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Simulating the effects of thinning and species mixing on stands of oak (*Quercus petraea* (Matt.) Liebl./*Quercus robur* L.) and pine (*Pinus sylvestris* L.) across Europe

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ABSTRACT

Tree species mixing of oak (*Quercus petraea* (Matt.) Liebl./*Quercus robur* L.) and pine (*Pinus sylvestris* L.) has been shown to have positive effects on ecosystem service provision. From a management perspective, however, it is still uncertain which thinning regime provides the highest possible productivity of mixed oak–pine forests in the long term. Because of a lack of empirical studies dealing with thinning and species mixing effects on oak–pine forests, we simulated forest growth in order to test which thinning type and intensity may provide the highest productivity in the long-term. To achieve this, we simulated the growth of pure and mixed stands of oak and pine for 100 years in 23 triplets located on an ecological gradient across Europe. For this purpose, we applied four different growth simulators and compared their results: the distance-independent single-tree simulator PROGNAUS, the distance-dependent single-tree simulator SILVA, the gap model ForCEEPS, and the process-based simulator 3D-CMCC-FEM. We investigated the effects of species mixing and thinning from the upper (thinning from above) and lower tail (thinning from below) of the diameter distribution by reducing the stand basal area to 50 and 80% of the maximum basal area. We compared simulated results of the relative volume productivity of mixed versus pure stands and of thinned versus unthinned stands to empirical results previously obtained on the same set of triplets. Simulated relative volume productivity ranged between 61 and 156%, although extremes of 10% and of 300% could be observed. We found the relative volume productivity to be influenced by stand age, but not by stand density, except for PROGNAUS. Relative volume productivity did not increase with the site water supply of the triplet location. Highest long-term productivity for oak, pine and oak–pine stands can be expected in consequence of thinning from above, but the effect of thinning intensity differed between simulators. Thinning effects were positively affected by stand density, but not by stand age, except for thinning from above predicted by PROGNAUS. Predicted thinning effects showed good approximation of results from thinning experiments for oak, but not for pine stands. We hypothesize the results might be caused by the insufficient simulator representation of climate and its interaction with other site variables and stand structure. Further work is needed to reduce the revealed limitations of the existing growth models, as we currently see no alternative to such kind of studies and simulators.

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1. Introduction

Pedunculate oak (*Quercus robur* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.) and Scots pine (*Pinus sylvestris* L.) are widely distributed tree species in Europe. Both oak species are found in a large area ranging from Southern Scandinavia to the Iberian Peninsula, with the distribution area of sessile oak being slightly smaller. The two oak species have a large ecological amplitude, and are well adapted to fertile and moist soils. Both oaks are light demanding trees, and their canopies permit a good deal of light to pass through to the undergrowth. Therefore, oak rarely forms pure forests under natural conditions (Eaton et al., 2016). *Pinus sylvestris L.*, Scots pine, is a pioneer species able to grow on very poor soils. Hence, it can be found in many ecologically diverse habitats from Northern Scandinavia (70° N) to southern Spain (37° N). As a pioneer species it is light demanding, with a good frost and drought tolerance (Houstan Durrant et al., 2016). Both oak and Scots pine are commercially important tree species. Due to the capacity of both tree species to produce large volumes of valuable timber, they have been managed in pure and mixed stands for centuries.

Commercial forestry aims to maximize production at the stand level. Numerous studies of oak and pine have investigated the effect of thinning on total yield. These experiments consistently show, that maximum production was often achieved in unthinned stands (Utschig and Pretzsch, 2001; Utschig et al., 1993; Lockow, 2006; Montero et al., 2001; del Rio et al., 2008; Kramer and Röös, 1989). Depending on the thinning intensity, here defined as remaining basal area after thinning in percent of pre-thinning (or 'initial') basal area, light (80–95% of maximum basal area) (Preuhsler et al., 1993; Juodvalkis et al., 2005; Mäkinen and Isomäki, 2004; Kramer and Jünemann, 1984; Juodvalkis et al., 2005) or moderate (65–79%) (Juodvalkis et al., 2005; Mäkinen and Isomäki, 2004; Juodvalkis et al., 2005) intensities may result in increased productivity. However, high (50–64%) thinning intensities in oak and pine usually result in large stand growth reductions (Dong et al., 1997; Lockow, 2003, 2006; Nickel et al., 2007; del Rio et al., 2008; Mäkinen and Isomäki, 2004). A maximum increase of 25% and 15%, compared to unthinned stands, has been reported for oak and pine at the age of 10–20 years (Juodvalkis et al., 2005). Comparing both tree genera, oak compensates for density reductions by thinning slightly better than pine (Assmann, 1970; Juodvalkis et al., 2005). Without considerable reductions in productivity, oak can be thinned to approximately 80% of the maximum basal area, which is the basal area of unthinned stands, and pine to 90–95% of the maximum basal area Assmann (1970). In summary, both species possess a rather small range of stand densities, for which thinning does not result in increment losses.

The positive reaction to thinning declines with age (Attocchi, 2015; Utschig et al., 1993; Juodvalkis et al., 2005; Montero et al., 2001). Substantial increases are only found in thinning experiments in very young stands (e.g. Juodvalkis et al., 2005), whereas in medium-age or old stands little or no increase of stand level productivity with thinning is observed. For example, the above-mentioned study of Juodvalkis et al. (2005), reported increases of stand-level productivity of 5% or less at the age of 60 years. These experimental findings led to the recommendation, that the main treatment should take place in the first half of the rotation period (Montero et al., 2001). The influence of the thinning intensity on the total yield pattern varies only slightly with site (del Rio et al., 2008; Mäkinen and Isomäki, 2004). For example, the analysis of various long-term thinning experiments by Attocchi (2015) did not show any significant site effects. Similarly, thinning experiments in pine stands in Finland showed negative effects on stand-level volume increments, irrespective of the site fertility (Mäkinen and Isomäki, 2004). However, it may be noteworthy, that the study by del Rio et al. (2008) found greater volume losses at better sites, even though they were not statistically significant (del Río et al., 2017). With respect to a regional assessment, volume losses for pine are reported to be higher in Northern or Central Europe than in SW-Europe (del Río et al., 2017).

Results from thinning experiments have been primarily reported for pure stands, see e.g., Montero et al. (2001); long-term experiments under mixture scenarios with the latter both species are lacking (Utschig, 1992). Because less is known about the complex inter-tree relationships in mixed-species stands, the possible effects of thinning activities are hard to predict. It is particularly unclear to which extent the productivity of mixed species stands might change under different thinning regimes (Pretzsch and Zenner, 2017). Thus so far, only overall assessments of species mixture on productivity rates have been accomplished and possible interaction effects with thinning have been neglected in past studies.

Species mixture has been reported to provide higher resistance against weather extremes (Pretzsch et al., 2013), minimizes production risks (Reif et al., 2010), enhances resistance against pathogens and herbivory by insects (Jactel and Brockerhoff, 2007) and produces enhanced ecosystem services (Gamfeldt et al., 2013).

In terms of production, mixing of two tree species can be beneficial, particularly if both tree species behave complementary. Both oak and pine species are characterized by different light-use regimes, even though they are both light demanding tree species. However, both species show a complementary consumption of below-ground resources that is expressed by a spatial divergence and a temporal asynchronism in their water and nutrient demands (Prieto et al., 2012; Pretzsch, 2014; Goisser et al., 2016; Brinkmann et al., 2018). Compared with pure stands, species mixing can increase stand-level productivity rates. For pine, productivity rates in mixed-stands were on average 9% higher than in pure stands, oak productivity increased by 7%, but this increase was statistically not significant (Pretzsch et al., 2019). Thus, productivity gains in oak–pine mixtures are obviously smaller than for other species, for which productivity gains of up to 30% were reported (Pretzsch and Zenner, 2017). This is primarily due to different functional traits of different tree species (Lu et al., 2016; Mina et al., 2017). The relative volume productivity can differ greatly from average reported values between 61 and 156% for single plots (Pretzsch et al., 2019).

The relative volume productivity for particular tree species is affected by manifold factors. The most important ones are site conditions (Forrester and Albrecht, 2014), stand age (Cavard et al., 2011; Bielak et al., 2014; Thurm and Pretzsch, 2016), stand density (Condés et al., 2013; Bielak et al., 2014) and spatial arrangement (Pretzsch et al., 2012). For Scots pine and oak only site effects were detected. For example, Steckel et al. (2019) found that mixed oak–pine stands showed higher productivity rates in favorable years with higher water supply. That is, mixture effects in his study were more pronounced on better sites. The study of Pretzsch et al. (2019) also reported an increase with site index for Scots pine, whereas the opposite was found for oak. For Scots pine and Norway spruce mixtures there is evidence of an increasing benefit of Scots pine over stand age when growing in a joint mixture with Norway spruce (Bielak et al., 2014). Positive mixture effects for both species become more pronounced with age, although an overyielding is also evident at early stand ages (Bielak et al., 2014).

The intensity of interrelationships between different tree species is often dependent on the stand density. As a lowered density reduces interspecific competition, a mixture effect is less likely in lighter forests. Vice versa, an overyielding effect more likely occurs in dense stands (Kelty and Cameron, 1995). For example, Condés et al. (2013) reported more positive effects of admixture of beech on pine at higher stocking degrees. But they complemented the results by stating that most pronounced effect is not necessarily found at maximum density. In the same way, the spatial arrangement of species is also an important factor, as reduction of competition can be lower when mixture pattern tends toward grouping (Pretzsch et al., 2012).

The major goal of the present study was to investigate which thinning type and intensity may be applied to mixed oak–pine forests

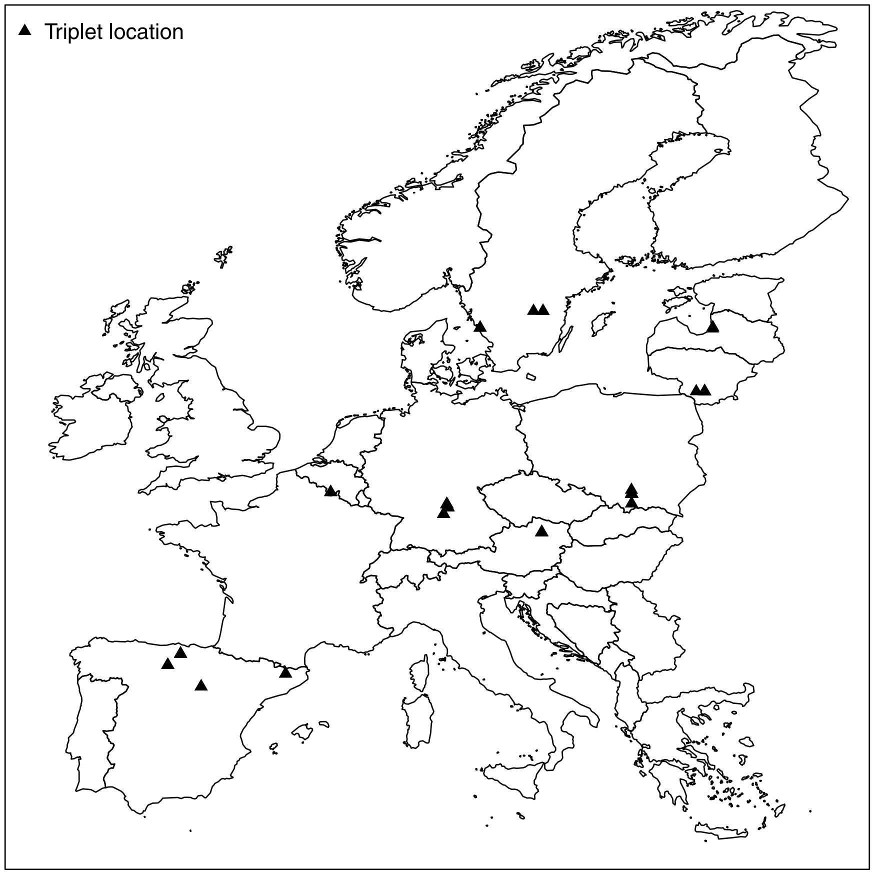

Fig. 1. Oak–pine triplet locations shown as triangles. Every triplet contains pure stands of oak and pine and one mixed oak–pine stand. On some locations, more than one triplet was established for thinning experiments. These thinning experiments are not part of this study.

in order to achieve maximum stand-level productivity. Because data from repeated measurements is so far lacking for representative mixed species trials, a sound empirical analysis of possible mixture effects in conjunction with management activities is generally hindered. As an alternative, the possible outcomes of a mixed species forestry can be also quantified by means of comprehensive simulations with growth models. For this purpose, thinning effects in pure and mixed stands of oak and pine were analyzed by means of simulations achieved with selected well-established growth models able to model mixture effects. We used the distance-independent single-tree simulator PROGNAUS (Sterba and Monserud, 1997; Ledermann, 2006), the distance-dependent single-tree simulator SILVA (Pretzsch et al., 2002), the gap model ForCEEPS (Morin, 2019), and the process-based simulator 3D-CMCC-FEM (Collalti et al., 2019). The statistical models PROGNAUS and SILVA have been parameterized by means of long-term experimental and inventory data, the models used in ForCEEPS are calibrated with inventory data. The ForCEEPS and 3D-CMCC-FEM models are based on a mathematical representation of the ecological processes. The use of different model types further facilitates the understanding of their functioning and predictive abilities.

All simulators were applied to a comprehensive set of experimental oak–pine plots established along a broad ecological gradient throughout the entire European region to quantify the effects of different thinning scenarios on the yield achieved with mixed and pure stands of oak and pine. Simulated stand-level productivity is compared to estimates reported in Steckel et al. (2019) and Pretzsch et al. (2019). Based on the findings from existing studies, we hypothesized that (1) stand-level productivity of mixed oak–pine stands is higher than those of pure oak or pine stands, (2) the relative volume productivity of mixed oak–pine stands increases with the site water supply, (3) the relative volume productivity increases with stand density and stand age (4) long-term positive thinning effects on stand-level productivity in pure and mixed stands occur only under moderate thinning intensities, and (5) relative thinning effects increase with stand density but decrease with stand age.

2. Material

2.1. Oak-pine-triplets

A total of 23 triplets of oak and pine have been established from 2017 to 2018 in the ERA-Net SUMFOREST project “REFORM — mixed species forest management. Lowering risk, increasing resilience”. German triplets used in this study have been previously investigated in Steckel et al. (2019) and all triplets are part of a greater network of 36 triplets investigated in Pretzsch et al. (2019). Sites selected for triplets span a large ecological gradient ranging from Mediterranean to boreal areas (Fig. 1 & Table 1). Survey plots belonging to one triplet are arranged in close proximity to each other representing similar site conditions. Plots were established on both flat and steep terrain with altitudes ranging from low elevations near the coast (100 m) to mountainous areas (1661 m). Mean annual temperature varied between 6 °C and 11.4 °C, whereas the annual precipitation sum ranged between 598–819 mm. We used the de Martonne aridity index dMI_k as a measure of the annual water supply for a specific triplet k, which is calculated as (de Martonne, 1926):

$$dMI_k = \frac{P_k}{T_k + 10} \quad (1)$$

where P denotes the annual precipitation sum and T denotes the annual mean temperature. The greater the index dMI_k, the higher is the annual water supply at a given site. We averaged annual de

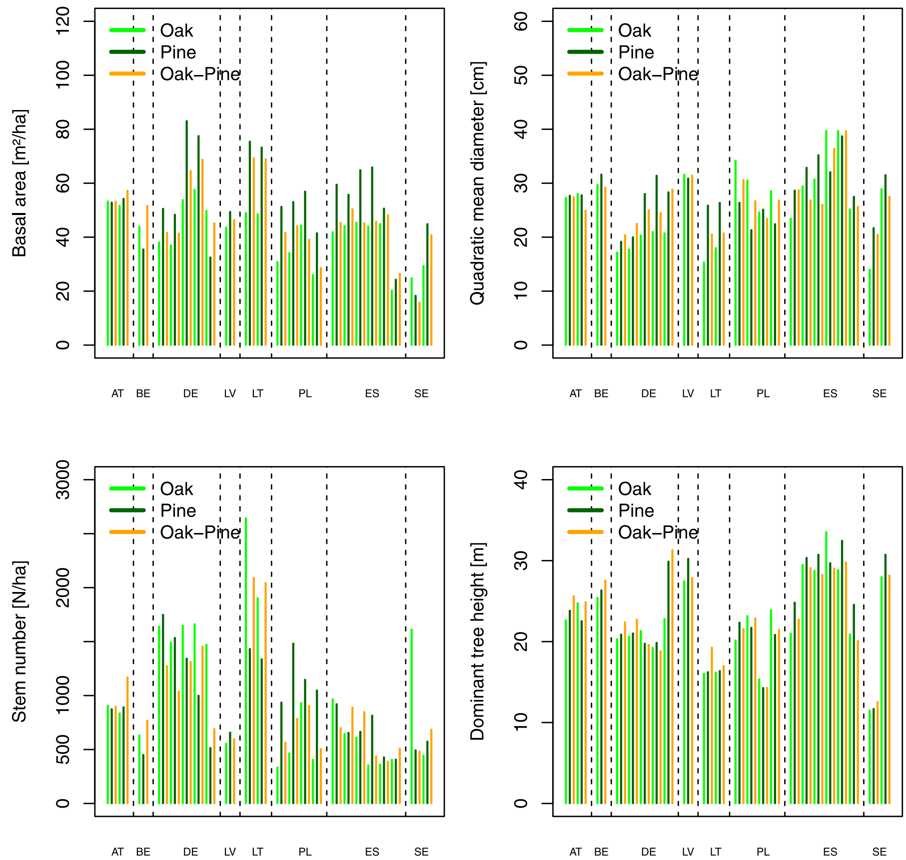

Fig. 2. Stand-level summary characteristics per plot for participating countries: "AT" Austria, "BE" Belgium, "DE" Germany, "LV" Latvia, "LT" Lithuania, "PL" Poland, "ES" Spain, and "SE" Sweden. Triplet plots are arranged in the subsequent order: pure oak, pure pine, mixed oak–pine. Triplet plots of a particular country are separated by dashed lines.

Martonne indices over the period from 1987 to 2017 to gain a long-term average that might characterize the site water supply of a given triplet.

In summary, the selected sites show large differences with respect to their climate variables and soil conditions. Each of the triplets comprises three survey plots. One survey plot is a single-tree mixture of oak and pine with nearly equal species-proportions of the respective stand basal areas, while the other plots are single-species stands of pine and oak. Plots were established in mature stands with a plot age between 40 and 138 years. Detailed information on plot measurement can be found in (Pretzsch et al., 2019)

Survey plots were established in closed, fully stocked stands. Basal area of plots varied between 15.9 m^2 ha^{-1} and 83.1 m^2 ha^{-1} (Fig. 2). A similarly high variation was observed for the quadratic mean diameter as well as for the stem number (Fig. 2). These differences are probably caused by variations in environmental conditions, past treatment and stand age (see Table 1).

2.2. Climate data

Triplet-specific climate data was used as input to all simulators, except for PROGNAUS, which used information on triplet plot altitude, exposition, and slope inclination only. SILVA used long-term averages for the temperature difference between the coldest and warmest month of the year, the number of days with mean temperature greater than 10 °C, the mean temperature within the growing season (°C) as well as precipitation sums within the growing season (Pretzsch et al., 2002). The process-based simulator 3D-CMCC-FEM used climate data on a daily basis instead (Collalti et al., 2019). Daily climate data (precipitation, temperature, vapor pressure deficit) for the period 1975–2018 (1980–2018 for Southern Sweden) was downloaded from the JRC Database AGRI4CAST (http://agri4cast.jrc.ec.europa.eu/DataPortal/Index.aspx?o=d) for every triplet location provided in Fig. 1. The AGRI4CAST data has a 25x25 km grid resolution. In addition, for each site local climate data was available. For each site, it was checked, if the local mean monthly values, corresponded to the gridded data set. For this purpose, daily climate data for maximum and minimum temperatures and precipitations sums of one year from the reference period 1975 (1980) to 2017 were randomly associated to one year in the future (2017–2117). Such a recombination of the 1975–2017 scenario up to 2100 allowed us to simulate a climate not affected by further climate change (Collalti et al., 2018). Inter-annual weather correlations were not considered. From this recombination, aggregated measures of monthly precipitation and temperature were obtained and used by the process-based gap model ForCEEPS.

2.3. Forest simulators

The simulations were carried out with three very different types of forest growth models: two individual tree-growth models, a gap model, and a process-based model. PROGNAUS (Sterba and Monserud, 1997; Ledermann, 2006) and SILVA (Pretzsch et al., 2002) are individual-tree growth models. Individual tree growth models are statistical models that rely on a collection of data that characterize the targeted population and their primary interest is in the prediction of forest stand development. They typically consist of functions for basal area increment, height increment, crown ratio, mortality and ingrowth. Measures of changes for the stand development are simply derived by aggregations of the individual tree increments as well as by simultaneously considering removals and ingrowing trees. The primary objectives of individual tree growth models are to provide credible predictions of stand development as well as to quantify the outcome and effects of

Table 1
Triplet plot data. “Size” provides the plot size ranges in ha, “Age” provides the age range of the triplet plots, ”Slope” gives the range of inclination in degrees, “Alt” gives the altitude range of the plots, “emp” the average annual temperature in °C 1987–2017 and “Prec” the average annual precipitation sum in mm 1987–2017, and “dMI” denotes the de Martonne aridity index (de Martonne, 1926).

	Country	Size	Age	Slope	Alt	Temp	Prec	dMI
1	Austria	1.6–3	94–118	0–0	450–450	8.7	658	35
2	Austria	1.2–2.1	44–65	0–0	450–450	8.7	658	35
3	Belgium	2.59–9.39	62–76	0–0	166–187	9.3	929	48
4	Germany	0.88–1.61	105–115	15–19	310–355	8.5	615	33
5	Germany	0.49–1.41	105–115	14–17	310–355	8.5	615	33
6	Germany	1.04–2	105–110	4.1–13.8	318–345	8.4	663	36
7	Germany	0.41–1.8	40–50	2–7	465–473	8.1	718	40
8	Germany	0.64–2.8	40–50	2–3	463–479	8.1	718	40
9	Latvia	0.76–1.85	66–74	0–0	60–60	5.5	657	42
10	Lithuania	0.67–1.73	49–66	0–0	59–80	6.6	614	37
11	Lithuania	1.15–2.43	80–90	0–0	76–80	6.6	614	37
12	Poland	1.12–3	65–65	0–0	210–220	8.4	671	36
13	Poland	1.12–3	65–65	0–0	210–220	8.4	671	36
14	Poland	1.2–3.3	75–75	0–0	200–200	8.4	680	37
15	Poland	1.65–4.25	85–85	0–0	200–200	8.4	680	37
16	Spain	0.62–0.89	52–71	10–16	1066–1512	9.9	793	40
17	Spain	0.6–0.91	49–60	15–17	1185–1188	9.9	793	40
18	Spain	0.55–0.65	41–50	22–34	760–810	11.4	819	38
19	Spain	0.51–0.67	41–49	20–35	765–815	11.4	819	38
20	Spain	1.09–1.4	40–81	10–22	1616–1661	10	586	29
21	Spain	0.52–2.19	50–58	35–45	1139–1149	10.9	846	40
22	Sweden	0.77–2.5	63–96	0–5.2	100–130	7.2	891	52
23	Sweden	0.62–1.48	102–138	21–25.9	110–130	6	598	37

thinning and harvesting scenarios over time (Weiskittel et al., 2011). Individual-tree growth models can be further classified into spatial and non-spatial models. Spatial models use measures of competition for the prediction of growth and mortality that require tree coordinates, whereas non-spatial models can only use competition indices that can be derived from tree-list (Weiskittel et al., 2011). According to this sub-classification, PROGNAUS can be regarded as a non-spatial individual tree growth model and SILVA as a spatial individual-tree growth model.

The distance-independent single-tree growth simulator PROGNAUS consists of an individual-tree basal area increment model (Monserud and Sterba, 1996), an individual-tree height increment model (Schieler, 1997), an individual-tree mortality model (Monserud and Sterba, 1999), and an ingrowth model (Ledermann, 2002). PROGNAUS has been originally developed to predict tree and forest stand growth based on repeated measures on forest inventory plots in Austria (Ledermann, 2006). The broad data material used for parameterization enables a wide application of the simulator across all forest types in Austria.

The distance-dependent single-tree simulator SILVA (Pretzsch et al., 2002) is based on a long-term trial plot network distributed over Germany (Kahn and Pretzsch, 1997) and is designed to analyze tree and stand reactions to changing environmental conditions. The plots used for model parameterization represent a wide range of site conditions and stand structures. In contrast to PROGNAUS, inter-tree competition is spatially modeled by means of rotation-symmetric tree crowns (Pretzsch, 1995).

ForCEEPS is a process-based gap model inspired by the forest succession model ForClim (Didion et al., 2009), which was originally developed for simulations over a wide range of environmental conditions. Gap models explore long-term ecological processes. Major impetus for the development of gap models was to understand the interactions that control forest species succession (Taylor et al., 2009). Light interception is described at the tree level, and light availability for the dominated trees is calculated according to the Beer Lambert law. Successional processes such as tree establishment, growth and mortality are described for each patch (Bugmann, 2001). ForCEEPS was designed to investigate the long-term changes in the structure, composition and functioning of forest communities, while being individual-based. ForCEEPS is essentially based on the following principle: at each time step maximum possible tree growth under optimum conditions is subsequently reduced by light availability, nitrogen availability, soil moisture and growing season temperature. Light availability is regulated by the identity and size of neighboring trees, allowing a competition for light. This is in strong contrast to SILVA and PROGNAUS, which use competition indices. For the main French forest tree species, including sessile oak and Scots pine, growth models were calibrated using data from the French national forest inventory. Moreover, model validation was performed by means of an independent data set from the network of forest monitoring plot belonging to ICP Forests level 2.

Process-based models attempt to mechanistically represent processes that influence tree growth. They are based on theoretical plant reactions, which allow them to be extended to novel situations. Processes typically depicted by process-based models are light interception, photosynthesis, stomatal conductances, respiration, carbon allocation, soil water and nutrients. Model coefficients are typically obtained from experimental trials and they are difficult to parameterize because of the high data input requirements (Weiskittel et al., 2011). The output of process-based models is net primary production for different components (stem, leaves, roots), but does not contain tree list data. Hence, the traditional applications of process-based models are not focused on growth and yield predictions, but rather comprise the testing of ecological hypotheses as well as the teaching of fundamental physiological principles. 3D-CMCC-FEM represents a typical example of a process-based model.

The process-based 3D-CMCC-FEM simulator calculates biochemical, biophysical, and physiological processes in order to predict carbon, energy and water fluxes that are coupled with forest stand development (Collalti et al., 2014, 2019). The model describes photosynthesis, respiration as well as hydrological processes on a daily time scale, which is in strong contrast to the previous simulators operating on a yearly scale. The 3D-CMCC-FEM model but represents horizontal and vertical forest structure with tree crowns arranged as in the “Perfect Plasticity Approximation” (Purves et al., 2008), which assumes that the crown surface areas above a certain height threshold have unrestricted sunlight absorption, whereas the remaining crown surface areas in the understorey receive only limited radiation. The height threshold depends on the tree height and crown geometry in the stand. The 3D-CMCC-FEM model uses a total of 55 species-specific ecophysiological, biophysical, biogeochemical and structural time-independent parameters. Such parameters have been gleaned mostly from the existing literature or previous model calibration in order to increase generalization of the model use (Collalti et al., 2019).

3. Methods

3.1. Simulation experiments

To test for possible long-term effects of thinning, a set of five different management scenarios was applied in 100 replications of 100 years simulations with each growth model:

1. control variant, no thinning
2. Above 50: thinning from the upper tail of the diameter distribution, while reducing stand basal area to 50% of the maximum stand basal area
3. Above 80: thinning from the upper tail of the diameter distribution, while reducing stand basal area to 80% of the maximum stand basal area
4. Below 50: thinning from the lower tail of the diameter distribution, while reducing stand basal area to 50% of the maximum stand basal area
5. Below 80: thinning from the lower tail of the diameter distribution, while reducing stand basal area to 80% of the maximum stand basal area

We replicated simulation runs to account for random effects in model subroutines, which were mortality for PROGNAUS, SILVA and ForCEEPS and climate for SILVA, ForCEEPS, and 3D-CMCC-FEM. During the 100-yr simulation period, only tree growth and mortality were considered, while tree regeneration, either natural or artificial, was not taken into account.

The present state of the triplet data was used as initial values for the simulations of tree growth and stand development over 100 years in the future. Edge effects at the plot boundaries were not corrected in simulations with PROGNAUS and ForCEEPS, but were indirectly corrected for 3D-CMCC-FEM by using the grid-cell canopy cover in mortality routines (Collalti et al., 2014). Edge effects in SILVA are corrected by linear expansion (Martin et al., 1977).

The maximum basal area as reference for thinning scenarios was obtained from the control variant where thinning was not applied. Simulated basal areas were however constrained by country-specific maximum basal area functions (Table 2). If such functions were not available for every triplet location and country, those with the least regional distances to the triplet location and least difference to observed stand basal areas were applied as reference for thinning applications. In the case of mixed oak–pine stands, which may naturally show higher stand densities, maximum basal area functions for oak and pine were applied, which possibly underestimates the maximum basal area of mixed oak–pine stands. For the thinning scenarios (2.–5.), a thinning was applied each time the simulated stand basal area exceeded the targeted basal area of 50 or 80% of the maximum basal area. Consequently, the frequency of thinning varied among the applied simulators, triplet plots, and thinning scenarios. Single trees were selected with a probability of 30% until the predefined basal area reduction was reached. In oak–pine mixtures the basal area reduction was proportionally assigned to both species with respect to their basal areas so that species proportions remained unchanged during the simulation. Hence, the species proportion remained constant during the simulation time.

For the process-based simulator 3D-CMCC-FEM,thinning variants were accomplished by setting the target basal area and applying a shift to the quadratic mean diameter, which is different for thinning from the upper or lower tail of the diameter distribution. The relative shift was calculated before the simulation started.

3.2. Thinning effects

Stand-level productivity was assessed in terms of the simulated annual volume increment per hectare iV. The ratio between $iV_k^{(t)}$ of the thinning scenario and the no-thinning scenarios for every triplet plot k in time step t provides the relative thinning effect $\delta V_k^{(t)}$ that informs about positive (values greater than 1) or negative (values less than 1) effects of the thinning scenario. As no information on thinning effects was available from the triplet plots in this study, we compared our simulated thinning effects with those that have been observed in thinning experiments with pure oak and pine stands (Table 3), which were restricted to thinning-from-above for oak and to thinning-from-below for pine.

Table 2
References for applied maximum basal area functions by countries.

	Country	Basal area function pine	Basal area function oak
1	Austria	Vospernik and Sterba (2015)	Vospernik and Sterba (2015)
2	Belgium	Pretzsch and Biber (2005)	Charru et al. (2012)
3	Germany	Pretzsch and Biber (2005)	Pretzsch and Biber (2005)
4	Latvia	Hynynen (1993)	Charru et al. (2012)
5	Lithuania	Hynynen (1993)	Pretzsch and Biber (2005)
6	Poland	Condés et al. (2017)	Charru et al. (2012)
7	Spain	del Rio et al. (2001)	Charru et al. (2012)
8	Sweden	Pretzsch and Biber (2005)	Charru et al. (2012)

Table 3
Observed thinning effects on stand-level volume increments for oak and pine stands. ”Age” denotes the stand age range in the respective study. “BA-rel” denotes the basal area relative to an unthinned variant [%]. “iV-rel” provides the stand volume increments relative to an unthinned variant [%]. Thinning from the upper tail of the diameter distribution was applied for oak stands, while pine stands were subject to thinning from the lower tail of the diameter distribution.

Species	Country	References	Age	BA-rel	iV-rel
oak	Germany	Preuhsler et al. (1993)	70–123	0.85	1.06[a]
oak	Germany	Lockow (2006)	183–193	0.83	0.95
oak	Germany	Preuhsler et al. (1993)	70–123	0.79	0.99[a]
oak	Germany	Utschig and Pretzsch (2001)	48–113	0.7	0.85
oak	Germany	Utschig et al. (1993)	61–71	0.7	0.87
oak	Germany	Lockow (2006)	183–193	0.57	0.72
oak	Germany	Utschig and Pretzsch (2001)	48–113	0.5	0.58
oak	Germany	Utschig et al. (1993)	61–71	0.48	0.76
pine	Germany	Kramer and Jünemann (1984)	35–40	0.9	1.01
pine	Germany	Kramer and Röös (1989)	40–46	0.88	0.85
pine	Finland	Mäkinen and Isomäki (2004)	16–124	0.88	0.96[b]
pine	Spain	del Rio et al. (2008)	35–80	0.83	0.92
pine	Germany	Kramer and Röös (1989)	40–46	0.73	0.74
pine	Finland	Mäkinen and Isomäki (2004)	16–124	0.73	0.86[b]
pine	Germany	Kramer and Jünemann (1984)	35–40	0.72	0.88
pine	Spain	del Rio et al. (2008)	35–80	0.7	0.83
pine	Spain	del Rio et al. (2008)	35–80	0.61	0.81
pine	Germany	Nickel et al. (2007)	92–126	0.6	0.92
pine	Sweden	Valinger et al. (2000)	34–40	0.6	0.67
pine	Finland	Mäkinen and Isomäki (2004)	16–124	0.58	0.75[b]

[a]Denotes thinning started after half of the experiment time.
[b]Denotes average values out of multiple experiments.

3.3. Mixing effects in no thinning scenarios

The relative volume productivity $O_k^{(t)}$ of the stand-level productivity $iV_k^{(t)}$ was quantified according to Pretzsch et al. (2015), who compares the observed productivity from mixed species stands and those expected from the respective monospecific stands. The simulated annual volume increment $iV_{mixed}^{(t)}$ for a mixed species plot and time step t is divided by the expected annual volume increment $\widehat{iV}_{mixed}^{(t)}$ calculated as the weighted mean of the annual volume increments of the respective monospecific stands $iV_{oak}^{(t)}$ and $iV_{pine}^{(t)}$:

$$O_k^{(t)} = \frac{iV_{mixed}^{(t)}}{\widehat{iV}_{mixed}^{(t)}} = \frac{iV_{mixed}^{(t)}}{iV_{oak}^{(t)} * m_{oak} + iV_{pine}^{(t)} * m_{pine}} \tag{2}$$

where m_{oak} and m_{pine} are the corresponding mixing proportions of oak and pine in the simulated mixed plots. If $O_k^{(t)}$ is greater than 1, positive mixing effects on stand-level productivity are observed indicating overyielding. If $O_k^{(t)}$ is smaller than 1, negative mixing effects on stand-level productivity are observed, indicating underyielding.

The mixing proportions of oak and pine were calculated according to Steckel et al. (2019) based on considerations by Dirnberger and Sterba (2014) and Sterba et al. (2014). In this approach, mixing proportions are calculated based on the stand density index SDI (Reineke, 1933). The ratio $e_1 = \frac{SDIMAX_1}{SDIMAX_2}$ of the maximum stand density index for each species reflects the growing space requirements of species 1 relative to species 2 in monoculture (Steckel et al., 2019). As an example, the ratio for oak relative to pine would be $e_{oak} = \frac{SDIMAX_{oak}}{SDIMAX_{pine}}$ and the mixing proportion m for the species oak in mixture with pine is calculated as (Steckel et al., 2019):

$$m_{oak} = \frac{SDI_{oak}}{SDI_{oak} + SDI_{pine} * e_{oak}} \tag{3}$$

where e_{oak} denotes the growing space requirements of oak in monoculture relative to pine in monoculture and SDI_{oak} and SDI_{pine} denote the stand density index of oak and pine in mixture. We calculated relative volume productivity for the unthinned simulation results only in order to facilitate a comparison to Pretzsch et al. (2019) by providing differences $\delta O_k^{(t)}$ of simulated to observed relative volume productivity. The volume increment in Pretzsch et al. (2019) is based on reconstruction from increment cores and height growth models for the most recent period, which is considerably different from the 100 years simulation period of the present study. However, the simulations in this study were performed on triplet plots that were also investigated in Pretzsch et al. (2019), which enables an indirect comparison of simulated and observed (reconstructed) range of relative volume productivity. This enabled us to examine whether the simulated relative volume productivity of mixed oak–pine stands lies within the range obtained via reconstructions. Furthermore, it is assessed which simulator shows the least differences across the entire ecological gradient.

3.4. Climate influences on mixing effects

To assess whether the relative volume productivity is dependent on the long-term climate conditions at the respective plot sites, a possible relationship of $O_k^{(t)}$ with the de Martonne aridity index (de Martonne, 1926) was examined.

3.5. Analyzing influences on relative thinning effects and relative volume productivity

The results analyzed in this study are based on simulations that can be easily replicated. As statistical significance is dependent on the number of replications, we do not report p-values from frequency statistics (Fritz and Morris, 2012; White et al., 2013). Instead, we provide graphical material showing the effects of stand age and stand density in terms of the Stand Density Index SDI (Reineke, 1933) on the relative volume productivity and relative thinning effects. For this purpose, we classified values of the relative volume productivity $O_k^{(t)}$ and relative thinning effect $\delta V_k^{(t)}$ into narrow classes of 5-year stand age and classes of 5 for the SDI in order to derive descriptive statistics.

4. Results

PROGNAUS and ForCEEPS accomplished each of the 100 simulations until the fixed predefined time of 100 years. However, with SILVA the simulations for 13 out of 69 plots ended before 100 years due to the forest aging process and subsequent tree mortality. With 3D-CMCC-FEM, the simulations did not reach the final time step for 30 plots due to climatic constraints that caused an increase in tree mortality and subsequent forest stand death. Tree-species mixture ratios in mixed oak–pine stands changed but a complete death of either species was not observed for all simulations. Simulations accomplished with ForCEEPS also showed some years with zero growth rates as a consequence of the

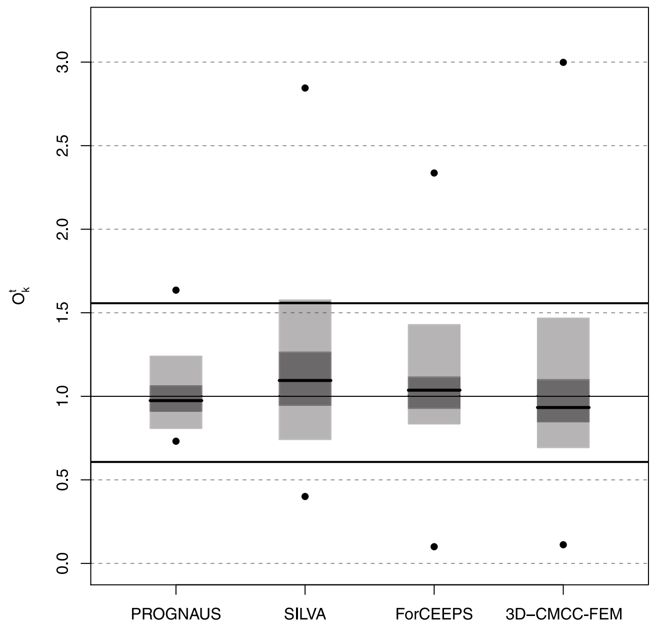

Fig. 3. Relative volume productivity $O_k^{(t)}$, i.e the ratio between the volume productivity of the mixed stand and that expected based on the monocultures, for every simulator applied over all triplets for the complete simulation time. Simulated $O_k^{(t)}$ are only reported for the unthinned variant. Simulated $O_k^{(t)}$ are provided with their maximum and minimum (black dots), median (short horizontal lines) and quantiles 0.05, 0.25, 0.75, and 0.95 (light and dark gray areas). Maximum and minimum observed relative volume productivity on 23 triplet locations are given as bold horizontal lines (Pretzsch et al., 2019).

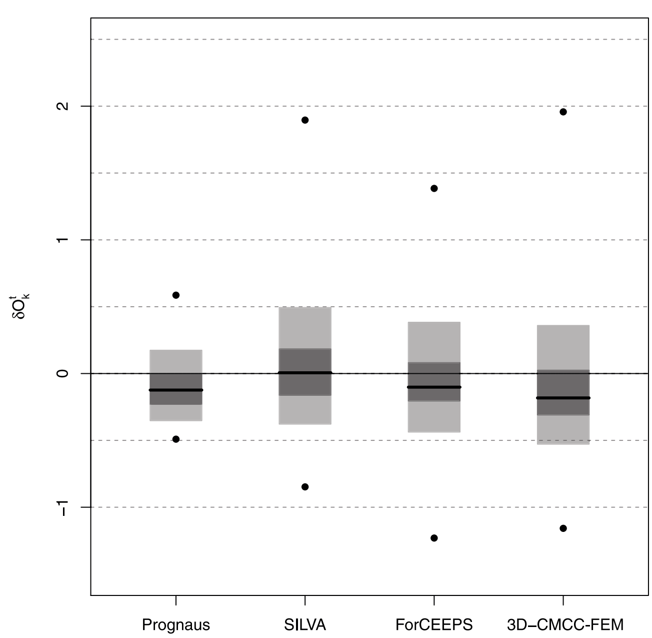

Fig. 4. Differences between simulated and observed relative volume productivity reported in Pretzsch et al. (2019) for mixed oak–pine triplet plots $\delta O_k^{(t)}$ for every simulator applied over all triplets for the complete simulation time. $\delta O_k^{(t)}$ are only reported for the unthinned variant. $\delta O_k^{(t)}$ are provided with their maximum and minimum (black dots), median (short horizontal lines) and quantiles 0.05, 0.25, 0.75, and 0.95 (light and dark gray areas).

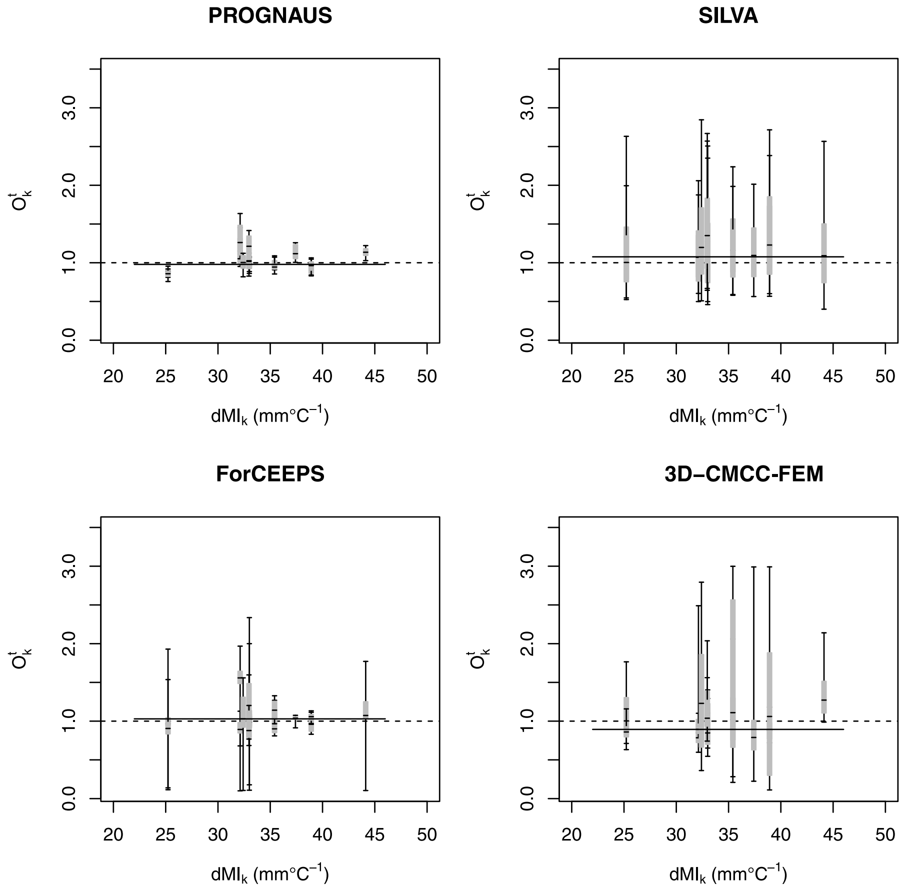

Fig. 5. Relative volume productivity $O_k^{(t)}$, i.e the ratio between the volume productivity of the mixed stand and that expected based on the monocultures, for every simulator applied over all triplets for the complete simulation time. Simulated $O_k^{(t)}$ are ordered according to the de Martonne aridity index (de Martonne, 1926) given in Table 1. The overall median over all triplets is given as horizontal line. Boxplots provide the values between the 5th and 95th quantile and maximum and minimum values.

simulated climate sequences. We excluded years without tree and stand growth from further analysis of relative thinning effects and relative volume productivity.

4.1. Mixing effects

Simulated $O_k^{(t)}$ over the complete simulation time and all triplets is provided in Fig. 3. Simulated $O_k^{(t)}$ from the 5th to 95th quantile range between the maximum (1.56) and minimum (0.61) observed relative volume productivity for the investigated 23 triplets reported in Pretzsch et al. (2019). Simulations for all simulators provide both over- and underyielding with extreme values achieved with ForCEEPS and 3D-CMCC-FEM between 0.1 and 3, meaning an underyielding of 90% and an overyielding of 300%. The median $O_k^{(t)}$ values were greater than 1 for simulations accomplished with SILVA and ForCEEPS, but lower than 1 for PROGNAUS and 3D-CMCC-FEM.

However, we found large differences between simulated and observed relative volume productivity on the level of individual triplets (Fig. 4). Differences $\delta O_k^{(t)}$ between the 5th and 95th quantile range between an underestimation of −53% (3D-CMCC-FEM) and an overestimation of 49% (SILVA). The least differences are achieved with the simulator PROGNAUS. In terms of their median, PROGNAUS, ForCEEPS, and 3D-CMCC-FEM tend to underestimate the relative volume productivity $O_k^{(t)}$ reported in Pretzsch et al. (2019)

We ordered the simulated relative volume productivity $O_k^{(t)}$ for every simulator applied over all triplets for the complete simulation time according to the de Martonne aridity index (de Martonne, 1926) given in Table 1. We could not find any relationship between $O_k^{(t)}$ and the de Martonne aridity index (Fig. 5).

We found an increase of the simulated relative volume productivity $O_k^{(t)}$ with the respective stand age for PROGNAUS and SILVA (Fig. 6). In the case of 3D-CMCC-FEM, $O_k^{(t)}$ increases for some simulations but did not show a clear trend for the median. In the case of ForCEEPS, the median $O_k^{(t)}$ decreases with stand age.

We found no clear relationship between the median $O_k^{(t)}$ of the unthinned scenario and the SDI of the mixed oak–pine stand, except a slightly increasing trend for the simulations accomplished with PROGNAUS (Fig. 7). Both PROGNAUS and ForCEEPS reached implausibly high SDI values greater than 1500 trees per hectare.

4.2. Thinning effects

We provide relative thinning effects $\delta V_k^{(t)}$ for every simulator applied over all triplets for the complete simulation time in Fig. 8. The results show that the highest $\delta V_k^{(t)}$ are reached for thinning from above. Both PROGNAUS and ForCEEPS showed that the moderate reductions in stand basal area of 80% of the maximum basal area (Above 80) provided the highest relative thinning effects. Contrary, SILVA predicted the highest $\delta V_k^{(t)}$ for a strong thinning from above (Above 50). The simulations with 3D-CMCC-FEM showed no clear differences between the thinning scenarios, although highest $\delta V_k^{(t)}$ were reached with a strong thinning from above (Above 50). PROGNAUS and ForCEEPS provided predictions within the observed values from thinning experiments for oak, but not for pine, where the predicted thinning effects $\delta V_k^{(t)}$ were much lower than observed for strong thinning from below (Below 50), but lesser for moderate thinning from below (Below 80). SILVA showed a good approximation of a strong thinning from above for oak (Above 50), and a moderate thinning from below for pine (Below 80). SILVA

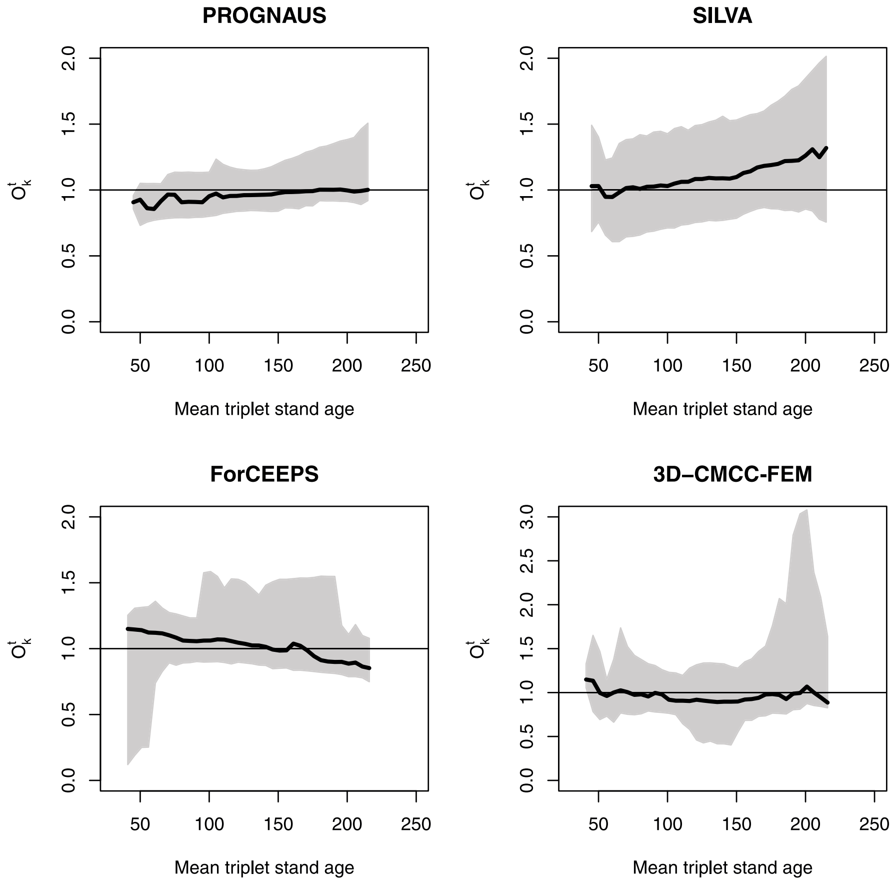

Fig. 6. Relative volume productivity $O_k^{(t)}$, i.e the ratio between the volume productivity of the mixed stand and that expected based on the monocultures, for every simulator applied over all triplets for the complete simulation time over the respective stand age. Simulated $O_k^{(t)}$ are only reported for the unthinned variant. Bold black lines show the median, gray areas the 95% confidence interval. Simulated $O_k^{(t)}$ have been classified into 5-year stand age classes.

underestimated the thinning effects $\delta V_k^{(t)}$ of the moderate thinning from above for oak and of the strong thinning from below for pine. The simulator 3D-CMCC-FEM showed good approximation of the moderate thinning from above for oak. This simulator also showed a much larger variability in the mixed stands compared to the monocultures.

We found no clear age trend of the median relative thinning effects $\delta V_k^{(t)}$. In general, median $\delta V_k^{(t)}$ remained stable or decreased over stand age. Median relative thinning effects $\delta V_k^{(t)}$ for mixed oak–pine stands simulated with 3D-CMCC-FEM and thinning from above for oak, pine and oak–pine stands simulated with PROGNAUS increased (Fig. 9).

Contrary to our findings about the effects of stand age on median relative thinning effects $\delta V_k^{(t)}$, we found an increasing trend with stand density for oak, pine, and mixed oak–pine stands, except for the oak and pine stands simulated with 3D-CMCC-FEM (Fig. 10).

5. Discussion

We simulated stand growth on 23 triplets with a total of 69 plots with four different simulators and predicted stand-level productivity in mixed oak–pine stands. All simulators predicted both over- and underyielding across the entire set of triplets and the complete simulation time. Simulated median relative productivity lay within the observed range between 61% and 156% for the 23 triplets out of 36 reported in Pretzsch et al. (2019). This indicates that the simulators can be applied over the investigated ecological gradient in this study and that plausible results can be expected. However, an extreme underyielding of 10% or an overyielding of 300%, such as accomplished with the simulator ForCEEPS and 3D-CMCC-FEM, has not been observed in other empirical studies (Steckel et al., 2019; Pretzsch et al., 2019). Differences to the values reported in Pretzsch et al. (2019) are large, but may also origin from the different methodological approaches used in these studies. The study of Pretzsch et al. (2019) used reconstructed stand volume increments for a 5-year period prior to the tree increment core drilling, whereas our study simulated 100 years of stand development. The triplet establishment and time of field measurement of the triplet plots are, nevertheless, identical. In conformance with Pretzsch et al. (2019) and Steckel et al. (2019), we did not find a constant overyielding across all triplets. Therefore, we have to partly reject our first hypothesis stating that stand-level productivity, in terms of annual volume increment, of mixed oak–pine stands is higher than those of pure oak and pine stands. Overyielding might be present at a few sites, but does not hold under all growing conditions. In addition, we found that over- or underyielding is driven by the initial stand age and stocking of the mixed oak–pine stands, i.e. a positive effect was found on older and fully stocked stands. This phenomenon is likewise in conformance with empirical findings (Cavard et al., 2011; Condés et al., 2013; Bielak et al., 2014; Thurm and Pretzsch, 2016). However, we cannot confirm a clear influence of site conditions as reported in Forrester and Albrecht (2014).

We have to reject our second hypothesis that the relative volume productivity of mixed oak–pine stands increases with the site water supply. We did not find evidence that the de Martonne index influenced our simulation results. This is in contrast to the findings in Pretzsch et al. (2019) and Steckel et al. (2019). This discrepancy might be associated with the different approach of climate-sensitive modeling in the growth simulators. However, even the simulators, that use monthly or daily climate data, did not show climate-growth relationships. In particular, the ecophysiological parameters of 3D-CMCC-FEM have been kept constant across triplets in order to make the results comparable.

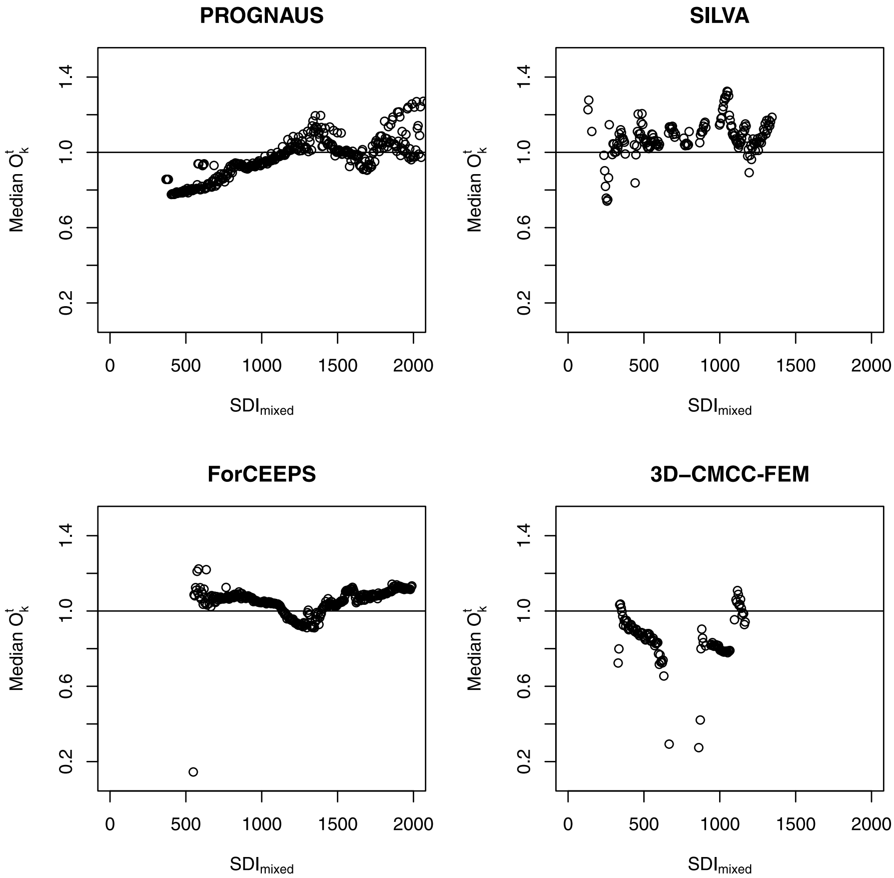

Fig. 7. Median relative volume productivity $O_k^{(t)}$, i.e the ratio between the volume productivity of the mixed stand and that expected based on the monocultures, for every triplet and simulator for mixed oak–pine stands. Simulated $O_k^{(t)}$ are only reported for the unthinned variant. Simulated $O_k^{(t)}$ are classified into 5-year classes of the respective Stand Density Index (SDI) of the mixed oak–pine stand. The median $O_k^{(t)}$ is reported for every SDI-class.

However, this is probably a too strong assumption, as ecological performances of the species may vary along the explored gradient. This might also be the reason why simulations with 3D-CMCC-FEM ended before the predefined time of 100 years. In addition, Steckel et al. (2019) assumed that triplet-level differences of the relative volume productivity might have been caused by complex inter-related factors such as crown architectures and soil dynamics. However, none of these possible interaction effects is sufficiently represented by the simulators. Thus, the future inclusion of crown and soil dynamics along with plant-atmosphere interactions may reveal additional insights in the dynamics of mixed-species forests. This is further supported by the high relevance of the specific tree functional traits (Lu et al., 2016; Mina et al., 2017) for the outcome of mixing effects in terms of stand-level productivity.

Another reason for the discrepancy between observed and simulated effects of the site water supply on the relative volume productivity might be the different number of triplet plots and associated range of ecological conditions. The study of Steckel et al. (2019) focused on 7 triplets in Germany and Denmark and showed a clear increase, whereas Pretzsch et al. (2019) focused on a larger ecological gradient across Europe with a total of 36 triplets and showed an increasing trend that is biased by a lack of triplets with high de Martonne indices. In this study stand growth at 23 triplet sites that have been already examined in Pretzsch et al. (2019) was predicted. Thus, the range of de Martonne indices in the mentioned studies differs, which affects the comparability. Further, Pretzsch et al. (2019) focused on periodical productivity and the long-term annual water supply at each investigated site, whereas Steckel et al. (2019) focused on an annual resolution of both water supply and productivity. Therefore, a final conclusion about the simulators' ability to capture the effects of site water supply on stand productivity cannot be drawn.

We found an increasing trend of the relative volume productivity with stand age for the simulations with PROGNAUS and SILVA and likewise some signs of a trend for simulations with 3D-CMCC-FEM on a few plots. In contrast, ForCEEPS showed a decreasing trend with stand age. The particular trend is also in agreement with studies on mixed pine–spruce (Bielak et al., 2014) and mixed douglas-fir-beech (Thurm and Pretzsch, 2016) forests. The only slightly increasing trend on some triplets with 3D-CMCC-FEM and the decreasing trend of the median relative volume productivity with ForCEEPS might be explained by the climate impact on tree growth in both simulators. Further, the trend of the simulations with 3D-CMCC-FEM might be biased due to the large number of incomplete simulations (30 out of 69 triplet plots).

We only found a slight increase of the relative volume productivity with stand density for PROGNAUS, whereas a clear relationship could not be found for the other simulators. This stands in contrast to empirical findings (Condés et al., 2013; Bielak et al., 2014). Additionally, PROGNAUS and ForCEEPS predicted unplausible high stand density indices (SDI) for the unthinned variant. This might be caused by an overestimation of tree growth probably resulting from biased crown model predictions and/or underestimates of tree mortality. These problems with sub-model routines have been previously evaluated for the simulators PROGNAUS, SILVA, MOSES, and BWIN (Vospernik et al., 2015) and point to a need for further refinement of the model parameterization. Thus, we can only partly confirm our third hypothesis in that only PROGNAUS and SILVA showed a clear increase of the relative volume productivity with stand age.

Our fourth hypothesis stated that highest stand-level productivity, in terms of annual volume increment, is found under moderate thinning intensities. This hypothesis was strongly supported by numerous thinning experiments for oak (Preuhsler et al., 1993; Utschig et al.,

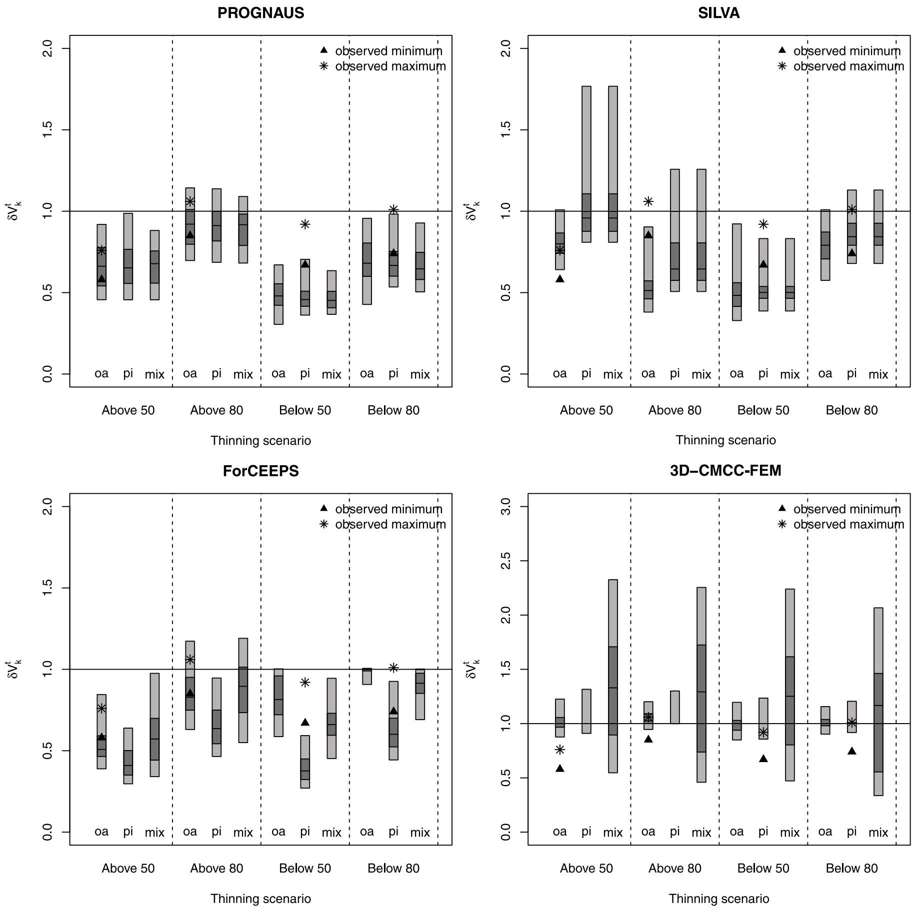

Fig. 8. Relative thinning effects $\delta V_k^{(t)}$ for every simulator applied over all triplets for the complete simulation time. Relative thinning effects $\delta V_k^{(t)}$ are provided for oak ("oa"), pine ("pi"), and mixed species ("mix") stands. Simulated $\delta V_k^{(t)}$ are provided for every simulator with their median and quantiles 0.05, 0.25, 0.75, and 0.95. Applied thinning scenarios are thinning from above with stand basal area reduction to 50 and 80% (Above 50 and Above 80) and thinning from below with stand basal area reduction to 50 and 80% (Below 50 and Below 80). Observed minimum and maximum relative thinning effects are derived from thinning experiments given in Table 3.

1993; Utschig and Pretzsch, 2001; Lockow, 2006) and pine (Kramer and Jünemann, 1984; Kramer and Röös, 1989; Valinger et al., 2000; Mäkinen and Isomäki, 2004; del Rio et al., 2008). In agreement with empirical findings, we found highest relative thinning effects for moderate thinning, except for SILVA and 3D-CMCC-FEM, which predicted highest relative thinning effects for a strong thinning intensity. In the case of 3D-CMCC-FEM large numbers of incomplete simulations might have biased the outcome of the relative thinning effect.

Mixed stands of oak and pine showed highest relative productivity for thinning from the upper tail of the diameter distribution, but with moderate (PROGNAUS, ForCEEPS) and strong (SILVA and 3D-CMCC-FEM) intensities. Thus, thinning from above seems to be more favorable, since this result is consistent across simulators. A fully comprehensive comparison of thinning type with empirical results is not possible, because experiments with oak where restricted to thinning from above, whereas experiments in Scots pine were restricted to thinning from below. Thus, we can partly confirm that moderate thinning intensities under a thinning from above yield the highest long-term productivity for mixed oak–pine stands.

The differences between observed and simulated relative thinning effects may be caused by highly variable thinning procedures with different basal area reductions, times of thinning, and time scale of observed effects as in the reference studies. This is the reason why we did not compare single study results but only ranges of relative thinning effects. The stand ages of simulations comprises a range between 16 and 193 years, which is wider than the range of stand ages of our triplet plots. Moreover the applied maximum basal area functions might have been inadequate for some triplet plots and the different approaches on how inter-tree competition is represented in the different simulators might have produced biased predictions of the thinning reactions. Hence, our results of the predicted relative thinning effects may hinder further interpretations and must be rather treated with caution.

Relative thinning effects did not show a clear decreasing age trend, but an increasing trend with stand density. Thus, we can only partly confirm our fifth hypothesis.

Mixed species forests represent very complex forest structures and theoretical reasoning suggests that more ecologically oriented and complex models are better suited to simulate such processes. However, even in ecological models some processes, such as light use, are described in detail whereas other processes such as energy, carbon, nutrient and water cycles are not included (Mäkelä et al., 2000). Moreover, the degree of upscaling required for these models is very high and processes at the leaf-level do not account for forest structure or management. The output of 3D-CMCC-FEM, however, shows that with careful modeling, growth and yield predictions similar to that of individual tree growth models are achievable. Recent research integrates such additional management parameters (Collalti et al., 2014), so that such modeling approaches are well suited to understand species mixture effects, which are caused by subtle ecological differences. Given that for mixture effects empirical knowledge is far from complete (Pretzsch and Zenner, 2017), this is a remarkable development.

Individual tree growth models, at the other end of the model spectrum, might be too coarse for the simulation of the spatial heterogeneity in mixed species forests and the sometimes missing causing link makes is difficult to understand the observed ecological processes. Moreover, such models are calibrated from large scale data sets, and might not

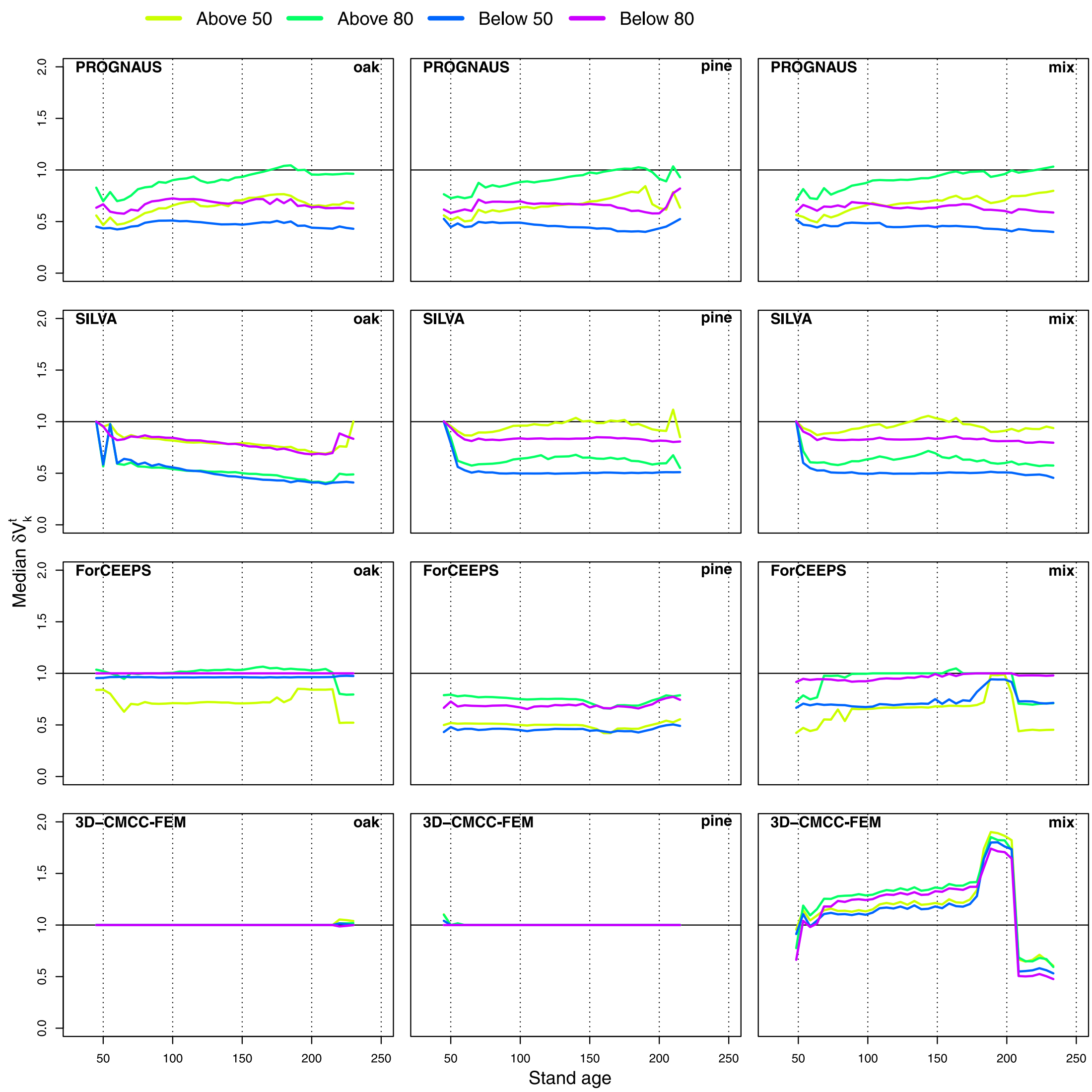

Fig. 9. Relative thinning effects $\delta V_k^{(t)}$ for every simulator applied over all triplets for the complete simulation time over the respective stand age. Median relative thinning effects $\delta V_k^{(t)}$ are provided for oak ("oak"), pine ("pine"), and mixed species ("mix") stands. Median $\delta V_k^{(t)}$ are provided with their median over 5-year stand age classes. Applied thinning scenarios are thinning from above with stand basal area reduction to 50 and 80% (Above 50 and Above 80) and thinning from below with stand basal area reduction to 50 and 80% (Below 50 and Below 80).

well adapt to each particular site. The approach in this paper however shows that the outputs from such models conform to results from empirical research. This is probably due to the fact, that the final outcome of ecological processes is reflected by the observed data, and with careful choice of variables in statistical models ecologically plausible patterns emerge. Individual tree growth models can be improved in the future by a careful choice of causal variables and better fit for particular sites could be obtained by regionalization.

Interestingly, all four models very well extrapolate to other regions in the prediction of average growth and yield rates, even though each model was developed for a particular region within the triplet gradient. Probably oak–pine mixed species forests establish in a similar ecological niche throughout Europe and the development from the data of a specific sub-region does not seem to hamper their use in a wider, geographical area.

The results from the four models further stress the large heterogeneity in model predictions, which can partly be attributed to different parameterization data sets and model approaches, but ensemble models show that also different parameterization techniques on the same data sets can result in different predictions (Araùjo et al., 2005; Grenouillet et al., 2011). Thus, the use of different models can help to document a wider range of responses.

In practical forest management, a spatially explicit and site specific decision is required. Silviculture in mixed species stands typically aims at maintaining stand compositional and structural diversity. An optimal forest management concept may vary from site to site and management practices can differ between countries (Bauhus et al., 2017). Accordingly, and because differences in yield due to different management strategies are subtle, the overall best management concept between simulators varies. Thus model prediction for mixed species forest and model predictions in general may be improved by blending different approaches, whether it be linking models of different spatial resolution or bridging spatial and non-spatial approaches (Weiskittel et al., 2011).

Despite large differences between experimental results and simulations, there is currently no alternative in applying different simulators to field data in order to clarify which management option appears optimal for a specific goal, e.g. maximizing stand-level productivity in the long run. It is hardly possible to investigate the behavior of mixed species stands from inventory data or existing yield tables for single-species stands or to infer possible outcomes from currently applied stand treatments in mixed-species forests. In fact, the further enhancement of existing growth models is necessary when the goal is to evaluate the ecological consequences and management options of a mixed-species forestry.

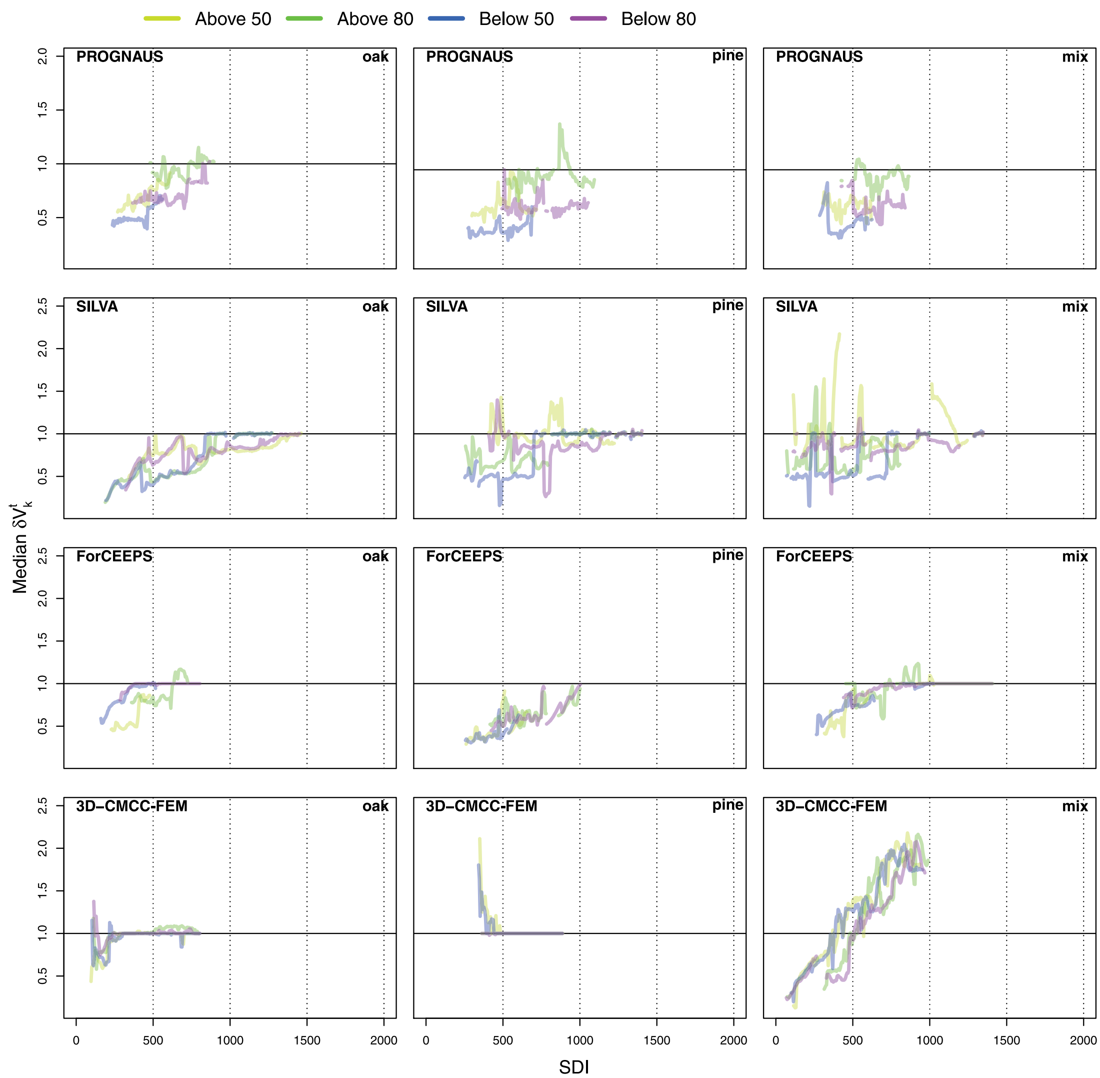

Fig. 10. Relative thinning effects $\delta V_k^{(t)}$ for every simulator applied over all triplets for the complete simulation time over the respective Stand Density Index (SDI). Median relative thinning effects $\delta V_k^{(t)}$ are provided for oak ("oak"), pine ("pine"), and mixed species ("mix") stands. Median $\delta V_k^{(t)}$ are provided with their median over SDI classes of 5. Applied thinning scenarios are thinning from above with stand basal area reduction to 50 and 80% (Above 50 and Above 80) and thinning from below with stand basal area reduction to 50 and 80% (Below 50 and Below 80).

6. Conclusion

Our study revealed that simulations were within empirical ranges previously found on the investigated triplet plots, although large discrepancies occurred at the individual triplet level. Nevertheless, we conclude that the applied simulators are able to provide plausible results for the relative volume productivity, because median predictions were within the observed ranges and models reflect the positive effects of stand age. However, we could not find a positive effect of stand density and of the site water supply on the relative volume productivity in conjunction with mixed oak–pine forests.

Our results revealed that highest long-term productivity can be expected with a thinning from above, whereas the simulators PROGNAUS and ForCEEPS demonstrated positive effects of moderate thinning intensities, SILVA and 3D-CMCC-FEM predicted the highest productivity under strong thinning. The predicted relative thinning effects showed an overall good approximation to results from thinning experiments for oak, but not for pine stands. Relative thinning effects were positively influenced by stand density, but not by stand age.

Our simulations did not show an increasing trend of the relative volume productivity with the site water supply. However, possible trends dependent on stand age and stocking density became evident. Further, we found the influence of climate and its interaction with other site variables and stand structure is so far not sufficiently represented by the models. This might have contributed to inconsistent results. The same applies to the effects of various thinning regimes, for which the simulators achieved divergent predictions.

Concluding from these findings, further work is required in order to decrease the revealed limitations of the existing growth models, as there is currently no alternative to such kind of studies and growth simulators.

CRediT authorship contribution statement

Markus Engel: Conceptualization, Methodology, Software, Formal analysis, Visualization, Writing Original Draft. **Sonja Vospernik:** Conceptualization, Resources, Methodology, Software, Writing review & editing, Project administration. **Maude Toïgo:** Software, Resources, Methodology, Writing Review & editing. **Xavier Morin:** Software, Resources, Methodology, Writing Review & editing. **Antonio Tomao:** Software, Resources, Methodology, Writing Review & editing. **Carlo Trotta:** Software, Resources, Methodology. **Mathias Steckel:** Software, Resources, Methodology, Writing review & editing. **Anna Barbati:** Resources. **Arne Nothdurft:** Resources, Methodology, Writing review &

Editing. **Hans Pretzsch:** Resources. **Miren del Rio:** Supervision. **Jerzy Skrzyszewski:** Resources. **Quentin Ponette:** Resources. **Magnus Löf:** Resources. **Āris Jansons:** Resources. **Gediminas Brazaitis:** Resources.

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.

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References

Araùjo, M.B., Whittaker, R.J., Ladle, R.J., Erhard, M., 2005. Reducing uncertainty in projections of extinction risk from climate change. Global Ecol. Biogeogr. 14, 526–538.

Assmann, E., 1970. The Principles of Forest Yield Study. Studies in Organic Production, Structure, Increment and Yield of Forest Stands. Pergamon Press, Oxford, New York, Toronto, Sydney, Braunschweig, p. 506.

Attocchi, G., 2015. Silviculture of Oak for High-Quality Wood Production. Effects of Thinning on Crown Size, Volume Growth and Stem Quality in Even-Aged Stands of Penduncculate Oak (*Quercus Robur* L.) in Northern Europe (Doctoral thesis). Swedish University of Agricultural Sciences, Alnarp, p. 506.

Bauhus, J., Forrester, D.I., Pretzsch, H., Felton, A., Pyttel, P., Benetter, A., 2017. Silvicultural options for mixed species stands. In: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), Mixed-Species Forest. Springer Verlag, Berlin-Heidelberg, pp. 433–501.

Bielak, K., Dudzińska, M., Pretzsch, H., 2014. Mixed stands of scots pine and Norway spruce can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. For. Syst. 23 (3), 573–589.

Brinkmann, N., Seeger, S., Weiler, M., Buchmann, N., Eugster1and, W., Kahmen, A., 2018. Employing stable isotopes to determine the residence times of soil water and the temporal origin of water taken up by *Fagus sylvatica* and *Picea abies* in a temperate forest. New Phytol. 219, 1300–1313.

Bugmann, H., 2001. A review of forest gap models. Clim. Change 51, 259–305.

Cavard, X., Bergeron, Y., Chen, H.Y.H., Paré, D., Laganière, J., Brassard, B., 2011. Competition and facilitation between tree species change with stand development. Oikos 120, 1683–1695.

Charru, M., Seynave, I., Morneau, F., Rivoire, M., Bontemps, J.-D., 2012. Significant differences and curvilinearity in the self-thinning relationships of 11 temperate tree species assessed from forest inventory data. Ann. For. Sci. 69 (2), 195–205.

Collalti, A., Perugini, L., Santini, M., Chiti, T., Nolè, Matteucci, G., Valentini, R., 2014. A process-based model to simulate growth in forests with complex structure: Evaluation and use of 3D-CMCC forest ecosystem model in a deciduous forest in central Italy. Ecol. Model. 272, 362–378.

Collalti, A., Thornton, P.E., Cescatti, A., Rita, A., Borghetti, M., Nole, A., Trotta, C., Ciais, P., Matteucci, G., 2019. The sensitivity of the forest carbon budget shifts across processes along with stand development and climate change. Ecol. Appl. 19 (2), e01837.

Collalti, A., Trotta, C., Keenan, T.F., Ibrom, A., Bond-Lamberty, B., Grote, R., Vicca, S., Reyer, C.P.O., Migliavacca, M., Veroustraete, F., Anav, A., Campioli, M., Scoccomarro, E., Šigut, L., Grieco, E., Cescatti, A., Metteucci, G., 2018. Thining can reduce losses in carbon efficiency and carbon stocks in managed forests under warmer climate. J. Adv. Model. Earth Syst. 10, 2427–2452.

Condés, S., del Rio, M., Sterba, H., 2013. Mixing effect on volume growth of *Fagus sylvatica* and *Pinus sylvestris* is modulated by stand density. For. Ecol. Manage. 292, 86–95.

Condés, S., Vallet, P., Bielak, P., Bravo-Oviedo, A., Coll, L., Ducey, M.J., Pach, M., Pretzsch, H., Sterba, H., Vayreda, J., del Rio, M., 2017. Climate influences on the maximum size-density relationship in Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) stands. Forest Ecol. Manag. 385, 295–307.

de Martonne, 1926. Une novel fonction climatologique: L'indice d'aridité. Météroligie 21, 449–458.

del Río, M., Bravo-Oviedo, A., Pretzsch, H., Löf, M., Ruiz-Peinado, R., 2017. A review of thinning effects on Scots pine stands: From growth and yield to new challenges under global change. For. Syst. 26 (2), eR03S.

del Rio, M., Calama, R., Cañellas, I., Roig, S., Montero, G., 2008. Thinning intensity and growth response in SW-European Scots pine stands. Ann. For. Sci. 65, 308.

del Rio, M., Montero, G., Bravo, F., 2001. Analysis of diameter-density relationships and self-thinning in non-thinned even-aged Scots pine stands. Forest Ecol. Manag. 142, 79–87.

Didion, M., Kupferschmid, A.D., Zingg, A., Fahse, L., Bugmann, H., 2009. Gaining local accuracy while not losing generality – extending the range of gap model applications. Can. J. Forest Res. 39, 1092–1107.

Dirnberger, G.F., Sterba, H., 2014. A comparison of different methods to estimate species proportions by area in mixed stands. For. Syst. 23, 534–546.

Dong, P.H., Muth, M., Roeder, A., 1997. Traubeneichen-Durchforstungsversuch in den Forstämtern Elmstein-Nord und FischbacH. Forst Holz 52, 34–38.

Eaton, E., Caudullo, G., Oliveira, S., de Rigo, D., 2016. Quercus robur and Quercus petrea in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, de Rigo, D., Caudullo, G., Houstan Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree Species. Publ. Off. Eu, Luxembourg.

Forrester, D.I., Albrecht, A.T., 2014. Light absorption and light-use efficiency in mixtures of *Abies alba* and *Picea abies* along a productivity gradient. Forest Ecol. Manag. 328, 94–102.

Fritz, C.O., Morris, P.E., 2012. Effect size estimates: current use, calculations, and interpretation. J. Exp. Psychol. 141 (1), 2–18.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusinski, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Commun. 4 (1340).

Goisser, M., Geppert, U., Rötzer, T., Paya, A., Huber, A., Kerner, R., Bauerle, T., Pretzsch, H., Pritsch, K., Häberle, K.H., Matyssek, R., Grams, T.E.E., 2016. Does belowground interaction with Fagus sylvatica increase drought susceptibility of photosynthesis and stem growth in Picea abies? Forest Ecol. Manag. 375, 268–278.

Grenouillet, G., Buisson, L., Casajus, N., Lek, S., 2011. Ensemble modelling of species distribution: the effects of geographical and environmental ranges. Ecography 34, 9–17.

Houstan Durrant, T., de Rigo, D., Caudullo, G., 2016. Pinus sylvestris in europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanze, de Rigo, D., Caudullo, G., Houstan Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg.

Hynynen, J., 1993. Self-thinning models for even-aged stands of Pinus sylvestris, Picea abies and Betula pendula. Scan. J. For. Res. 8, 226–336.

Jactel, H., Brockerhoff, E.G., 2007. Tree diversity reduces herbivory by forest insects. Ecol. Lett. 10 (9), 835–848.

Juodvalkis, A., Kairiukstis, L., Vasilianskas, R., 2005. Effects of thinning on growth of six tree species in north-temperate forests of Lithuania. Eur. J. For. Res. 124, 187–192.

Kahn, M., Pretzsch, H., 1997. Das Wuchsmodell SILVA – Parametrisierung der Version 2.1 für Rein- und Mischbestände aus Fichte und Buche. AFZ 168 (6–7), 115–123.

Kelty, M.J., Cameron, I., 1995. Plot designs for the analysis of species interactions in mixed stands. Commonw. For. Rev. 74, 322–332.

Kramer, H., Jünemann, D., 1984. Bestandesentwicklung und Erstdurchforstung in einem weitständig begründetem Kiefernbestand. Forstarchiv 55, 10–17.

Kramer, H., Röös, M., 1989. Durchforstungsversuch in einem weitständig begründetem Kiefernbestand. Forst Holz 44, 139–144.

Ledermann, T., 2002. Ein Einwuchsmodell aus den Daten der Österreichischen Waldinventur 1981-1996. Centralblatt Gesamte Forstwesen 119, 40–77.

Ledermann, T., 2006. PROGNAUS - Ein Waldwachstumsmodell Zur Fortschreibung Von Inventurdaten. Federal Research and Training Centre for Forests Natural Hazards and Landscape.

Lockow, K.W., 2003. Traubeneichen-Durchforstungsversuch Schönholz 3. AFZ – Der Wald 58, 115–118.

Lockow, K.W., 2006. Traubeneichen-Durchforstungsversuch Freienwalde (Maienpfuhl) 172. AFZ – Der Wald 61, 1040–1043.

Lu, H., Mohren, G.M.J., den Ouden, J., Goudiaby, V., Sterck, F.J., 2016. Overyielding of temperate mixed forests occur in evergreen-deciduous but not in deciduous-deciduous species mixtures over time in the Netherlands. Forest Ecol. Manag. 376, 321–332.

Mäkelä, A., Landsberg, J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Ågren, G.I., Oliver, C.D., Puttonen, P., 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. Tree Physiol. 20 (5–6), 289–298.

Mäkinen, H., Isomäki, A., 2004. Thinning intensity and growth of Scots pine stands in Finland. Forest Ecol. Manag. 201, 311–325.

Martin, G.L., Ek, A.R., Monserud, R.A., 1977. Control of plot-edge bias in forest stand growth simulation models. Can. J. Forest Res. 7 (1), 100–105.
Mina, M., Huber, M.O., Forrester, D.I., Thürig, E., Rohner, B., 2017. Multiple factors modulate tree growth complementarity in central European mixed forests. J. Ecol. 106, 1106–1119.
Monserud, R.A., Sterba, H., 1996. A basal area increment model for individual trees growing in even- and unevenaged forest stands in Austria. Forest Ecol. Manag. 80, 57–80.
Monserud, R.A., Sterba, H., 1999. Modelling individual tree mortality for Austrian forest species. Forest Ecol. Manag. 113, 109–123.
Montero, G., Cañella, I., Ortega, C., del Rio, M., 2001. Results from a thinning experiment in a Scots pine (*Pinus sylvestris* L.) natural regeneration stand in the Sistema Ibérico Mountain Range (Spain). Forest Ecol. Manag. 201, 311–325.
Morin, X., 2019. ForCEEPS. http://capsis.cirad.fr/capsis/help_en/forceeps.
Nickel, M., Klemmt, H.-J., Uhl, E., Pretzsch, H., 2007. Der Kiefern-Standraum und Durchforstungsversuch Weiden 611. AFZ – Der Wald 24, 1316–1319.
Pretzsch, H., 1995. Zum Einfluß des Baumverteilungsmusters auf den Bestandeszuwachs. Allg. For. Jagdztg. 166, 190–201.
Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. Forest Ecol. Manag. 327, 251–264.
Pretzsch, H., Biber, P., 2005. A re-evaluation of Reineke's rule and stand density index. For. Sci. 51 (4), 304–320.
Pretzsch, H., Biber, P., Durský, J., 2002. The single tree-based stand simulator SILVA: construction, application and evaluation. Forest Ecol. Manag. 162, 3–21.
Pretzsch, H., Dieler, J., Seifert, T., Rötzer, T., 2012. Climate effects on productivity and resource-use efficiency of Norway spruce (Picea abies [L.] Karst.) and European beech (Fagus sylvatica [L.]) in stands with different spatial mixing patterns. Trees-Struct. Funct. 1–18.
Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbetto, 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., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Schweig, J., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Vanhellemont, M.Svoboda.M., Verheyen, K., Wellhausen, K., Zlatanov, T., 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. Eur. J. For. Res. 134, 927–947.
Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by interspecific facilitation. Plant Biol. 15, 483–495.
Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehbrecht, M., Bielak, K., Bravo, F, Ordóñez, C., Collet, C., Vast, F., Droessler, L., Brazaitis, G., Jansons, A., Coll, L., Löf, M., Aldea, J., Korboulewsky, N., Reventlow, D.O.J., Nothdurft, A., Engel, M., Pach, M., Skrzyszewski, J., Pardos, M., Ponette, Q., Sitko, R., Fabrika, M., Svoboda, M., Černý, J., Wolff, B., Ruiz-Peinado, R., del Rio, M., 2019. Stand growth and structure of monospecific and mixed-species stands of Scots pine (*Pinus sylvestris*) L. and oak (*Q. robur* L. *Quercus petraea* (MATT.) LIEBL.) analysed along a productivity gradient through Europe. Eur. J. For. Res. http://dx.doi.org/10.1007/s10342-019-01233-y.
Pretzsch, H., Zenner, E.K., 2017. Toward managing mixed-species stands: from parametrization to prescription. For. Ecosyst. 4, 1–17.
Preuhsler, T., Kiefl, J., Meyer, F., 1993. Der Eichen-Durchforstungsversuch ROH 90 im FA Rohrbrunn. AFZ – Der Wald 6, 276–280.
Prieto, I., Armas, C., Pugnaire, F.I., 2012. Water release through plant roots: new insights into its consequences at the plant and ecosystem level. New Phytol. 193 (4), 830–841.
Purves, D., Lichstein, J., Strigul, N., Pacala, S., 2008. Predicting and understanding forest dynamics using a simple tractable model. Proc. Natl. Acad. Sci. USA 105, 17018–17022.
Reif, A., Brucker, U., Kratzer, R., Bauhus, J., 2010. Waldbewirtschaftung in Zeiten des Klimawandels – Synergien und Konfliktpotenziale zwischen Forstwirtschaft und Naturschutz. Nat. Landschaftsplanung 42, 261–266.
Reineke, L.H., 1933. Perfecting a stand density index for even-age forests. J. Agric. Res. 46, 627–638.
Schieler, K., 1997. Methode Der Zuwachsberechnung Der österreichischen Waldinventur Dissertation. Universität für Bodenkultur, Wien, p. 92 p.
Steckel, M., Heym, M., Wolff, B., Reventlow, D.O.J., Pretzsch, H., 2019. Transgressive overyielding in mixed compared with monospecific Scots pine (Pinus sylvestris L.) and oak (Quercus robur L., Quercus petraea (Matt.) Liebl.) stands – Productivity gains increase with annual water supply. Ann. For. Sci. 65 (308).
Sterba, H., Monserud, R.A., 1997. Applicability of the forest stand growth simulator PROGNAUS for the Austrian part of the Bohemian Massif. Ecol. Model. 98, 23–34.
Sterba, H., del Rio, M., Brunner, A., Condés, S., 2014. Effect of species proportion definition on the evaluation of growth in pure vs. mixed stands. For. Syst. 23, 547–559.
Taylor, A.R., Chen, H.Y.H., VanDamme, L., 2009. A review of forest succession models and their suitability for forest management planning. For. Sci. 55 (1), 22–36.
Thurm, E.A., Pretzsch, H., 2016. Improved productivity and modified tree morphology of mixed versus pure stands of European beech (*Fagus sylvatica*) and Douglas-fir (*Pseudotsuga menziesii*) with increasing precipitation and age. Ann. For Sci. 73, 1047–1061.
Utschig, H., 1992. Zielsetzung des ertragskundlichen Versuchswesens im Wandel – dargestellt am Beispiel langfristiger Eichenversuche. Forstw. Cbl. 111, 117–128.
Utschig, H., Bachmann, M., Dursky, J., 1993. Traubeneichen-Durchforstungsversuch Rohrbrunn 620. Wirkung verschiedener Durchforstungen auf Struktur und Wachstum. AFZ – Der Wald 48, 271–274.
Utschig, H., Pretzsch, H., 2001. Der Eichen-Durchforstungsversuch Waldleinigen 88. Auswirkungen unterschiedlicher Eingriffsstärken nach 65 Jahren Beobachtung. Forstw. Cbl. 120, 90–113.
Valinger, E., Elfring, B., Mörling, T., 2000. Twelve-year growth response of Scots pine to thinning and nitrogen fertilization. Forest Ecol. Manag. 134, 45–53.
Vospernik, S., Monserud, R.A., Sterba, H., 2015. Comparing individual-tree growth models using principles of stand growth for Norway spruce, Scots pine and European beech. Can. J. Forest Res. 45 (8), 1006–1018.
Vospernik, S., Sterba, H., 2015. Do competition-density rule and self-thinning rule agree? Ann. For. Sci. 72 (3), 379–390.
Weiskittel, A.R., Hann, D.W., Kershaw, J.A., Vanclay, J.K., 2011. Forest Growth and Yield Modeling. John Wiley & Sons, Ltd, West Sussex, UK, p. 415 p..
White, J.W., Rassweiler, A., Samhouri, J.F., Stier, A.C., White, C., 2013. Ecologists should not use statistical significance tests to interpret simulation model results. Oikos 123, 385–388.