926). L'indice d'aridité. *Bulletin de l'Association de Géographes Français*, *3*(9), 3–5. https://doi.org/10.3406/BAGF.1926.6321

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27–46.

Duarte, M. M., Moral, R. d. A., Guillemot, J., Zuim, C. I. F., Potvin, C., Bonat, W. H., Stape, J. L., & Brancalion, P. H. S. (2021). High tree diversity enhances light interception in tropical forests. *Journal of Ecology*, *109*(7), 2597–2611. https://doi.org/10.1111/1365-2745.13669

Dufour-Kowalski, S., Courbaud, B., Dreyfus, P., Meredieu, C., & de Coligny, F. (2012). Capsis: An open software framework and community for forest growth modelling. *Annals of Forest Science*, *69*(2), 221–233. https://doi.org/10.1007/s13595-011-0140-9

FAO and UNEP. (2020). The state of the world's forests 2020. In *The state of the world's forests 2020—Forests, biodiversity and people*. FAO and UNEP. https://doi.org/10.4060/ca8642en

Forrester, D. I. (2014). The spatial and temporal dynamics of species interactions in mixed-species forests: From pattern to process. *Forest Ecology and Management*, *312*, 282–292. https://doi.org/10.1016/j.foreco.2013.10.003

Forrester, D. I., Baker, T. G., Elms, S. R., Hobi, M. L., Ouyang, S., Wiedemann, J. C., Xiang, W., Zell, J., & Pulkkinen, M. (2021). Self-thinning tree mortality models that account for vertical stand structure, species mixing and climate. *Forest Ecology and Management*, *487*, 118936. https://doi.org/10.1016/J.FORECO.2021.118936

García-Valdés, R., Estrada, A., Early, R., Lehsten, V., & Morin, X. (2020). Climate change impacts on long-term forest productivity might be driven by species turnover rather than by changes in tree growth. *Global Ecology and Biogeography*, *29*(8), 1360–1372. https://doi.org/10.1111/GEB.13112

Godoy, O., Gómez-Aparicio, L., Matías, L., Pérez-Ramos, I. M., & Allan, E. (2020). An excess of niche differences maximizes ecosystem functioning. *Nature Communications*, *11*(1), 1–10. https://doi.org/10.1038/s41467-020-17960-5

Grainger, T. N., Senthilnathan, A., Ke, P. J., Barbour, M. A., Jones, N. T., Delong, J. P., Otto, S. P., O'connor, M. I., Coblentz, K. E., Goel, N., Sakarchi, J., Szojka, M. C., Levine, J. M., & Germain, R. M. (2022). An empiricist's guide to using ecological theory. *The American Naturalist*, *199*(1), 1–20. https://doi.org/10.1086/717206

Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., Schlesinger, W. H., Shoch, D., Siikamäki, J. V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R. T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M. R., … Fargione, J. (2017). Natural climate solutions. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(44), 11645–11650. https://doi.org/10.1073/PNAS.1710465114

Guillemot, J., Kunz, M., Schnabel, F., Fichtner, A., Madsen, C. P., Gebauer, T., Härdtle, W., von Oheimb, G., & Potvin, C. (2020). Neighbourhood-mediated shifts in tree biomass allocation drive overyielding in tropical species mixtures. *New Phytologist*, *228*(4), 1256–1268. https://doi.org/10.1111/NPH.16722

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., Gonzalez, A., Duffy, J. E., Gamfeldt, L., & O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, *486*(7401), 105–108. https://doi.org/10.1038/Nature11118

Hordijk, I., Maynard, D. S., Hart, S. P., Lidong, M., ter Steege, H., Liang, J., de-Miguel, S., Nabuurs, G. J., Reich, P. B., Abegg, M., Adou Yao, C. Y., Alberti, G., Almeyda Zambrano, A. M., Alvarado, B. V., Esteban, A. D., Alvarez-Loayza, P., Alves, L. F., Ammer, C., Antón-Fernández, C., … Crowther, T. W. (2023). Evenness mediates the global relationship between forest productivity and richness. *Journal of Ecology*, *111*(6), 1308–1326. https://doi.org/10.1111/1365-2745.14098

Hurtt, G. C., & Pacala, S. W. (1995). The consequences of recruitment limitation: Reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, *176*(1), 1–12. https://doi.org/10.1006/JTBI.1995.0170

Jucker, T., Avăcăriței, D., Bărnoaiea, I., Duduman, G., Bouriaud, O., & Coomes, D. A. (2016). Climate modulates the effects of tree diversity on forest productivity. *Journal of Ecology*, *104*(2), 388–398. https://doi.org/10.1111/1365-2745.12522

Jucker, T., Bouriaud, O., Avacaritei, D., & Coomes, D. A. (2014). Stabilizing effects of diversity on aboveground wood production in forest ecosystems: Linking patterns and processes. *Ecology Letters*, *17*(12), 1560–1569. https://doi.org/10.1111/Ele.12382

Jucker, T., Bouriaud, O., & Coomes, D. A. (2015). Crown plasticity enables trees to optimize canopy packing in mixed-species forests. *Functional Ecology*, *29*, 1078–1086. https://doi.org/10.1111/1365-2435.12428

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*(1), 1–20. https://doi.org/10.1038/sdata.2017.122

Koenker, R. (2022). *quantreg*: *Quantile Regression* (R package version 5.88).

Koenker, R., & Bassett, G. (1978). Regression Quantiles. *Econometrica*, *46*(1), 33–50.

Levins, R. (1966). The strategy of model building in population ecology. *American Scientist*, *54*, 421–451.

Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A. D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C. B., Glick, H. B., Hengeveld, G. M., Nabuurs, G.-J., Pfautsch, S., … Reich, P. B. (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science*, *354*(6309), aaf8957.

Loreau, M. (1998). Separating sampling and other effects in biodiversity experiments. *Oikos*, *82*(3), 600–602.

Loreau, M., & Hector, A. (2019). Not even wrong: Comment by Loreau and Hector. *Ecology*, *100*, e02794.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D., & Wardle, D. A. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, *294*(5543), 804–808.

Maréchaux, I., & Chave, J. (2017). An individual-based forest model to jointly simulate carbon and tree diversity in Amazonia: Description and applications. *Ecological Monographs*, *87*(4), 632–664. https://doi.org/10.1002/ecm.1271

Maréchaux, I., Langerwisch, F., Huth, A., Bugmann, H., Morin, X., Reyer, C. P. O., Seidl, R., Collalti, A., de Paula, M. D., Fischer, R., Gutsch, M., Lexer, M. J., Lischke, H., Rammig, A., Rödig, E., Sakschewski, B., Taubert, F., Thonicke, K., Vacchiano, G., & Bohn, F. J. (2021). Tackling unresolved questions in forest ecology: The past and future role of simulation models. *Ecology and Evolution*, *11*(9), 3746–3770. https://doi.org/10.1002/ECE3.7391

Morin, X. (2024). ICP forests data for Morin et al. [Data set]. *Zenodo* https://doi.org/10.5281/zenodo.13952979

Morin, X., Bugmann, H., de Coligny, F., Martin-StPaul, N., Cailleret, M., Limousin, J.-M., Ourcival, J.-M., Prevosto, B., Simioni, G., Toigo, M., Vennetier, M., Catteau, E., & Guillemot, J. (2021). Beyond forest succession: A gap model to study ecosystem functioning and tree community composition under climate change. *Functional Ecology*, *35*(4), 955–975. https://doi.org/10.1111/1365-2435.13760

Morin, X., Damestoy, T., Toigo, M., Castagneyrol, B., Jactel, H., de Coligny, F., & Meredieu, C. (2020). Using forest gap models and experimental data to explore long-term effects of tree diversity on the productivity of mixed planted forests. *Annals of Forest Science*, *77*(2), 1–19. https://doi.org/10.1007/S13595-020-00954-0

Morin, X., & de Coligny, F. (2022). ForCEEPS simulator 1.1 (1.1). *Zenodo*. https://doi.org/10.5281/zenodo.6303305

Morin, X., Fahse, L., de Mazancourt, C., Scherer-Lorenzen, M., & Bugmann, H. (2014). Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. *Ecology Letters*, *17*(12), 1526–1535. https://doi.org/10.1111/ele.12357

Morin, X., Fahse, L., Jactel, H., Scherer-Lorenzen, M., García-Valdés, R., & Bugmann, H. (2018). Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. *Scientific Reports*, *8*, 5627. https://doi.org/10.1038/s41598-018-23763-y

Morin, X., Fahse, L., Scherer-Lorenzen, M., & Bugmann, H. (2011). Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, *14*(12), 1211–1219.

Morin, X., Vallet, P., & Toïgo, M. (2022a). Data supporting publication by Morinetal [Data set]. *Zenodo*. https://doi.org/10.5281/zenodo.6320862

Morin, X., Vallet, P., & Toïgo, M. (2022b). R codes for some analysis of Morinetal [Data set]. *Zenodo*. https://doi.org/10.5281/zenodo.6425394

Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Kobe, R. K., & Ribbens, E. (1996). Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecological Monographs*, *66*(1), 1–43.

Pachauri, R. K., & Meyer, L. A. (2014). AR5 synthesis report: Climate change 2014—IPCC. In *Climate change 2014: Synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (p. 151). IPCC.

Paquette, A., & Messier, C. (2011). The effect of biodiversity on tree productivity: From temperate to boreal forests. *Global Ecology and Biogeography*, *20*(1), 170–180. https://doi.org/10.1111/j.1466-8238.2010.00592.x

Pardos, M., del Río, M., Pretzsch, H., Jactel, H., Bielak, K., Bravo, F., Brazaitis, G., Defossez, E., Engel, M., Godvod, K., Jacobs, K., Jansone, L., Jansons, A., Morin, X., Nothdurft, A., Oreti, L., Ponette, Q., Pach, M., Riofrío, J., … Calama, R. (2021). The greater resilience of mixed forests to drought mainly depends on their composition: Analysis along a climate gradient across Europe. *Forest Ecology and Management*, *481*, 118687. https://doi.org/10.1016/J.FORECO.2020.118687

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2020). *nlme: Linear and nonlinear mixed effects model* (R package version 3.1-149).

Pretzsch, H. (2014). Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *Forest Ecology and Management*, *327*, 251–264. https://doi.org/10.1016/j.foreco.2014.04.027

Pretzsch, H., & Biber, P. (2016). Tree species mixing can increase maximum stand density. *Canadian Journal of Forest Research*, *46*(10), 1179–1193. https://doi.org/10.1139/cjfr-2015-0413

Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Dirnberger, G., Drössler, L., Fabrika, M., Forrester, D. I., Godvod, K., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Matović, B., … Bravo-Oviedo, A. (2015). Growth and yield of mixed versus pure stands of scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *European Journal of Forest Research*, *134*(5), 927–947. https://doi.org/10.1007/s10342-015-0900-4

Ratcliffe, S., Liebergesell, M., Ruiz-Benito, P., Madrigal González, J., Muñoz Castañeda, J. M., Kändler, G., Lehtonen, A., Dahlgren, J., Kattge, J., Peñuelas, J., Zavala, M. A., & Wirth, C. (2016). Modes of functional biodiversity control on tree productivity across the European continent. *Global Ecology and Biogeography*, *25*(3), 251–262. https://doi.org/10.1111/GEB.12406

Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C. C., Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., … Baeten, L. (2017). Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology Letters*, *20*(11), 1414–1426. https://doi.org/10.1111/ELE.12849

R-Core-Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Reineke, L. H. (1933). Perfecting a stand-density index for even-aged forest. *Journal of Agricultural Research*, *46*, 627–638.

Rissanen, K., Martin-Guay, M.-O., Riopel-Bouvier, A.-S., & Paquette, A. (2019). Light interception in experimental forests affected by tree diversity and structural complexity of dominant canopy. *Agricultural and Forest Meteorology*, *278*, 107655. https://doi.org/10.1016/j.agrformet.2019.107655

Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, *48*(2), 1–36.

Rüger, N., Condit, R., Dent, D. H., DeWalt, S. J., Hubbell, S. P., Lichstein, J. W., Lopez, O. R., Wirth, C., & Farrior, C. E. (2020). Demographic trade-offs predict tropical forest dynamics. *Science*, *368*(6487), 165–168. https://doi.org/10.1126/SCIENCE.AAZ4797/SUPPL_FILE/AAZ4797_RUGER_SM_.PDF

Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., & Loreau, M. (2014). Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology*, *95*(9), 2479–2492. https://doi.org/10.1890/13-1366.1

Schnabel, F., Schwarz, J. A., Dănescu, A., Fichtner, A., Nock, C. A., Bauhus, J., & Potvin, C. (2019). Drivers of productivity and its temporal stability in a tropical tree diversity experiment. *Global Change Biology*, *25*, 4257–4272. https://doi.org/10.1111/gcb.14792

Schwinning, S., & Weiner, J. (1998). Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, *113*(4), 447–455. https://doi.org/10.1007/S004420050397

Sebald, J., Thrippleton, T., Rammer, W., Bugmann, H., & Seidl, R. (2021). Mixing tree species at different spatial scales: The effect of alpha, beta and gamma diversity on disturbance impacts under climate change. *Journal of Applied Ecology*, *58*(8), 1749–1763. https://doi.org/10.1111/1365-2664.13912

Storch, D., Bohdalková, E., & Okie, J. (2018). The more-individuals hypothesis revisited: The role of community abundance in species richness regulation and the productivity–diversity relationship. *Ecology Letters*, *21*(6), 920–937. https://doi.org/10.1111/ELE.12941

Tatsumi, S., & Loreau, M. (2023). Partitioning the biodiversity effects on productivity into density and size components. *Ecology Letters*, *26*(11), 1963–1973. https://doi.org/10.1111/ELE.14300

Thom, D., Golivets, M., Edling, L., Meigs, G. W., Gourevitch, J. D., Sonter, L. J., Galford, G. L., & Keeton, W. S. (2019). The climate sensitivity of carbon, timber, and species richness covaries with forest age in boreal–temperate North America. *Global Change Biology*, *25*(7), 2446–2458. https://doi.org/10.1111/GCB.14656

Toïgo, M., Castagneyrol, B., Jactel, H., Morin, X., & Meredieu, C. (2022). Effects of tree mixture on forest productivity: Tree species addition versus substitution. *European Journal of Forest Research*, *2021*(141), 165–175. https://doi.org/10.1007/S10342-021-01432-6

Toïgo, M., Perot, T., Courbaud, B., Castagneyrol, B., Gégout, J.-C., Longuetaud, F., Jactel, H., & Vallet, P. (2018). Difference in shade tolerance drives the mixture effect on oak productivity. *Journal of Ecology*, *106*(3), 1073–1082. https://doi.org/10.1111/1365-2745.12811

Toigo, M., Vallet, P., Perot, T., Bontemps, J. D., Piedallu, C., & Courbaud, B. (2015). Overyielding in mixed forests decreases with site productivity. *Journal of Ecology*, *103*, 502–512. https://doi.org/10.1111/1365-2745.12353

Trogisch, S., Liu, X., Rutten, G., Xue, K., Bauhus, J., Brose, U., Bu, W., Cesarz, S., Chesters, D., Connolly, J., Cui, X., Eisenhauer, N., Guo, L., Haider, S., Härdtle, W., Kunz, M., Liu, L., Ma, Z., Neumann, S., … Bruelheide, H. (2021). The significance of tree-tree interactions for forest ecosystem functioning. *Basic and Applied Ecology*, *55*, 33–52. https://doi.org/10.1016/J.BAAE.2021.02.003

Turnbull, L. A., Levine, J. M., Loreau, M., & Hector, A. (2013). Coexistence, niches and biodiversity effects on ecosystem functioning. *Ecology Letters*, *16*, 116–127. https://doi.org/10.1111/Ele.12056

Ulrich, W., Sewerniak, P., Puchałka, R., & Piwczyński, M. (2017). Environmental filtering triggers community assembly of forest understorey plants in Central European pine stands. *Scientific Reports*, *7*, 274. https://doi.org/10.1038/s41598-017-00255-z

Vila, M., Carrillo-Gavilan, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., Haase, J., Kunstler, G., Schelhaas, M., & Trasobares, A. (2013). Disentangling biodiversity and climatic determinants of wood production. *PLoS One*, *8*(2), e53530. https://doi.org/10.1371/journal.pone.0053530

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G. G., Gough, L., Dodson, S. I., Juday, G. P., & Parmenter, R. (1999). The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, *30*, 257–300.

Williams, L. J., Butler, E. E., Cavender-Bares, J., Stefanski, A., Rice, K. E., Messier, C., Paquette, A., & Reich, P. B. (2021). Enhanced light interception and light use efficiency explain overyielding in young tree communities. *Ecology Letters*, *24*(5), 996–1006. https://doi.org/10.1111/ele.13717

Williams, L. J., Paquette, A., Cavender-Bares, J., Messier, C., & Reich, P. B. (2017). Spatial complementarity in tree crowns explains overyielding in species mixtures. *Nature Ecology & Evolution*, *1*(4), 0063. https://doi.org/10.1038/s41559-016-0063

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R. Statistics for biology and health*. Springer.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix A. Description of the ForCEEPS model.

Appendix B. Validation of ForCEEPS for European forests.

Appendix C. Supplementary information about complementarity analyses about management.

Appendix D. Supplementary information about the simulations and their analyses.

How to cite this article: Morin, X., Toigo, M., Fahse, L., Guillemot, J., Cailleret, M., Bertrand, R., Cateau, E., de Coligny, F., García-Valdés, R., Ratcliffe, S., Riotte-Lambert, L., Zavala, M. A., & Vallet, P. (2025). More species, more trees: The role of tree packing in promoting forest productivity. *Journal of Ecology*, *113*, 371–386. https://doi.org/10.1111/1365-2745.14460