How dominant height responds to mixing species: Effect of traits and height difference between species

Matthieu Combaud, Thomas Cordonnier, Thomas Pérot, Xavier Morin, Patrick Vallet

To cite this version:

Matthieu Combaud, Thomas Cordonnier, Thomas Pérot, Xavier Morin, Patrick Vallet. How dominant height responds to mixing species: Effect of traits and height difference between species. Forest Ecology and Management, 2024, 572, pp.122298. 10.1016/j.foreco.2024.122298 . hal-04722944

Forest Ecology and Management 572 (2024) 122298

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

How dominant height responds to mixing species: Effect of traits and height difference between species

Matthieu Combaud[a], Thomas Cordonnier[b], Thomas Pérot[c], Xavier Morin[d], Patrick Vallet[a,*]

[a] Univ. Grenoble Alpes, INRAE, LESSEM, F-38402 St-Martin-d'Hères, France
[b] Office National des Forêts, Recherche Développement et Innovation, 21 rue du Muguet, Dole 39100, France
[c] INRAE, EFNO, Domaine des Barres, Nogent-sur-Vernisson, F-45290, France
[d] CEFE UMR 5175, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France

ARTICLE INFO

Keywords:
Species interactions
Temperate forest
National forest inventory
Shade tolerance
Specific leaf area
Wood density

ABSTRACT

Adapting forests to climate change is a major challenge for forest ecology and forestry. Among the management options available, encouraging the use of mixtures is a promising way forward. However, this practice requires a thorough understanding of how species respond to mixing. In this article, we analyzed species dominant height responds to mixing and how species ontogeny and traits drive this response. We compared species observed dominant height in mixed even-aged stands with the expected dominant height of the same species in a monospecific stand under the same environmental conditions. We then related this dominant height variation due to mixing to between-species dominant height difference and to species traits linked to competition (shade tolerance, wood density, specific leaf area).

We focused our analyses on 76 pairs of forest tree species. We used data from the French National Forest Inventory to calculate species dominant height in 1368 mixed stands. We then used previously developed models to estimate the expected dominant height in virtual monospecific stands with the same environmental conditions.

We found that mixture had a significant impact on species dominant height for 15 out of 50 species-combination considered. Dominant height of a given species was higher in mixture than in pure stands when this species had a lower dominant height in pure stands, a lower shade tolerance, a lower specific leaf area or a higher wood density than its companion species.

Our results suggest that species dominant height response to mixing depends on how mixture influences the competition for light. Our results will help inform strategies aiming to diversify species in forests, and will be especially useful in anticipating a given species' behavior in response to competition for light when it is mixed with other species.

1. Introduction

Climate change raises a double challenge for forests: they must adapt to rapid changes in their environmental conditions while also ensuring their contribution to climate change mitigation. Promoting mixed forests, *i.e.* forests combining different tree species at the stand scale, is a relevant adaptation strategy in the face of climate change and its associated pressures (Messier et al., 2022) due to two main advantages. First, mixing species may create an "insurance effect" in case one species declines. Second, mixing may create complementarity effects that may decrease the impact of biotic and abiotic stresses in the forest stand (Jactel et al., 2017). These effects of species mixing are dependent on site conditions, on species combinations (Grossiord, 2020; Toïgo et al., 2015a) and on management (Pretzsch et al., 2017, chapter 9). Depending on the species considered, mixing may also influence the contribution of forests to climate change mitigation, because the mixing strategy can have a positive impact on stand productivity, thereby increasing carbon storage (Liang et al., 2016; Zhang et al., 2012).

Trees grow differently in mixed stands than they do in monospecific stands (*i.e.* stands dominated by a single species) due to differences between interspecific *versus* intraspecific competition, and/or to facilitation effects (Pretzsch et al., 2017). In particular, light distribution among coexisting trees, which impacts tree growth, differs between monospecific and mixed stands (Jucker et al., 2014). It is therefore

---

* Corresponding author.
E-mail address: patrick.vallet@inrae.fr (P. Vallet).

https://doi.org/10.1016/j.foreco.2024.122298
Received 12 June 2024; Received in revised form 9 September 2024; Accepted 10 September 2024

crucial to have thorough knowledge of how different species behave in mixtures in order to define an efficient adaptation and mitigation strategy. More specifically, such knowledge may help managers choose compatible species and other aspects of their management strategies, and better evaluate carbon sequestration capacity.

In this paper, we focus on even-aged stands, which represent around 75 % of Europe's forests (Forest Europe, 2020). In such systems, key variables are species dominant heights, defined for each species as the mean height of the trees of the species belonging to the largest trees of the stand (details in 2.1.1) (del Río et al., 2016). In even-aged mixtures, there is a vertical hierarchy among species, which depends on each species' dominant height. This hierarchy influences access to light, thus impacting the ability of the species to grow and thrive together (Kothari et al., 2021). It is therefore important to have information on species vertical hierarchy in mixtures, and this requires assessing the effect of mixing species on species dominant height. However, the response of species dominant height to mixing has been less studied than the response of tree diameter or stand productivity (but see Del Rio et al., 2019). For example, Toïgo, et al. (2015a) found that mixed stands had increased basal area increment at the stand level for five combinations of European species, compared to corresponding pure stands. They also showed that the effect of mixing species on basal area increment differed between the two species involved in the mixture, with a negative impact in some cases. Further empirical results on stand productivity can be found in Pretzsch et al. (2017) (chapter 4, point 4.2.2.2). The relatively low number of large-scale studies on the impact of mixing species on height is probably due to scarcer data, due to measurement complexity. Moreover, some large-scale studies focus on the effect of competition on height and not the effect of mixing species (see for example Lines et al., 2012).

Because height responds to competition for light in temperate forests (Kothari et al., 2021; Lines et al., 2012), it is essential to explore how variables linked to light acquisition and light use influence the response of species dominant height to mixing species. Herein, for a given stand at a given development stage, we consider three important variables that influence light acquisition (Fig. 1). First, the between-species difference in expected dominant height, defined as the dominant height that would be achieved in the same environment in the absence of other species. This between-species dominant height difference determines if a species will be subject to size-asymmetric competition for light, because this type of competition mainly affects smaller species (Biber and Pretzsch, 2022). Second, the shade tolerance of the dominated species, which reflects its ability to survive, grow or reproduce in low light conditions (Niinemets and Valladares, 2006). Third, the shading effect of the dominant species due to light interception, which reflects its competitive effect on smaller trees. The shading effect is positively related to shade tolerance (Canham et al., 1994; Kulha et al., 2023) because shade-tolerant species develop crowns that intercept more light (Pacala et al., 1996; Petrovska et al., 2021). In this paper, we have defined shade tolerance and shading effect as intrinsic species traits, independent of the species' position in the stand vertical hierarchy.

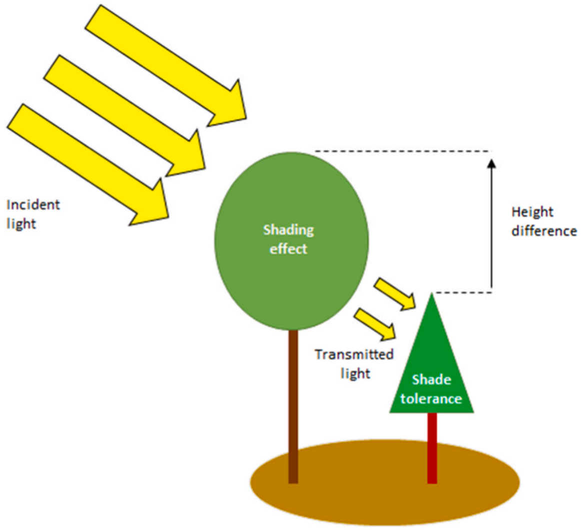

Fig. 1. The three variables involved in the acquisition of light in mixtures: height difference between species, shading effect of the height-dominant species, and shade tolerance of the height-dominated species. Shading effect is positively linked with shade tolerance.

Several studies have analyzed the impact of species traits and height difference on the response of height to mixing species. By fitting height-diameter allometries for 13 species, Rodríguez de Prado et al. (2022) found that mixture influenced species height in a different direction depending on whether the species was deciduous (positive effect) or coniferous (negative effect). Del Río et al. (2019) focused on ten species-pairs and found that shade-intolerant species had higher height in mixtures and that shade-tolerant species had lower height in mixtures. For even-aged stands, Vallet and Perot (2016) found a "compensation effect", *i.e.* the taller species of the mixture had a lower height in mixture compared to pure stands and the smaller species of the mixtures had a higher height in mixture compared to pure stands. They related this effect to the fact that mixtures reduce light competition for the height-dominant species and increase light competition for the height-dominated species. Other functional traits related to light competition or integrative of several processes, in particular specific leaf area (SLA) and wood density, have been mobilized to study the impact of mixture on diameter increment (Kunstler et al., 2016). However, to our knowledge, the simultaneous impact of species height difference and of traits on the response of height to mixing species remains largely unexplored.

In this article, we studied the response of species dominant height to mixing species in even-aged two-species mixed stands in France (without overseas territories). We focused on interactions linked to light acquisition. Taking advantage of the extensive French National Forest Inventory dataset, we selected a subset of 1368 even-aged mixed stands that covers 76 species–pairs. We explored two questions: (i) how does mixing species affect species dominant height in even-aged stands; (ii) what is the respective influence of between-species expected dominant height difference and species traits on the mixture effect on species dominant height?

For a given stand, we refer to the species under scrutiny as the "focal species" and to the other species as the "companion species". We call "mixture effect on species dominant height" the response of the focal species dominant height to mixing species, and we write "mixture effect" if there is no ambiguity.

Using these definitions, we formulated the following hypotheses:

- H1: The mixture effect on species dominant height depends on the between-species excepted dominant height difference: (i) the taller is the companion species compared to the focal species, the more positive is the mixture effect and (ii) the mixture effect is positive (resp. negative) when the focal species has a lower (resp. higher) expected dominant height than its companion species. We made this hypothesis assuming that mixture effect on dominant height is driven by access to light and that access to light is strongly linked with vertical hierarchy, following Vallet and Pérot (2016);
- H2: Differences in shade tolerance between the companion and the focal species should influence the mixture effect on species dominant height. In particular, if the focal species has a lower expected dominant height than its companion species, a higher difference in shade tolerance should increase the mixture effect. We made this hypothesis assuming that in mixtures, the focal species would need to increase its height to access light even more if (i) it is less shade-tolerant than the companion species, and (ii) the companion species intercepts more light, which can be related to the shade

tolerance of the companion species (Canham et al., 1994; Kulha et al., 2023).

In addition to these hypotheses, we analyzed the impact of differences in wood density and SLA on the mixture effect on species dominant height, because Kunstler et al. (2016) found an important role for these variables in species interactions.

2. Data and methods

To compute the mixture effect on species dominant height, we followed Vallet and Perot (2016): for each stand and each species, we compared observed dominant height to the expected dominant height in case the species had grown in a monospecific stand under the same environmental conditions (hereafter, "expected dominant height"). To assess this expected dominant height, we used the models calibrated in Combaud et al. (2024). Next, we used a stepwise model-selection procedure to model the mixture effect as a function of the between-species difference in expected dominant height and of the difference of trait value between species. As defined in the introduction, "focal species'' refers to the species for which the mixture effect is evaluated, and "companion species" refers to the accompanying species. For each stand, we successively considered both species involved in the mixture as the focal species.

2.1. Data

2.1.1. Dendrometric data

We used data from the French National Forest Inventory (NFI) temporary plots collected between 2006 and 2020 (IGN, 2022). For each plot, the NFI protocol defines three concentric circles from the plot center, with radii of 6 m, 9 m and 15 m, for a maximum surface area of around 700 m^2. In each of these circles, NFI data provides diameter measurements and species identity for all the trees with a diameter at a height of 1.3 m from 7.5 cm to 22.5 cm for the 6 m-radius circle, from 22.5 cm to 37.5 cm for the 9 m-radius circle, and greater than 37.5 cm for the 15 m-radius circle. The NFI also provides the canopy cover (*i.e.* cover having vertical access to light) per species within a 25 m-radius circle. The NFI also identifies the six dominant trees in each stand as those with the largest diameter among all the measured trees across the three circles. The NFI provides age and height measurements for two randomly selected dominant trees per plot. If one species represents more than 75 % of the canopy cover of the dominant trees, both dominant trees selected for age measurement are of this species. If no single species reaches 75 % of the canopy cover, one dominant tree of each of the two main species is measured. Hereafter, we refer to the dominant trees with height and age measurements as "measured dominant trees", and the species of these trees as the "dominant species". We defined stand age as the mean age of the two measured dominant trees.

Herein, we focused on even-aged two-species mixed stands. As in Combaud et al. (2024), the even-aged plots we selected were those labeled "even-aged" in the NFI database and for which the relative age difference between the oldest and the youngest measured dominant trees was less than 25 %. Among these plots, we considered mixed stands to be the ones where (i) the two measured dominant trees were of different species, and (ii) the sum of the canopy cover of the two dominant species within the 25 m radius circle was more than 50 % of the stand canopy cover. The first criterion ensured that the stand was indeed mixed, and the second criterion ensured that the mixture was mainly composed of the two species. We kept only the plots for which both dominant species were in the list of the 20 species considered in Combaud et al. (2024) because our modeling strategy relied on the models calibrated in that paper. We also restricted our dataset to stands with a relative density index superior to 0.5 to ensure that present and past densities were high enough to have a between-species interaction effect. The relative density index is defined as the ratio of the observed number of trees over the maximum number of trees that could be reached due to self-thinning induced by competition (Reineke, 1933). We computed this index following the method described by Aussenac et al. (2021). Even though the NFI data do not provide explicit localisation of the species in the mixtures, the small size of the 15 m-radius plot for tree measurements (700 m^2) allowed us to consider that the mixtures were intimate.

In even-aged monospecific stands, dominant height is usually defined per hectare as the mean height of the 100 trees with the largest diameters (Assmann and Davis, 1970), or, if the plot is less than one hectare in size, of n-1 trees where n is the number of 100-m^2 subunits in the plot (Vallet and Pérot, 2016). For example, for a plot of around 700 m^2, the dominant height in monospecific stands can be estimated as the mean height of the six trees with the largest diameters in the plot. In mixed stands, to determine the dominant height of each species, del Río et al. (2016), citing Zingg (1994), recommend first determining the dominant trees without taking into account species identity, and second computing the mean height of the dominant trees for each species. To apply this method to the selected NFI stands in our study where only one tree per dominant species was measured for age and height, we estimated the dominant height for each dominant species from the height of the measured dominant tree belonging to this species. This is a valid proxy for species dominant height *sensu* del Río et al. (2016) because for each dominant species, the measured dominant tree is randomly selected among all the dominant trees belonging to this species. Fig. A.1 in the Supplementary Materials summarizes how we computed dominant height.

2.1.2. Environmental data

We used the models provided in Combaud et al. (2024) to assess each dominant species' expected dominant height, therefore we calculated the NFI environmental data in the same way as in this latter study. More specifically, we used NFI data on soil depth, soil texture, flora, and FYRE and Safran climate data (Devers et al., 2020a, 2020b, 2021). The variables we computed included both soil variables (C:N ratio, pH, soil water holding capacity) and climatic variables (temperature, precipitation, sum of degree-days and climate water balance - defined as the difference between precipitation and potential evapotranspiration). We also took some environmental variables directly from the NFI database (slope, aspect, bedrock type). We restricted our database to NFI mixed stands for which the environmental variables were within the calibration range of the models for dominant height developed in Combaud et al. (2024).

2.1.3. Trait data and type of mixture

We tested the impact of three species traits that are directly or indirectly related to light interception or use: shade tolerance, wood density and specific leaf area (SLA, *i.e.* leaf area per unit of leaf mass). We considered these traits as fixed values per species, independently of species vertical hierarchy. We analyzed the impact of shade tolerance for two reasons. First, this variable provides information on the ability of the trees of the species to survive and develop when they are height dominated (Valladares and Niinemets, 2008). Second, it is a good proxy for the shading effect created by trees of this species when they are height dominant, *i.e.* shade tolerance informs on how the trees of one species shade dominated trees of other species (Fig. 1). This positive relationship stems notably from the ability of shade-tolerant species to develop deeper and denser crowns thanks to a better resistance to self-shading (Canham et al., 1994; Kulha et al., 2023; Petrovska et al., 2021). We also analyzed the impact of SLA and wood density because these variables reflect trade-offs between longevity and construction costs of some tissues and have proven useful in analyzing species interactions (Kunstler et al., 2016). In particular, wood density relates to crown shape and the speed of height growth and therefore influence resource foraging and competition for resources (Poorter et al., 2012a; Woodall et al., 2015). There was no correlation between these three traits among the 20 species we studied, except for a negative correlation between wood density and shade tolerance for gymnosperms (correlation coefficient −0.019, p-value = 0.01038 based on a linear model) (cf. Supplementary Materials, fig. B.1). We used the shade tolerance index of Niinemets and Valladares (2006) (higher values mean stronger shade-tolerance), the wood density values from the XyloDensMap database (Leban et al., 2022) and the SLA values from Carmona et al. (2021). For each species, we retained the mean value in the corresponding database. We completed these databases with data from other sources for missing species. For *Pinus nigra var. corsicana (Loudon, Hyl.)*, we used the shade tolerance provided in Thuiller et al. (2014) and for *Pinus pinaster subsp. pinaster (Aiton)*, we used the shade tolerance provided in Poorter et al. (2012a). Table 1 provides trait values for the 20 species we studied. We also considered the type of mixture, *i.e.* the combination between the group of the focal species (gymnosperm or angiosperm) and the group of the companion species. For 19 species out of the 20 species considered, the group matches the difference between evergreen and deciduous. Only *Larix decidua subsp. decidua (Mill.),* is a deciduous gymnosperm.

2.2. *Height variables calculations*

For each stand, we focused on each of the two dominant species successively. We used the models provided in Combaud et al. (2024) to assess the expected dominant height for each species as if it had grown in a monospecific stand under the same conditions as in the observed environment. We applied these models using the NFI age and environmental data for each dominant species. In the rest of this paper, we use the term “height-dominated species” (resp. “height-dominant species”) to refer to the species having the smallest (resp. highest) expected dominant height.

We computed the mixture effect on the dominant height of species i in stand k ($ME_{i,k}$) as in Vallet and Pérot (2016), *i.e.* as the difference between the observed and expected dominant heights of the focal species, divided by the expected dominant height of the focal species. This gave us a relative value (Eq. 1). In Eq. (1), $H_{obs,i,k}$ is the observed dominant height of the focal species i in the mixed stand k, and $H_{\exp,i,k}$ is the expected dominant height of species i in a monoculture with the same environment as in stand k. It is worth noting that we computed the mixture effect on a state variable (dominant height) and not on a flux variable (dominant height growth). We also computed the difference between the expected dominant height of the companion species and the expected dominant height of the focal species. We divided the difference by the focal species expected dominant height to obtain a relative value (Eq. 2). We called this variable the “between-species expected dominant height difference” ($\Delta H_{\exp,i,k}$). In Eq. (2), $H_{\exp,c,k}$ is the expected dominant height of the companion species c in stand k in a monoculture with the same environment as in stand k.

$$ME_{i,k} = \frac{H_{obs,i,k} - H_{\exp,i,k}}{H_{\exp,i,k}} \tag{1}$$

$$\Delta H_{\exp,i,k} = \frac{H_{\exp,c,k} - H_{\exp,i,k}}{H_{\exp,i,k}} \tag{2}$$

2.3. *Final stand selection*

To have observation data on tree age and height for the two species in the mixture, we focused on stands where both species were present in the dominant stratum, as defined by the NFI. However, if mixture negatively impacts the growth of the height-dominated species, this species may not be observed in the dominant stratum, even though it should be found there according to its expected dominant height in monospecific stands. To avoid a stand selection biased against stands for which mixture has a negative impact on the dominant height of the height-dominated species, we restricted our calibration sample to stands where the expected dominant height difference between the two species was between −20 % and +20 %. In this range, it is unlikely that the mixture effect on species dominant height would exclude a species from the dominant stratum. Finally, we kept 1368 plots (Table 1), corresponding to 76 species-pairs, and therefore to 76 ×2 = 152 combinations of focal / companion species. The distribution of the plots by species-pair is provided in the Supplementary Materials (fig. C.1).

2.4. *Modeling the mixture effect on species dominant height*

2.4.1. *General form of the model*

For each trait (shade tolerance, wood density, SLA), we modeled the mixture effect on species dominant height using a linear mixed model. We treated each trait separately to avoid hard-to-interpret interactions between the different traits. We included the traits in the model as the difference between the trait values for the companion species and the focal species.

We included a stand-level random intercept to capture the structure of the data because we had two mixture-effect observations per stand (one for each species). We considered the following explanatory vari-

Table 1

Number of plots and trait values per species. Each plot is counted twice because two species are measured on each plot. The number of different plots is 1368, and the number of observations is 2736. 978 plots are angiosperm-angiosperm stands, 163 plots are gymnosperm-gymnosperm stands and 227 plots are angiosperm-gymnosperm stands. The shade tolerance index is taken from (Niinemets and Valladares, 2006), higher values indicate stronger shade-tolerance.

Species in the mixture	Number of plots	Shade tolerance index	Wood density (kg/m3)	Specific leaf area (mm^2/mg)	Group
Abies alba (Mill.),	148	4.60	417	6.1	Gymnosperm
Betula pendula (Roth),	75	2.03	532	17.7	Angiosperm
Carpinus betulus (L.),	107	3.97	615	21.0	Angiosperm
Castanea sativa (Mill.),	161	3.15	506	17.9	Angiosperm
Fagus sylvatica (L.),	360	4.56	607	20.2	Angiosperm
Fraxinus excelsior (L.),	185	2.66	594	18.5	Angiosperm
Larix decidua subsp. decidua (Mill.),	7	1.46	499	15.1	Gymnosperm
Picea abies subsp. abies (L., H.Karst.),	124	4.45	388	4.5	Gymnosperm
Picea sitchensis (Bong., Carrière),	11	3.85	399	9.6	Gymnosperm
Pinus halepensis (Mill.),	3	1.35	537	11.2	Gymnosperm
Pinus nigra subsp. nigra (J.F.Arnold),	15	2.10	524	5.2	Gymnosperm
Pinus nigra var. corsicana (Loudon, Hyl.),	21	2.	491	5.2	Gymnosperm
Pinus pinaster subsp. pinaster (Aiton),	24	1.35	444	4.9	Gymnosperm
Pinus sylvestris (L.),	178	1.67	459	5.1	Gymnosperm
Pseudotsuga menziesii (Mirb., Franco),	22	2.78	456	7.4	Gymnosperm
Quercus petraea subsp. petraea (Matt., Liebl.),	551	2.73	650	16.7	Angiosperm
Quercus pubescens (Willd.),	44	2.31	721	10.3	Angiosperm
Quercus robur var. robur (L.),	659	2.45	630	16.8	Angiosperm
Quercus rubra (L.),	5	2.75	656	16.6	Angiosperm
Robinia pseudoacacia (L.),	36	1.72	640	23.5	Angiosperm

ables: expected dominant height difference between the two species in the mixture, trait difference between the companion and the focal species, the type of mixture (*i.e.* whether the companion and focal species are angiosperm / gymnosperm), age difference between species and stand age. We also tested for interactions between expected dominant height difference and all the other variables, because the compensation effect emphasized by Vallet and Pérot (2016) suggests that the sign of certain types of impact could depend on the species' vertical hierarchy. Finally, we tested the interactions between the traits and the type of mixture to account for differences in the distribution of wood density and SLA between angiosperm and gymnosperm species (Supplementary Materials, fig. B.2). We centered and scaled each quantitative variable by subtracting the mean and dividing by the standard deviation (Table 2). The general form of the models we tested is provided in Eq. 3, and Table 2 provides the mean and standard deviations for the potential explanatory variables.

$$\begin{aligned} ME_{i,k} = \quad & \mu_0 + \mu_k + \Delta H_{\exp,i,k} \\ & \times \left(\Delta Trait_{i,c,k} + \Delta Age_{i,c,k} + Age_k + TypeMixture_{i,k} \right) + \Delta Trait_{i,c,k} \\ & \times TypeMixture_{i,k} \quad + \epsilon_{i,k} \end{aligned} \tag{3}$$

In Eq. (3), k is the stand index: i is the focal species; c is the companion species; μ_0 is a common intercept; μ_k is a stand-specific random effect assumed to follow a normal distribution, independently and identically distributed across stands; $\epsilon_{i,k}$ is an error term for species i and stand k assumed to follow a normal distribution, independently and identically distributed across observations; and the "x" symbol represents interactions.

2.4.2. Model selection and parameter inference

For each species trait (shade tolerance, wood density, SLA), we combined a k-fold procedure and a stepwise selection procedure to select the best variables. First, we randomly divided our sample into five groups. Second, we implemented five stepwise model selections, each of them based on a calibration subsample composed of four groups (therefore based on 80 % of the data), so that each subsample was left outside the calibration subsample once. The stepwise procedure was both forward and backward. Because the random-effect structure was the same for all models and because we were interested only in fixed effects, we used the maximum likelihood estimator (Cheng et al., 2010) to estimate the parameters; we selected the model with the lowest AIC at each step. We stopped the selection process when an Anova test showed no significant (pvalue = 0.05) improvement of the model in two successive steps. Third, we defined the final model for a given trait as the model with the variables that consistently appeared in each of the five models (one per calibration subsample). This choice was made to ensure robustness and the parsimony of our models. To estimate the fixed effect of the final model, we used a restricted maximum likelihood estimator (Toïgo et al., 2015b). Our model selection strategy is summarized in the Supplementary Materials (fig. D.1).

To avoid including highly-correlated variables in the same model, we excluded models for which the variance inflation criteria (VIF) (O'Brien, 2007) was above 2. In the VIF computation, we excluded interaction variables and species group (angiosperm / gymnosperm). Indeed, we included the "group" variable precisely to account for the correlation between group and certain traits. We visually checked the normality of the random effects, the normality of the errors, and the homoscedasticity of the error of the final model (Pinheiro and Bates, 2006). We used the *lme* function of the R *nlme* package (version 3.1–157) (Pinheiro et al., 2023) in version 4.2.0 of the R software (R Core Team, 2022).

Table 2
Description of the explanatory variables over the 1368 plots (2736 observations). Q5 and Q95 are respectively the quantile at the 5 % and the 95 % levels. Mean and standard deviations are used to compute the centered-scaled variables used in the model. "difference" refers to difference between the value for the companion species and the value for the focal species. For example, if the focal species is shade-intolerant (low shade tolerance index) and the companion species is shade-tolerant (high shade tolerance index), then the shade tolerance difference is positive.

Variable	Mean	Standard deviation	Q5	Q95
Stand age (years)	74.71	27.89	30.00	123.00
Age difference between species (years)	0.00	8.59	−15.00	15.00
Expected DH difference (relative)	0.01	0.11	−0.15	0.18
Specific leaf area difference (mm2/mg)	0.00	5.85	−11.74	11.74
Shade tolerance difference	0.00	1.20	−1.90	1.90
Wood density difference (kg/m3)	0.00	87.31	−170.74	170.74

3. Results

3.1. Computed mixture effect on species dominant height per species-pair

Out of 50 combinations for which at least 10 observations were available (involving 13 species), we found a significant mixture effect on species dominant height (pvalue = 0.05) for 15 focal species-companion species combinations (involving 9 species): for 12 combinations, the focal species dominant height was higher in mixture than in pure stand, and for 3 combinations, the focal species dominant height was lower in mixture than in pure stands (Fig. 2).

3.2. Models of mixture effect on species dominant height

Between-species expected dominant height difference and stand age were selected in the three final models, with respectively positive and negative impacts on the response of species dominant height to mixture (Table 3). Trait difference was also included in each selection procedure. In addition, mixture type was selected in the model based on wood density. In this model, the response of the focal species dominant height to mixture is higher (less negative or more positive) when the focal species is a gymnosperm and lower (more negative or less positive) when the companion species is a gymnosperm. The AIC was lower for the model involving shade tolerance than those involving SLA or wood density (a difference of more than 5 points). We checked that the hypotheses regarding residuals and random effects were respected for the three models (fig. E.1 to E.3 in Supplementary Materials). The models selected for the different calibration subsamples are presented in the Supplementary Materials (tab. E.1 to E.3).

We found that expected dominant height difference had the strongest impact on the mixture effect whatever the model considered: the mixture effect varied over around 13 percentage points within the range of expected dominant height difference in the calibration sample (Fig. 3). This means that in response to mixing, species dominant height increases by between 3.2 and 3.4 percentage points when the between-species expected dominant height difference increased by 10 percentage points. Shade tolerance difference, SLA difference and wood density difference had a lower impact: in response to mixing, species dominant height increases by +3, +3 and −7 percentage points, respectively, from the 5 % quantile to the 95 % quantile of the variable. For the different stand age classes, the graphs are provided in Supplementary Materials (fig. F.1 to F.3). The intercept was significantly positive in all the models. Fig. 4 illustrates the influence of expected dominant height difference, stand age and shade tolerance on the dominant height dynamics in mixed stands, compared to monospecific stands. Figures G.1 to G.5 in the Supplementary Materials address the other traits.

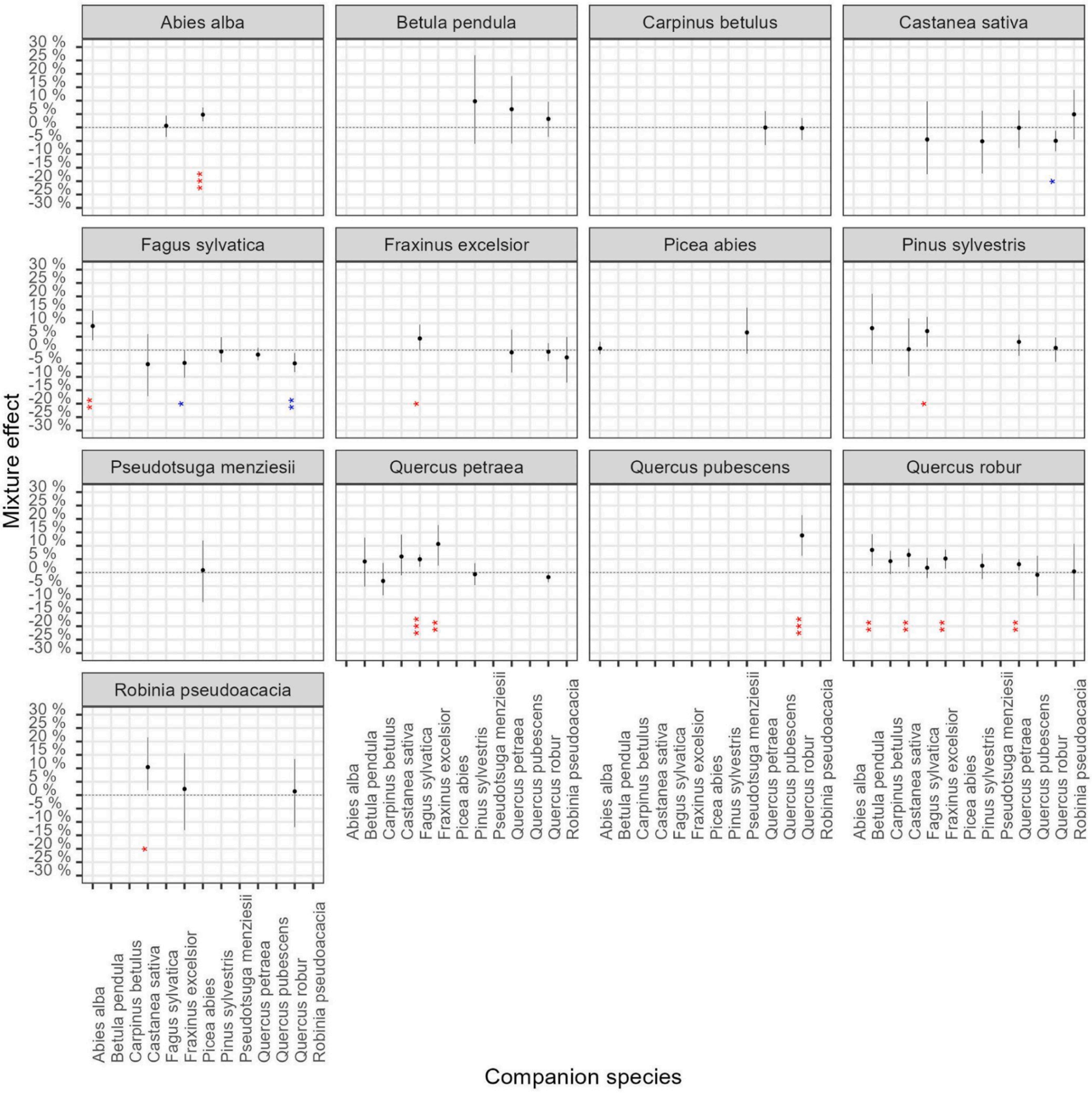

Fig. 2. Mixture effect on species dominant height for species-combinations with more than ten observations. The mixture effect is the relative difference between observed dominant height and expected dominant height. Each graph corresponds to a focal species; companion species are on the x-axis. Points are the mean values of the mixture effect; segments represent the confidence intervals (Wilcoxon test at the 0.05 level). Stars indicate whether the mean mixture effect is significantly different from 0 (no star: non- significant, *: significance level = 0.05, **: significance level = 0.01, ***: significance level = 0.001). Red star: significantly positive mixture effect; blue star: significantly negative mixture effect. For example, for the focal species Fagus sylvatica and the companion species Abies alba the mean mixture effect is 9 %, which means that the dominant height of Fagus sylvatica is on average 9 % higher in a mixture with Abies alba than when Fagus sylvatica grows in a monospecific stand under the same environmental conditions. Seven species are not represented because there were not enough observations: Larix decidua, Picea sitchensis, Pinus halepensis, Pinus nigra subsp. nigra, Pinus nigra var. corsicana, Pinus pinaster and Quercus rubra.

4. Discussion

4.1. Mixture effect on species dominant height, per species-pair

Our results show that mixture influenced species dominant height for a significant proportion of the species combinations (15 out of 50), which confirms the importance of taking this effect into account to anticipate stand development. The mixture effect on species dominant height we found was generally moderate (below 10 % in absolute terms), except for the focal species *Quercus pubescens* with the companion species *Quercus robur* combination (increase of *Quercus pubescens* dominant height in mixtures of +14 %). This contrasts with the response of basal area increment to mixing species, where effects above 20 % are common and may even exceed 40 % (Toïgo et al., 2018; Toïgo, Toïgo et al., 2015a). In some configurations, the predicted mixture effect is strong enough to reverse the vertical hierarchy expected in monospecific

Table 3

Parameter values and quality indicators for the three final models involving, respectively, shade tolerance difference, SLA difference and wood density difference (in columns).

	Model with shade tolerance	Model with specific leaf area	Model with wood density
Parameters			
Intercept	0.019 ***	0.019 ***	0.017 ***
Expected dominant height difference	0.034 ***	0.036 ***	0.034 ***
Stand age	−0.012 **	−0.012 **	−0.011 **
Shade tolerance difference	0.01 ***	.	.
Specific leaf area difference	.	0.008 ***	.
Wood density difference	.	.	−0.018 ***
Mixture type = AG	.	.	−0.039 **
Mixture type = GA	.	.	0.054 ***
Mixture type = GG	.	.	0.005
Standard deviation of the error term	0.099	0.099	0.098
Standard deviation of the random effects	0.12	0.12	0.121
Quality indicators	Shade tolerance	Specific leaf area	Wood density
AIC	−2971	−2962	−2965
r^2	0.06	0.06	0.06
RMSE	0.16	0.16	0.16

The explanatory variables are center-scaled (see Table 2). "Mixture type" is a discrete variable representing whether the focal species-companion species pair was angiosperm-angiosperm (reference case), angiosperm-gymnosperm (AG), gymnosperm-angiosperm (GA) or gymnosperm-gymnosperm (GG). r^2 is the share of variance explained by the model and RMSE is the root mean square error. Both were computed with unconditional residuals (i.e. without any random effects prediction). Stars indicate whether the parameters are significantly different from 0 at pvalue = 0.05(*), 0.01(**) or 0.001(***).

stands. In this case, predictions should be interpreted carefully because then the expected dominant height difference is probably an unsatisfactory explanatory variable.

Our results are partly consistent with those obtained by Vallet and Pérot (2016), who also used French NFI data to analyze five focal species. We had enough data to confirm their results for five out of the eight species combinations for which they found a significant mixture effect on species dominant height. For the three remaining cases, we did not find any significant effect. Discrepancies probably come from differences in the mixed stands selected, because we constrained our dataset to ensure that expected dominant height difference was between −20 % and +20 %. Our larger set of focal species and including *Fraxinus excelsior* in the list of companion species enabled us to identify significant mixture effects that Vallet and Pérot (2016) did not capture: increase of the dominant height of *Quercus robur* with four companion species, strong increase of the dominant height of *Quercus pubescens* when mixed with *Quercus robur*, and some responses of the dominant height to mixture for *Castanea sativa*, *Fraxinus excelsior* and *Robinia pseudoacacia*. These results are interesting for forest management strategies because they show significant mixture effects on economically important species in Europe (*e.g. Picea abies*, *Quercus petraea* and *Quercus robur*) (Hanewinkel et al., 2013; Ducousso and Bordacs, 2004) or potentially well-adapted to upcoming climate change (*e.g. Quercus pubescens*) (Illés and Móricz, 2022).

4.2. Models of mixture effect on species dominant height

4.2.1. Impact of between-species expected dominant height difference on the mixture effect on species dominant height

Our results confirm our first hypothesis that the mixture effect on species dominant height is more positive (or less negative) when the between-species expected dominant height difference increases. This effect dominates the effect of other variables, which confirms our hypothesis that mixing species tends to increase the dominant height of the height-dominated species and to reduce the dominant height of the height-dominant species. This result was consistent for all three of the final models resulting from our selection processes (one per trait). In all cases, we found an increase of dominant height between 3.2 percentage points and 3.4 percentage points, for an increase of 10 percentage points in expected dominant height difference. These effects in opposite directions for the height-dominant and the height dominated species, leading to a convergence of dominant height of both species, are consistent with the compensation effect found in Vallet and Pérot (2016). We can interpret these in relation to the impact of mixture on the asymmetric competition for light for both the height-dominated and the height-dominant species. Let us consider a mixed stand composed of two species with different expected dominant heights and similar traits (especially regarding shade tolerance and shading effect). In such a stand, the competition for light experienced by the height-dominated species is stronger than if this species grew in monospecific stands with similar density. Our findings of an increase in the height of this species compared to monospecific stands can be interpreted in a way to compensate for this increased competition. Such a behavior would be consistent with the findings of Lines et al. (2012): they found that for a given diameter, height increases when the asymmetric competition increases. Their studies used the basal area of the trees with larger diameter as the competition index. Our findings complement these results because they show that (dominant) height difference is an important variable to describe asymmetric competition. Del Rio et al. (2019) also found that height increased with asymmetric competition for two species out of the four they studied. Conversely, in the same stand, the competition for light experienced by the height-dominant species is lower than if it grew in monospecific stands. This could explain the decrease in the dominant height of this species compared to monospecific stands, because then resources can be allocated to other functions than light foraging (radial growth, water foraging, by allocating carbon to roots, reproduction, etc.) (Bebre et al., 2021, Durigan et al., 2012, Poorter et al., 2012b).

The positive intercept we found implies that, if the focal species has a higher expected dominant height, the mixture effect on species dominant height becomes negative only when the expected dominant height difference is large enough (expected dominant height difference is negative in this case).

4.2.2. Impact of traits on the mixture effect on species dominant height

We found that shade-tolerance, SLA and wood-density differences between species were useful to explain the mixture effect on species dominant height. However, the magnitude associated to these variables was lower than the magnitude of the expected dominant height difference. In our sample, there was no correlation between species traits (fig. B.1 in Supplementary Materials), except for a negative correlation between shade tolerance and wood density for gymnosperm species. This suggests that the traits we studied provide different information. Each of the three models we calibrated (one per trait) are useful. The shade tolerance index of Niinemets and Valladares (2006) is interesting because this index is available for a wide range of species. However, shade tolerance may depend on tree age as well as on biotic and abiotic factors, and the shade tolerance index can hardly be measured on the field because it is an indirect measure of several functional traits (Valladares and Niinemets, 2008). In contrast, SLA and wood density can be directly measured on the field, albeit with complex procedures for wood density. However, the models we calibrated involving these latter variables have a higher AIC.

4.2.2.1. Focus on the effect of shade tolerance. According to our results, the higher is the shade tolerance of the companion species compared to the focal species, the more positive (or less negative) is the mixture effect

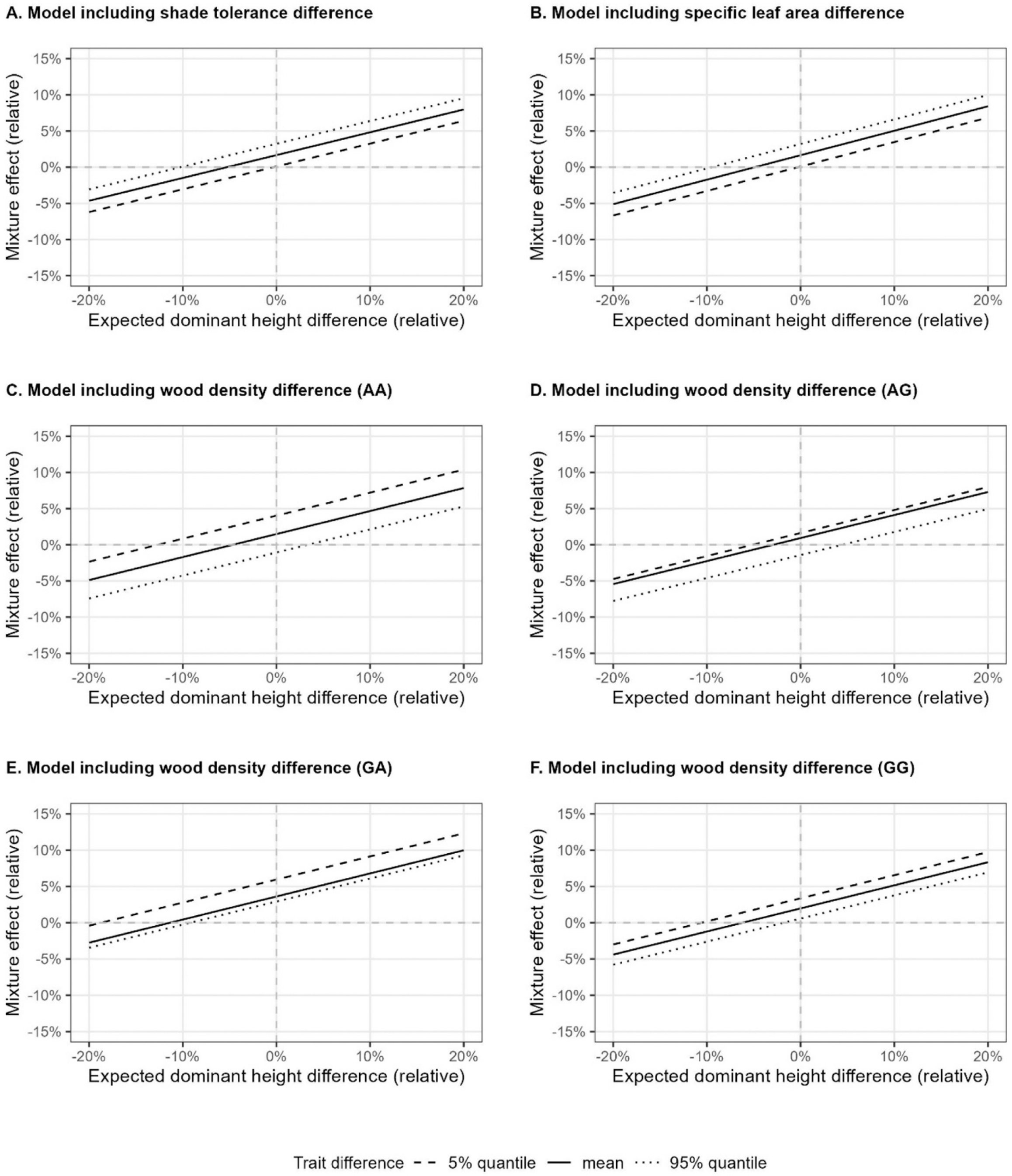

Fig. 3. Impact of expected dominant height difference (x-axis) and trait difference on the mixture effect on species dominant height (y-axis) in the model with shade tolerance (A), SLA (B) and wood density (C to F). Graphs C to F represent different focal-companion species combinations: angiosperm-angiosperm ("AA", graph C), angiosperm - gymnosperm ("AG", graph D), gymnosperm - angiosperm ("GA", graph E), and gymnosperm - gymnosperm ("GG", graph F). Computations were done for a mean age of 75 years. Line types represent different values of trait differences between species. Trait difference is computed as trait value for the companion species minus trait value for the focal species. Hence, the 5% quantile (resp. 95% quantile) of trait difference represents a case with relatively high (resp. relatively low) shade tolerance of the focal species compared to the companion species. The extreme values for trait differences are the 5 % and 95 % quantiles of the distribution in the calibration sample. Quantile values: for shade tolerance difference, Q5 % = −1.9, mean = 0, Q95 % = 1.9; for SLA difference, Q5 % = −11.7 mm^2/mg, mean = 0 mm^2/mg and Q95 % = 11.7 mm^2/mg; for wood-density difference: Q5 % = −171 kg/m^3, mean = 0 kg/m^3, Q95 % = 171 kg/m^3 (for angiosperm-angiosperm mixtures), Q5 % = −195 kg/m^3, mean = −161 kg/m^3, Q95 % = −47 kg/m^3 (for angiosperm-gymnosperm mixtures), Q5 % = 47 kg/m^3, mean = 161 kg/m^3, Q95 % = 195 kg/m^3 (for gymnosperm-angiosperm mixtures), Q5 % = −68 kg/m^3, mean = 0 kg/m^3, Q95 % = 68 kg/m^3 (for gymnosperm-gymnosperm mixtures).

on species dominant height. This finding is consistent with that of del Río et al. (2019). The stronger increase of dominant height in response to mixing for height-dominated shade-intolerant species (compared to shade-tolerant species) is consistent with shade-avoidance, our second hypothesis. This behavior consists in prioritizing height growth over other functions for shade-intolerant species under cover (Henry and Aarssen, 1999). Kothari et al. (2021) identified such a behavior for the shade-intolerant *Betula papyrifera*, for which they found stem elongation in case of stronger competition. They did not find the same pattern for the shade-tolerant species *Tilia americana* and *Acer negundo*. Lines et al.

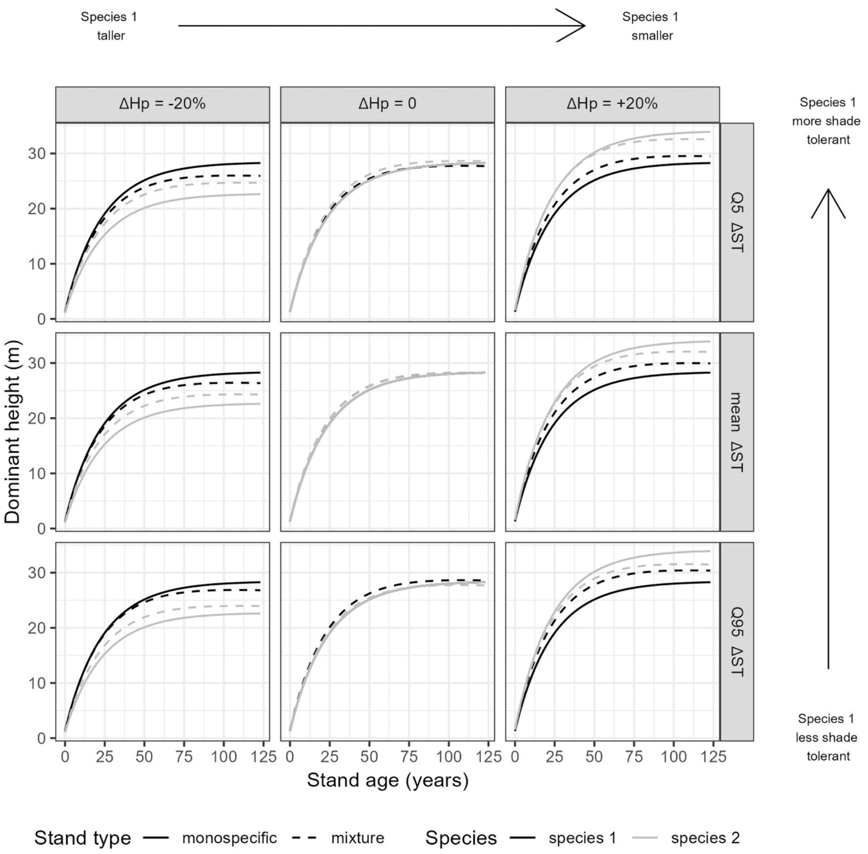

Fig. 4. Simulated dominant height dynamics for two virtual species in monospecific (solid line) and mixed stands (dashed line), for two virtual species (species 1 in black, species 2 in grey), depending on expected dominant height difference (ΔHp) and shade-tolerance difference (ΔST), where differences are computed as the value for species 2 minus the value for species 1. Hence, the 5% quantile (resp. 95% quantile) of trait difference represents a case with relatively high (resp. relatively low) shade tolerance of species 1 compared to species 2. Columns represent different values of the expected dominant height difference (-20 %, 0, 20 %). Rows represent different values of shade-tolerance difference (5 % quantile, mean, 95 % quantile, over the calibration sample). For example, the top left graph corresponds to the case where species 1 had a higher expected dominant height and a higher shade tolerance than species 2. Dominant height in monospecific stands for species 1 was computed from the parameters for Quercus petraea in Combaud et al. (2024), in the mean environment. Dominant height in monospecific stands for species 2 was computed as the dominant height of species 1 corrected by the expected dominant height difference. Dominant heights in the mixture for species 1 and 2 were computed as expected dominant height corrected by the mixture effect predicted by the model from shade tolerance difference. ΔHp: expected dominant height difference; ΔST: shade-tolerance difference. Quantile values for shade-tolerance difference: Q5 % = −1.9, mean = 0, Q95 % = 1.9. The maximum age represented corresponds to the 95 % quantile of the distribution in the calibration sample (123 years).

(2012) found results in the same direction: they show that at a given diameter of the focal tree, asymmetric competition tends to increase the height of shade-intolerant species more that the height of shade-tolerant ones.

We can also interpret our result focusing on the shade-tolerance of the companion species. The shade tolerance of the companion-species is a good proxy for its shading effect, notably because shade-tolerant species can develop deeper, denser crowns due to a better resistance to self-shading (Canham et al., 1994; Kulha et al., 2023; Petrovska et al., 2021). If the focal species is height-dominated, we can hypothesize that it needs to grow more in height to access light if the companion species has a stronger shading effect. This would be again consistent with a shade-avoidance behavior. Another possibility in such situations would be the inhibition of height growth of the height-dominated focal species, but we did not find this pattern. It is possible that in these situations, the height-dominated species dies, so we do not observe this in our data. It is also possible that our stand selection excludes such cases, as we only consider stands where both species are in the dominant strata, and a negative response of dominant height to mixture could lead to the exclusion of a species from this stratum. However, we tried to avoid such a selection effect by focusing on mixtures for which expected dominant height difference is below 20 %.

In case the focal species is height-dominant, we did not expect any effect of shade tolerance difference on the mixture effect on species dominant height. Therefore, we expected an interaction between the effect of shade-tolerance difference and expected dominant height difference, but this was not the case. This suggests that the positive effect of shade-tolerance difference also holds for a height-dominant focal species. However, such a positive effect is counterbalanced by the much stronger negative effect of expected dominant height difference. In addition, it is possible that the linear interaction framework we used in our study masked non-linear interactions between between-species shade tolerance difference and between-species expected dominant height difference.

4.2.2.2. Focus on the effect of wood density and specific leaf area. We found that higher wood-density difference was associated with lower mixture effect on species dominant height. This could appear in contradiction with our finding that higher shade tolerance difference is associated with a higher mixture effect, because studies have emphasized a positive correlation between wood density and shade tolerance for tropical species (Wright et al., 2010). However, we did not observe this correlation between wood density and shade tolerance in our dataset, after controlling for species group (angiosperm / gymnosperm). On the contrary, we observed a negative correlation for gymnosperm species (fig. B.1 in Supplementary Materials). This negative correlation was also found on a larger set of Northern-hemisphere coniferous species (Tucker et al., 2024). Our findings on the effect of wood density could reflect a relationship between wood density and shade tolerance for gymnosperms. It could also reflect other processes, because wood density is an integrative trait of diverse properties. For example, it relates to the resources required to creating wood fiber (Kunstler et al., 2016). In our model with wood density, the type of mixture was also among the selected variables. This accounts for the fact that wood density is very different in gymnosperms and angiosperms (fig. B.2 in Supplementary Materials), and therefore including the mixture type corrects for this difference. The negative impact of gymnosperm companion species on the mixture effect could be due to the fact that they keep their leaves all year long (except for *Larix decidua*), thus preventing the species below from benefitting from easy access to light in the early spring. The positive impact of gymnosperm focal species could relate to the ability of gymnosperms to photosynthesize in early spring in case of favorable temperatures, once again due to the fact that they are evergreen.

Our finding of a positive effect of SLA difference on the mixture effect on species dominant height is difficult to interpret because SLA is integrative of different processes and because it provides information on light interception at the leaf level, but not at the tree or stand level. In particular, for mature trees, light interception is determined by tree architecture rather than by SLA (Poorter et al., 2008). Therefore, it is difficult to directly interpret SLA as a proxy for competitive pressure.

Kunstler et al. (2016) focused on the competition effect on diameter increment and found effects of SLA and wood density. For temperate forests, they found that the companion tree’s SLA negatively related to the competitive pressure exerted by the companion tree, meaning that a higher SLA of the companion tree favored diameter growth. They also found a positive impact of focal-species wood density and a negative impact of companion-species wood density on diameter growth. It is worth noting that Kunstler et al., (2016) found no significant effect of SLA difference or wood-density difference on competition, after separately taking into account the effects of the focal-species and the companion-species trait. This suggests that individual traits may be more important than trait differences. However, we chose not to analyze individual trait to ensure a more robust k-fold model selection procedure.

4.2.3. Impact of stand age on the mixture effect on species dominant height

We did not expect stand age to be selected as an explanatory variable. However, it appeared consistently in the three models, albeit with a weak magnitude comparable to the one for shade-tolerance difference and specific-leaf-area difference. This may reflect how the impact of species interactions on growth can vary with stand age (Forrester et al., 2011). Plaga et al. (2023) found that the response of species diameter to mixture was stronger in early development phases. This could be due to greater competition pressure during these phases and to variations in the efficiency of light-harvesting with age (Niinemets, 2010). It is surprising that the age impact did not depend on the vertical hierarchy: if age modulates the amplitude of the mixture effect on species dominant height, we would have expected an interaction between age and expected dominant-height difference to capture the “compensation effect” mentioned above. Residual variability in our data may have masked this interaction.

4.2.4. Comparison with the impact of mixture on radial growth

The mixture effect on species dominant height that we found do not necessarily have the same sign as effects on radial increment found in the literature. The effect we found has the same sign as the one found by Toïgo et al. (2015a) on radial growth for *Fagus sylvatica* (mixed with *Abies alba*) or *Abies alba* (mixed with *Picea abies*). However we found opposite signs for *Quercus petraea* (mixed with *Fagus sylvatica*), and for a large number of combinations we did not find significant effect while they found some, and conversely. Under increased light competition, some species may prioritize height growth over diameter growth due to shade-avoidance behavior (Henry and Aarssen, 1997; Kothari et al., 2021), which could result in an opposite response of species diameter and height to mixing species. In other situations, increased light competition could decrease carbon assimilation so much that the response to mixing species of both diameter and height would be negative, even after carbon reallocation in favor of height growth. To get further insights on carbon allocation in response to mixing species, it would be useful to simultaneously analyze the impact of certain traits on the response to mixing species of both diameter and height growth.

4.3. Interest of our approach and working perspectives

Our results apply to mixtures that are effectively observed on the field; they do not reflect cases where the mixture effect on species dominant height leads to the death of one of the two species. Neither do our results apply in mixtures where the expected dominant-height difference is above 20 %, because we excluded such stands from our calibration sample to avoid potential bias linked to the NFI protocol (cf. Section 2.3). Extending our results to this latter category of stands would be interesting, but applying our approach to such stands would require age data for trees that are not necessarily in the dominant stratum.

One should keep in mind some caveats when interpreting our results. First, the independent variable in our model and one of the explanatory variables were computed based on simulated expected dominant height at the age of observation. Any uncertainty on the parameters used to simulate this variable affects the computation of the mixture effect. However, a sensitivity analysis shows that our main conclusions on the sign and the magnitude of the effects are robust to variations in the values of the parameters used to determine expected dominant height in mixtures (supplementary material H). Second, part of the mixture effect on species dominant height that we observe in our data may have been due to management choices. In particular, thinning can be designed to promote access to light for a given species, and stand density history may affect the competition for light experienced by the observed trees. It would therefore be useful to account for management history (del Río et al., 2019), but this would require stand level data unavailable from the French NFI. However, our focus on stands with a relative density index superior to 0.5 ensures that each stand has remained quite dense for a large part of its history. Third, we did not consider intraspecific trait variability because we lacked field measurements for traits. Studies confirm the existence of this variability depending on environmental conditions and tree age (Niinemets and Valladares, 2006; Valladares and Niinemets, 2008). The second and third points illustrate the trade-off between obtaining detailed stand data and the number of observations. One strength of our study is to take into account a large number of stands.

The large unexplained variability in our models is due to three main aspects. First, the mixture effect on species dominant height is a second order effect, because the main driver of species dominant height in mixed stands is species dominant height in monospecific stands, which depends on species ontogeny and environmental conditions (Combaud et al., 2024). Second, NFI data provides a high number of observations covering a wide range of species and environmental conditions, but at the cost of a low number of measurements per plot: in this study, we had only one height and age measurement per species for each stand. Third, it would be interesting to analyze the impact of the environment on the mixture effect on species dominant height to reduce the unexplained variability in our models. Analyzing environmental impact would require taking into account how the mixture effect is influenced by the environment depending on the nature of species interactions (Forrester and Bauhus, 2016). Dealing with all species-pairs together would therefore require more data, especially on traits, to control for varying interactions across species-pairs.

Despite these caveats, our study provides an interesting method to explore the consequences of mixing species on dominant height growth in even-aged stands. Using a large NFI database enabled us to cover a large number of species-pairs and environments, ensuring the genericity of our results in the context of European forests, which at least partly compensates for the above-mentioned drawbacks. In addition, our trait-based approach makes it possible to compute the mixture effect on species dominant height for European species not present in our database, provided the value of expected dominant height difference is available. Also, we contributed to the empirical literature on asymmetric competition by quantifying the role of height difference, while the majority of the papers on asymmetric competition focus on the basal area or volume of larger trees (Lines et al., 2012, Kothari et al., 2021).

Mixing species through species-diverse plantation, enrichment plantation or management favoring species-diverse natural regeneration is an important path to adapt forest to climate change (Kolström et al., 2011). Our results may help design management strategies to adapt forest to climate change, especially regarding the choice of species to favor in mixtures. First, our results contribute to better anticipate tree growth and therefore carbon sequestration and wood production, which is an important aspect for managers wanting to diversify forests. Second, our results inform on the species dominant height response to asymmetric competition for light. This can help assessing the ability of two species growing in the same stand to have sufficient access to light.

5. Conclusion

The response of species dominant height to mixture is important to take into account when anticipating how species react to changes in the light competition induced by mixing species. This mixture effect on species dominant height is linked to species characteristics involved in the acquisition of light (height difference and trait difference). Our results may help design and implement strategies to diversify tree species in European forests, which is an important avenue toward adapting forests to climate change.

CRediT authorship contribution statement

Thomas Cordonnier: Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization. **Thomas Pérot:** Writing – review & editing, Validation. **Xavier Morin:** Writing – review & editing, Validation. **Patrick Vallet:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Matthieu Combaud:** Writing – original draft, Validation, Methodology, Investigation, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Most of the data are available online (cf. references in the material and method). Some data are confidential (precise stand altitude)

Acknowledgements

This work was supported by the metaprogramme "Agriculture and forestry in the face of climate change: adaptation and mitigation" (CLIMAE) of the French National Research Institute for Agriculture, Food and Environment (INRAE) and the French National Forest Office (ONF). The authors wish to thank the French NFI for providing the stand data, Météo-France for providing the SAFRAN data, Jean-Claude Gégout for providing data on bioindication, Alexandre Devers and Jean-Philippe Vidal for exchanges on climate data, Christian Piedallu for exchanges about bioindicated values, Mathieu Jonard, Jordan Bello, François Morneau and Sylvain Dupire for discussing the general idea of the paper, and Anne Baranger, Julien Barrère, Nathéo Beauchamp, Maxime Jaunâtre, Georges Kunstler, and Björn Reineking for advice on some aspects of the paper. The authors also want to thank the participants of the 2024 FOREM seminar for their constructive inputs.

Data statement

Most of the data are available online (cf. references in the material and method). Some data are confidential (precise stand altitude).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122298.

References

Assmann, Ernst, & Davis, P.W. (1970). Principles of Forest Yield Study. Pergamon.

Aussenac, Raphaël, Pérot, Thomas, Fortin, Mathieu, de Coligny, François, Monnet, Jean-Matthieu, & Vallet, Patrick. (2021). The Salem simulator version 2.0: A tool for … | Open Research Europe. Open Research Europe. https://open-research-europe.ec.europa.eu/articles/1-61/v2.

Bebre, Ieva, Riebl, Hannes, Annighöfer, Peter, 2021. Seedling growth and biomass production under different light availability levels and competition types. Article 10. Forests *12* (10). https://doi.org/10.3390/f12101376.

Biber, P., Pretzsch, H., 2022. Tree growth at gap edges. Insights from long term research plots in mixed mountain forests. For. Ecol. Manag. *520*. https://doi.org/10.1016/j.foreco.2022.120383.

Canham, Charles D., Finzi, Adrien C., Pacala, Stephen W., Burbank, Diane H., 1994. Causes and consequences of resource heterogeneity in forests: Interspecific variation in light transmission by canopy trees. Can. J. For. Res. *24* (2), 337–349. https://doi.org/10.1139/x94-046.

Carmona, Carlos, Bueno, C.Guillermo, Toussaint, Aurele, Träger, Sabrina, Diaz, Sandra, Moora, Mari, Munson, Alison, Pärtel, Meelis, Zobel, Martin, & Tamme, Riin. (2021). Data from "Fine-root traits in the global spectrum of plant form and function" (Carmona et al. 2021 Nature) (p. 1115039 Bytes) [Dataset]. figshare. https://doi.org/10.6084/M9.FIGSHARE.13140146.V1.

Cheng, Jing, Edwards, Lloyd J., Maldonado-Molina, Mildred M., Komro, Kelli A., Muller, Keith E., 2010. Real longitudinal data analysis for real people: Building a good enough mixed model. Stat. Med. *29* (4), 504–520. https://doi.org/10.1002/sim.3775.

Combaud, Matthieu, Cordonnier, Thomas, Dupire, Sylvain, Vallet, Patrick, 2024. Climate change altered the dynamics of stand dominant height in forests during the past century – Analysis of 20 European tree species. For. Ecol. Manag. *553*, 121601. https://doi.org/10.1016/j.foreco.2023.121601.

del Río, Miren, Bravo-Oviedo, Andrés, Ruiz-Peinado, Ricardo, Condés, Sonia, 2019. Tree allometry variation in response to intra- and inter-specific competitions. Trees *33* (1), 121–138. https://doi.org/10.1007/s00468-018-1763-3.

del Río, Miren, Pretzsch, Hans, Alberdi, Iciar, Bielak, Kamil, Bravo, Felipe, Brunner, Andreas, Condés, Sonia, Ducey, Mark J., Fonseca, Teresa, von Lüpke, Nikolas, Pach, Maciej, Peric, Sanja, Perot, Thomas, Souidi, Zahera, Spathelf, Peter, Sterba, Hubert, Tijardovic, Martina, Tomé, Margarida, Vallet, Patrick, Bravo-Oviedo, Andrés, 2016. Characterization of the structure, dynamics, and productivity of mixed-species stands: Review and perspectives. Eur. J. For. Res. *135* (1), 23–49. https://doi.org/10.1007/s10342-015-0927-6.

Devers, Alexandre, Vidal, Jean-Philippe, Lauvernet, Claire, & Vannier, Olivier. (2020a). FYRE Climate: Precipitation (Version v1.0.0) [Dataset]. Zenodo. https://doi.org/10.5281/zenodo.4005573.

Devers, Alexandre, Vidal, Jean-Philippe, Lauvernet, Claire, & Vannier, Olivier. (2020b). FYRE Climate: Temperature (Version v1.0.0) [Dataset]. Zenodo. https://doi.org/10.5281/zenodo.4006472.

Devers, Alexandre, Vidal, Jean-Philippe, Lauvernet, Claire, Vannier, Olivier, 2021. FYRE Climate: A high-resolution reanalysis of daily precipitation and temperature in France from 1871 to 2012. Climate *17* (5), 1857–1879. https://doi.org/10.5194/cp-17-1857-2021.

Ducousso, Alexis, & Bordacs, Sandor. (2004). *EUFORGEN Technical Guidelines for genetic conservation and use for pedun- culate and sessile oaks (Quercus robur and Q. petraea)*. Interna- tional Plant Genetic Resources Institute, Rome, Italy.

Durigan, Giselda, Melo, Antonio C.G., Brewer, John S., 2012. The root to shoot ratio of trees from open- and closed-canopy cerrado in south-eastern Brazil. Plant Ecol. Divers. *5* (3), 333–343. https://doi.org/10.1080/17550874.2012.691564.

Forest Europe. (2020). *State of Europe's forests 2020*. https://foresteurope.org/wp-content/uploads/2016/08/SoEF_2020.pdf.

Forrester, David I., Bauhus, J.ürgen, 2016. A review of processes behind diversity—productivity relationships in forests. Curr. For. Rep. *2* (1), 45–61. https://doi.org/10.1007/s40725-016-0031-2.

Forrester, David I., Vanclay, Jerome K., Forrester, Robert I., 2011. The balance between facilitation and competition in mixtures of Eucalyptus and Acacia changes as stands develop. Oecologia *166* (1), 265–272. https://doi.org/10.1007/s00442-011-1937-9.

Grossiord, Charlotte, 2020. Having the right neighbors: How tree species diversity modulates drought impacts on forests. N. Phytol. *228* (1), 42–49. https://doi.org/10.1111/nph.15667.

Hanewinkel, Marc, Cullmann, Dominik A., Schelhaas, Mart-Jan, Nabuurs, Gert-Jan, Zimmermann, Niklaus E., 2013. Climate change may cause severe loss in the economic value of European forest land. Nat. Clim. Change *3* (3), 203–207. https://doi.org/10.1038/nclimate1687.

Henry, Hugh A.L., Aarssen, Lonnie W., 1997. On the Relationship between Shade Tolerance and Shade Avoidance Strategies in Woodland Plants. Oikos *80* (3), 575. https://doi.org/10.2307/3546632.

IGN. (2022). *Données brutes de l'inventaire forestier mises en ligne sur DataIFN - Version* 2.0. https://inventaire-forestier.ign.fr/dataIFN/.

Illés, G.ábor, Móricz, Norbert, 2022. Climate envelope analyses suggests significant rearrangements in the distribution ranges of Central European tree species. Ann. For. Sci. *79* (1), 35. https://doi.org/10.1186/s13595-022-01154-8.

Jactel, Hervé, Bauhus, J.ürgen, Boberg, Johanna, Bonal, Damien, Castagneyrol, Bastien, Gardiner, Barry, Gonzalez-Olabarria, Jose Ramon, Koricheva, Julia, Meurisse, Nicolas, Brockerhoff, Eckehard G., 2017. Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. Curr. For. Rep. *3* (3), 223–243. https://doi.org/10.1007/s40725-017-0064-1.

Jucker, Tommaso, Bouriaud, Olivier, Avacaritei, Daniel, Dănilă, Iulian, Duduman, Gabriel, Valladares, Fernando, Coomes, David A., 2014. Competition for light and water play contrasting roles in driving diversity–productivity relationships in Iberian forests. J. Ecol. *102* (5), 1202–1213. https://doi.org/10.1111/1365-2745.12276.

Kolström, M., Lindner, M., Vilén, T., Maroschek, M., Seidl, R., Lexer, M.J., Netherer, S., Kremer, A., Delzon, S., Barbati, A., Marchetti, M., Corona, P., 2011. Reviewing the Science and Implementation of Climate Change Adaptation Measures in European Forestry. Forests 2 (4). https://doi.org/10.3390/f2040961. Article 4.

Kothari, Shan, Montgomery, Rebecca A., Cavender-Bares, Jeannine, 2021. Physiological responses to light explain competition and facilitation in a tree diversity experiment. J. Ecol. *109* (5), 2000–2018. https://doi.org/10.1111/1365-2745.13637.

Kulha, Niko, Honkaniemi, Juha, Barrere, Julien, Brandl, Susanne, Cordonnier, Thomas, Korhonen, Kari T., Kunstler, Georges, Paul, Carola, Reineking, Björn, Peltoniemi, Mikko, 2023. Competition-induced tree mortality across Europe is driven by shade tolerance, proportion of conspecifics and drought. J. Ecol. *111* (10), 2310–2323. https://doi.org/10.1111/1365-2745.14184.

Kunstler, Georges, Falster, Daniel, Coomes, David A., Hui, Francis, Kooyman, Robert M., Laughlin, Daniel C., Poorter, Lourens, Vanderwel, Mark, Vieilledent, Ghislain, Wright, S.Joseph, Aiba, Masahiro, Baraloto, Christopher, Caspersen, John, Cornelissen, J.Hans C., Gourlet-Fleury, Sylvie, Hanewinkel, Marc, Herault, Bruno, Kattge, Jens, Kurokawa, Hiroko, Westoby, Mark, 2016. Plant functional traits have globally consistent effects on competition. Nature *529* (7585), 204–207. https://doi.org/10.1038/nature16476.

Leban, Jean-Michel, Lacarin, Maxime, Kerfriden, Baptiste, Jacquin, Philippe, Taupin, Amélie, Mola, Charline, Duprez, C.édric, Chabot, Sandrine, Dauffy, Vincent, Morneau, François, Wurpillot, Stéphanie, Hervé, Jean-Christophe, 2022. *Wood Basic Density for 156 tree forest species-V2* [Dataset]. Rech. Data Gouv. https://doi.org/10.57745/ZNFO7T.

Liang, Jingjing, Crowther, Thomas W., Picard, Nicolas, Wiser, Susan, Zhou, Mo, Alberti, Giorgio, Schulze, Ernst-Detlef, McGuire, A.David, Bozzato, Fabio, Pretzsch, Hans, de-Miguel, Sergio, Paquette, Alain, Hérault, Bruno, Scherer-Lorenzen, Michael, Barrett, Christopher B., Glick, Henry B., Hengeveld, Geerten M., Nabuurs, Gert-Jan, Pfautsch, Sebastian, Reich, Peter B., 2016. Positive biodiversity-productivity relationship predominant in global forests. Science *354* (6309), aaf8957. https://doi.org/10.1126/science.aaf8957.

Lines, Emily R., Zavala, Miguel A., Purves, Drew W., Coomes, David A., 2012. Predictable changes in aboveground allometry of trees along gradients of temperature, aridity and competition. Glob. Ecol. Biogeogr. *21* (10), 1017–1028. https://doi.org/10.1111/j.1466-8238.2011.00746.x.

Messier, Christian, Bauhus, J.ürgen, Sousa-Silva, Rita, Auge, Harald, Baeten, Lander, Barsoum, Nadia, Bruelheide, Helge, Caldwell, Benjamin, Cavender-Bares, Jeannine, Dhiedt, Els, Eisenhauer, Nico, Ganade, Gislene, Gravel, Dominique, Guillemot, Joannès, Hall, Jefferson S., Hector, Andrew, Hérault, Bruno, Jactel, Hervé, Koricheva, Julia, Zemp, Delphine Clara, 2022. For the sake of resilience and multifunctionality, let's diversify planted forests! Conserv. Lett. *15* (1), e12829. https://doi.org/10.1111/conl.12829.

Niinemets, Ülo, 2010. A review of light interception in plant stands from leaf to canopy in different plant functional types and in species with varying shade tolerance. Ecol. Res. *25* (4), 693–714. https://doi.org/10.1007/s11284-010-0712-4.

Niinemets, Ülo, Valladares, Fernando, 2006. Tolerance to Shade, Drought, and Waterlogging of Temperate Northern Hemisphere Trees and Shrubs. Ecol. Monogr. *76* (4), 521–547. https://doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2.

O'Brien, Robert M., 2007. A Caution Regarding Rules of Thumb for Variance Inflation Factors. Qual. Quant. *41* (5), 673–690. https://doi.org/10.1007/s11135-006-9018-6.

Pacala, Stephen W., Canham, Charles D., Saponara, John, Silander, John A., Kobe, Richard K., Ribbens, Eric, 1996. Forest Models Defined by Field Measurements: Estimation, Error Analysis and Dynamics. Ecol. Monogr. *66* (1), 1–43. https://doi.org/10.2307/2963479.

Petrovska, Roksolana, Brang, Peter, Gessler, Arthur, Bugmann, Harald, Hobi, Martina Lena, 2021. Grow slowly, persist, dominate—Explaining beech dominance in a primeval forest. Ecol. Evol. *11* (15), 10077–10089. https://doi.org/10.1002/ece3.7800.

Pinheiro, José, & Bates, Douglas. (2006). Mixed-Effects Models in S and S-PLUS. Springer Science & Business Media.

Pinheiro, José, Bates, Douglas, DebRoy, Saikat, Sarkar, Deepayan, EISPACK authors, Heisterkamp, Siem, Van Willigen, Bert, & Ranke, Johannes. (2023). nlme: Linear and Nonlinear Mixed Effects Models (Version 3.1-164) [Computer software]. https://cran.r-project.org/web/packages/nlme/index.html.

Plaga, Benjamin N.E., Bauhus, J.ürgen, Pretzsch, Hans, Pereira, M.ário Gonzalez, Forrester, David I., 2023. Influence of crown and canopy structure on light absorption, light use efficiency, and growth in mixed and pure Pseudotsuga menziesii and Fagus sylvatica forests. Eur. J. For. Res. https://doi.org/10.1007/s10342-023-01638-w.

Poorter, Lourens, Lianes, Elena, Moreno-de las Heras, Mariano, Zavala, Miguel A., 2012a. Architecture of Iberian canopy tree species in relation to wood density, shade tolerance and climate. Plant Ecol. *213* (5), 707–722. https://doi.org/10.1007/s11258-012-0032-6.

Poorter, Hendrik, Niklas, Karl J., Reich, Peter B., Oleksyn, Jacek, Poot, Pieter, Mommer, Liesje, 2012b. Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. N. Phytol. *193* (1), 30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x.

Poorter, Lourens, Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G., Harms, K.E., Licona, J.C., Martínez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Peña-Claros, M., Webb, C.O., Wright, I.J., 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. Ecology *89* (7), 1908–1920. https://doi.org/10.1890/07-0207.1.

Pretzsch, Hans, Forrester, David I., Bauhus, J.ürgen, 2017. Mixed-Species Forests. Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-54553-9.

R. Core Team. (2022). *R: A language and envi*ronment for statistical computing [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/.

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forest. J. Agric. Res. *46*, 627–638. ⟨https://www.fs.usda.gov/research/treesearch/60134⟩.

Rodríguez de Prado, Diego, Riofrío, Jose, Aldea, Jorge, McDermott, James, Bravo, Felipe, Herrero de Aza, Celia, 2022. Species mixing proportion and aridity influence in the height–diameter relationship for different species mixtures in Mediterranean forests. Article 1. Forests *13* (1). https://doi.org/10.3390/f13010119.

Thuiller, Wilfried, Münkemüller, Tamara, Schiffers, Katja H., Georges, Damien, Dullinger, Stefan, Eckhart, Vincent M., Edwards Jr, Thomas C., Gravel, Dominique, Kunstler, Georges, Merow, Cory, Moore, Kara, Piedallu, Christian, Vissault, Steve, Zimmermann, Niklaus E., Zurell, Damaris, Schurr, Frank M., 2014. Does probability of occurrence relate to population dynamics. Ecography *37* (12), 1155–1166. https://doi.org/10.1111/ecog.00836.

Toïgo, Maude, Perot, Thomas, Courbaud, Benoit, Castagneyrol, Bastien, Gégout, Jean-Claude, Longuetaud, Fleur, Jactel, Hervé, Vallet, Patrick, 2018. Difference in shade tolerance drives the mixture effect on oak productivity. J. Ecol. *106* (3), 1073–1082. https://doi.org/10.1111/1365-2745.12811.

Toïgo, Maude, Vallet, Patrick, Perot, Thomas, Bontemps, Jean-Daniel, Piedallu, Christian, Courbaud, Benoit, 2015a. Overyielding in mixed forests decreases with site productivity. J. Ecol. *103* (2), 502–512. https://doi.org/10.1111/1365-2745.12353.

Toïgo, Maude, Vallet, Patrick, Tuilleras, Valène, Lebourgeois, François, Rozenberg, Philippe, Perret, Sandrine, Courbaud, Benoit, Perot, Thomas, 2015b. Species mixture increases the effect of drought on tree ring density, but not on ring width, in Quercus petraea–Pinus sylvestris stands. For. Ecol. Manag. *345*, 73–82. https://doi.org/10.1016/j.foreco.2015.02.019.

Tucker, Gabriel F., Maguire, Douglas A., Tupinambá-Simões, Frederico, 2024. Associations between shade tolerance and wood specific gravity for conifers in contrast to angiosperm trees: Foundations of the conifer fitness-enhancing shade tolerance hypothesis. Plant-Environ. Interact. *5* (1), e10131. https://doi.org/10.1002/pei3.10131.

Valladares, Fernando, Niinemets, Ülo, 2008. Shade tolerance, a key plant feature of complex nature and consequences. Annu. Rev. Ecol., Evol., Syst. *39* (1), 237–257. https://doi.org/10.1146/annurev.ecolsys.39.110707.173506.

Vallet, Patrick, Pérot, Thomas, 2016. Tree diversity effect on dominant height in temperate forest. For. Ecol. Manag. *381*, 106–114. https://doi.org/10.1016/j.foreco.2016.09.024.

Woodall, C.W., Russell, M.B., Walters, B.F., D'Amato, A.W., Zhu, K., Saatchi, S.S., 2015. Forest production dynamics along a wood density spectrum in eastern US forests. Trees *29* (1), 299–310. https://doi.org/10.1007/s00468-014-1083-1.

Wright, S.Joseph, Kitajima, Kaoru, Kraft, Nathan J.B., Reich, Peter B., Wright, Ian J., Bunker, Daniel E., Condit, Richard, Dalling, James W., Davies, Stuart J., Díaz, Sandra, Engelbrecht, Bettina M.J., Harms, Kyle E., Hubbell, Stephen P., Marks, Christian O., Ruiz-Jaen, Maria C., Salvador, Cristina M., Zanne, Amy E., 2010. Functional traits and the growth-mortality trade-off in tropical trees. Ecology *91* (12), 3664–3674. https://doi.org/10.1890/09-2335.1.

Zhang, Yu, Chen, Han Y.H., Reich, Peter B., 2012. Forest productivity increases with evenness, species richness and trait variation: A global meta-analysis. J. Ecol. *100* (3), 742–749. https://doi.org/10.1111/j.1365-2745.2011.01944.x.

Zingg, A. (1994). Top heights in mixed stands—Their definition and calculation. Mixed Stands: Research Plots, Measurements and Results, Models. Proceedings from the Symposium of the IUFRO Working Groups S4.01. Mixed stands: research plots, measurements and results, models. Proceedings from the Symposium of the IUFRO Working Groups S4.01., Lousa/Coimbra, Portugal.