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Can mixing *Quercus robur* and *Quercus petraea* with *Pinus sylvestris* compensate for productivity losses due to climate change?

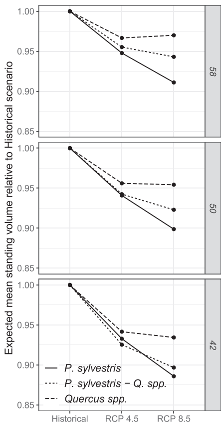
Sonja Vospernik [a,*], Carl Vigren [b], Xavier Morin [c], Maude Toïgo [c], Kamil Bielak [d], Gediminas Brazaitis [e], Felipe Bravo [f], Michael Heym [g], Miren del Río [h], Aris Jansons [i], Magnus Löf [j], Arne Nothdurft [a], Marta Pardos [h], Maciej Pach [k], Quentin Ponette [l], Hans Pretzsch [m]

[a] Department of Forest- and Soil Sciences, Institute of Forest Growth, BOKU, University of Natural Resources and Life Sciences Vienna, Peter-Jordan-Str. 82, A-1190 Vienna, Austria
[b] Department of Forest Resource Management, Swedish University of Agricultural Sciences, Skogsmarksgränd 17, 907 36 Umeå, Sweden
[c] Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175 CNRS, Univ. Montpellier, EPHE, IRD, 1919 route de Mende, 34293 Montpellier Cedex 5, France
[d] Department of Silviculture, Institute of Forest Sciences, Warsaw University of Life Sciences, Nowoursynowska 159/34, 02776 Warsaw, Poland
[e] Vytautas Magnus University, Department of Forest Science, Studentu 11, Akademija LT-53361, Kaunas dist, Lithuania
[f] Instituto de Investigación en Gestión Forestal Sostenible (iuFOR), Unidad Asociada de I+D+i al CSIC, ETS de Ingenierías Agrarias, Universidad de Valladolid, Avda. De Madrid 44, 34004 Palencia, Spain
[g] Bavarian State Institute of Forestry (LWF), Department Silviculture and Mountain Forest, Germany
[h] Instituto de Ciencias Forestales (ICIFOR- INIA), CSIC, Ctra. A Coruña km 7.5, 28040 Madrid, Spain
[i] Latvian State Forest Research Institute Silava, Rigas 111, Salaspils. Latvia
[j] Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, Box 190, 23422 Lomma, Sweden
[k] Department of Ecology and Silviculture, Faculty of Forestry, University of Agriculture in Krakow, al. 29-Listopada, 46 31-425 Kraków, Poland
[l] UCLouvain - Université catholique de Louvain, Earth & Life Institute, Croix du Sud 2 box L7.05.09, 1348 Louvain-la-Neuve, Belgium
[m] Chair of Forest Growth and Yield Science, Department of Life Science Systems, TUM School of Life Sciences, Technical University of Munich, Hans-Carl-Von-Carlowitz-Platz 2, 85354 Freising. Germany

HIGHLIGHTS

- Productivity losses increase with increasing severity of climatic scenario.
- Productivity decreases by 7.7 % and 11.6 % for *Q.* spp. and *P. sylvestris* for RCP 8.5.
- Climate change will shift the competitive advantage from *P. sylvestris* to *Q.* spp.
- Productivity losses can be mitigated but not compensated by the use of mixtures.
- Productivity losses at low latitudes are more severe than at high latitudes.

GRAPHICAL ABSTRACT



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* Corresponding author.
E-mail address: Sonja.Vospernik@boku.ac.at (S. Vospernik).

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ABSTRACT

The climate change scenarios RCP 4.5 and RCP 8.5, with a representative concentration pathway for stabilization of radiative forcing of 4.5 W m^{-2} and 8.5 W m^{-2} by 2100, respectively, predict an increase in temperature of 1–4.5° Celsius for Europe and a simultaneous shift in precipitation patterns leading to increased drought frequency and severity. The negative consequences of such changes on tree growth on dry sites or at the dry end of a tree species distribution are well-known, but rarely quantified across large gradients. In this study, the growth of *Quercus robur* and *Quercus petraea* (*Q.* spp.) and *Pinus sylvestris* in pure and mixed stands was predicted for a historical scenario and the two climate change scenarios RCP 4.5 and RCP 8.5 using the individual tree growth model PrognAus. Predictions were made along an ecological gradient ranging from current mean annual temperatures of 5.5–11.4 °C and with mean annual precipitation sums of 586–929 mm. Initial data for the simulation consisted of 23 triplets established in pure and mixed stands of *Q.* spp. and *P. sylvestris*. After doing the simulations until 2100, we fitted a linear mixed model using the predicted volume in the year 2100 as response variable to describe the general trends in the simulation results. Productivity decreased for both *Q.* spp. and *P. sylvestris* with increasing temperature, and more so, for the warmer sites of the gradient. *P. sylvestris* is the more productive tree species in the current climate scenario, but the competitive advantage shifts to *Q.* spp., which is capable to endure very high negative water potentials, for the more severe climate change scenario. The *Q.* spp.-*P. sylvestris* mixture presents an intermediate resilience to increased scenario severity. Enrichment of *P. sylvestris* stands by creating mixtures with *Q.* spp., but not the opposite, might be a right silvicultural adaptive strategy, especially at lower latitudes. Tree species mixing can only partly compensate productivity losses due to climate change. This may, however, be possible in combination with other silvicultural adaptation strategies, such as thinning and uneven-aged management.

1. Introduction

Recent climate scenarios for Europe predict an average rise in temperature for the medium and extreme emission scenario in the range of 1–4.5 °C for the RCP 4.5, and 2.5–5.5 C for the RCP 8.5 greenhouse gas emission scenarios (Jacob et al., 2014). The climate change scenarios represent concentration pathways for stabilization of radiative forcing of 4.5 and 8.5 W m^{-2} by 2100, respectively (Jacob et al., 2014). The large scale spatial patterns in high resolution climate ensemble models are similar for both scenarios and the predicted increase in temperature across Europe is particularly pronounced in Southern Europe (Jacob et al., 2014). Associated with rises in temperature are changes in precipitation patterns, predicting a decrease in Southern Europe and an increase in precipitation in Central and Northern Europe and a seasonal shift in precipitation (Jacob et al., 2014).

As a consequence, we would expect to observe an earlier occurrence of phenophases (Körner and Basler, 2010; Puchałka et al., 2017; Menzel et al., 2020; Puchałka et al., 2024), a northward migration of tree species (Ozolinčius et al., 2014; Giesecke et al., 2017) similar to the one observed in earlier warming phases (Giesecke et al., 2017), growth depression (Eilmann et al., 2006; Pardos et al., 2021; Salomón et al., 2022) due to an earlier cessation of growth (Strieder and Vospernik, 2021; Puchałka et al., 2024) due to a premature cessation of the cambial activity (Puchałka et al., 2024), increased tree mortality due to hydraulic failure or carbon starvation (Benito Garzón et al., 2018; Choat et al., 2018; Arend et al., 2021; Mantova et al., 2022; Hartmann et al., 2022; Hammond et al., 2022) reinforced by an increased risk of insect pests and tree pathogens (Venäläinen et al., 2020) and an increase of natural hazards and abiotic disturbances (Dupuy et al., 2020; Maurer and Heinimann, 2020; Romeiro et al., 2022). Recent climate warming has pushed many ecosystems to the margins of their ecological niche (Bebi et al., 2001; Camarero et al., 2021) and further rising global temperatures will continue to exacerbate the situation.

Oak (*Quercus* spp. (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.)) – Scots pine (*Pinus sylvestris* L.) mixed species forests are a plant association found on xeric, acidophilous sites (Müller, 1992) which are thought to be resistant and resilient to climatic warming (Pretzsch et al., 2020) since both tree genera are well adapted to drought.

Quercus spp. have deep penetrating tap roots and leaves with a thick-walled epidermis (Gil-Pelegrín et al., 2017). *Quercus* spp. can endure an extremely high negative water potential of −4 MPa and can withdraw considerable amounts of stored water from its stem and crown (Zweifel et al., 2009; Peters et al., 2023). As aniso-hydric tree species, they display very little climate sensitivity and quickly recover from summer drought, usually within 1–2 years (Gillner et al., 2013; Haerdtle et al., 2013; Vitasse et al., 2019). *Quercus* spp. are adopted to be productive even under high vapor pressure deficits, but extreme drought can move them to their physiological limit leading to premature leaf cessation (Zweifel et al., 2006).

P. sylvestris is a widely distributed tree species (Brus et al., 2012) that is also drought tolerant with its thick walled epidermis and inset stomata, which protect it from water loss (Zweifel et al., 2009). *P. sylvestris*, however, maintains a significantly higher water potential than do *Quercus* spp., not dropping below −1.5 and −2.5 MPa in leaves (Irvine et al., 1998; Zweifel et al., 2009) and it stores smaller amounts of water in its leaves and crown (Zweifel et al., 2007). The isohydric behavior and tighter stomatal control result in greater limitations of carbon assimilation than is observed for *Q.* spp. (Zweifel et al., 2009) resulting in more pronounced and longer lasting growth response to drought for *P. sylvestris* than for *Q.* spp. (Zweifel et al., 2009) and post-drought growth depression for *P. sylvestris* can last for up to 5 years (Galiano et al., 2011). Thus, while *P. sylvestris* is drought tolerant, it is better adapted to wet and cool conditions in dry environments, where it opens its stomata more widely than *Q.* spp. and then has a higher photosynthetic capacity (Zweifel et al., 2009; Peters et al., 2023).

Both *Q.* spp. and *P. sylvestris* are of high commercial importance (Durrant et al., 2016; Eaton et al., 2016) and many studies have investigated their productivity. At the same site *Q.* spp. were reported to maintain lower tree densities in terms of stem number, basal area and volume, but higher biomass productivity (Yuste et al., 2005), because of their higher wood density. Lower basal area for *Q.* spp. is also reflected by considerably lower maximum basal area per hectare attainable by this species in comparison to *P. sylvestris* (Vospernik and Sterba, 2015). Management concepts and commercial use for the two tree species differ considerably: *P. sylvestris* constitutes 20 % of the standing timber volume in Europe and has an easily workable wood for construction, furniture pulp and paper (Durrant et al., 2016), and can be more easily managed than *Q.* spp. In contrast, *Q.* spp. provides high quality hardwood, appreciated for its durability and hardness. The most valuable oak wood has narrow rings with long economic rotations and frequent management interventions (Eaton et al., 2016).

The increasing frequency of drought extremes associated with climate change is a key challenge to forest ecosystems. Consequently, the quantification of drought effects on tree growth and mortality is of the highest concern for forest management and forest science (Bhuyan et al., 2017). Selection of drought tolerant tree species (Thurm et al., 2018; Vospernik, 2021), managing tree species mixture (Steckel et al., 2020), climate adapted forest management and selection of suitable provenances (Taeger et al., 2013; Karrer et al., 2022) are all important strategies to mitigate climate change impacts. In particular, mixing tree species has been proposed as one of the solutions to promote adaptive forest management because mixed stands are supposed to be, on average, more productive, more resistant and resilient to drought (Pretzsch et al., 2020; Steckel et al., 2020; Pardos et al., 2021), herbivores and pathogens (Jactel et al., 2017, 2019) than pure stands – although the strength of the mixture effects may strongly vary with species and site conditions (Pardos et al., 2021; Strieder and Vospernik, 2021).

While mixing tree species is beneficial, growth depressions follow drought. These are well documented (*Quercus*: Toïgo et al., 2015; Prokop et al., 2016; Roibu et al., 2020; Vospernik et al., 2023; ***Pinus***: Rigling et al., 2002; Toïgo et al., 2015; Treml et al., 2022), since both tree species are well-represented in dendro-ecological studies. In general, *Q.* spp. tree ring chronologies correlate positively with precipitation in spring and early summer while during late-wood formation climate response is unstable and varying in sign from site to site (Prokop et al., 2016; Roibu et al., 2020; Vospernik et al., 2023). High autumn temperatures positively affect carbohydrate reserves and thus are positively associated with ring width for *Q.* spp. of the next year (Prokop et al., 2016; Roibu et al., 2020; Vospernik et al., 2023). Likewise, spring and early summer precipitation positively affect the growth of *P. sylvestris* on xeric sites (Rigling et al., 2002; Treml et al., 2022). Unlike *Q.* spp., *P. sylvestris* ring growth was reported to be positively affected by winter precipitation, which is important for successful shoot and root growth but *P. sylvestris* is negatively affected by high summer temperatures (Rigling et al., 2002; Treml et al., 2022). Fluctuations in the ring width of *P. sylvestris* are reported to be higher than that of *Q.* spp. because of its iso-hydric nature (Zweifel et al., 2009).

In Europe, additional growth depressions in future scenarios are thought to be most pronounced in Mediterranean areas (Aldea et al., 2018; Martínez-Sancho et al., 2021). Here, temperature rise is predicted to be highest (Jacob et al., 2014), and these sites are currently already particularly dry sites, with low water availability during summer (Aldea et al., 2018; Martínez-Sancho et al., 2021) with stressful site conditions. At these sites plant species are, however, genetically and phenologically adapted to low water availability (Martínez-Sancho et al., 2021), and trees at temperate or boreal sites with currently sufficient water availability and with currently larger absolute and relative growth rates, might be affected more by climatic warming, and decrease more in growth, while being still higher than in Mediterranean areas. At the north-eastern range limit, despite predicted maintaining their climatic niche, growth of *Q. robur* decreased in dry years (Puchałka et al., 2024), possibly because this widely distributed species has different ecotypes, which are only adapted to a proportion of the niche occupied by the species as a whole (Sáenz-Romero et al., 2019; Puchałka et al., 2024).

In order to supply decision makers, researchers and stakeholders with an in-depth information and quantification of the consequences of climate growth, it is imperative to integrate climate change scenarios with forest growth models. This can be done by using climate and mixture sensitive individual tree (*e.g.* Vospernik, 2021), gap (*e.g.* Morin et al., 2021) or process-based models (*e.g.* Gupta and Sharma, 2019; Bouwman et al., 2021). The first type of model predicts growth and mortality of individual trees, the second type uses a similar approach but focuses on grid cells and the latter focus on tree physiological processes such as photosynthesis, respiration, stomatal conductance or carbon allocation (Weiskittel et al., 2011). Individual tree growth models most easily integrate empirical research on tree rings and dendrometers and forest management scenarios because of the shared focus on the individual tree. Also, they are less computationally expensive than process based models assuring reasonable prediction times and the detailed output provided by these models is often not required. Therefore, they are the preferred means for simulating forest productivity (Weiskittel et al., 2011), but predictions of tree growth with climate change remain scarce (Bombi et al., 2017; Dyderski et al., 2018; Girardin et al., 2008; Bayat et al., 2022; De Wergifosse et al., 2022) and are still lacking for mixed *Q.* spp. and *P. sylvestris* stands.

Growth reactions for different climate scenarios have not yet been studied in detail for *Q.* spp.-*P. sylvestris* pure and mixed forests. In this study, we quantify growth reactions for *Quercus* and *Pinus* on different sites across Europe under different climate scenarios and compare pure and mixed species stand with respect to climatic resistance and resilience and productivity response.

1.1. Hypothesis

We hypothesize that:

1. The expected standing volume in 2100, decreases on average for all species with increased severity of the scenario (Historical ≪ RCP 4.5 ≪ RCP 8.5).
2. If hypothesis 1 holds, *Q.* spp. will be better able to buffer these changes than *P. sylvestris* (experience less of a decline with increased severity of scenario).
3. Additionally, we hypothesize that the mixed species stands will show less response in productivity than the single species stands do.
4. We expect that, in line with our current understanding of the species' climatic distribution, the volume fall-off with increased scenario severity will be stronger for lower-latitude plots, which are closer to their species distributional xeric limit.

2. Data

2.1. Tree data

Initial data for the simulation was data from *Q.* spp. – *P. sylvestris* triplets established as part of the ERA-Net SUMFOREST project REFORM ("REsilience of FORest Mixtures", reform-mixing.eu) across Europe. This is described in detail in previous studies focusing on stand productivity and tree drought resilience (Pretzsch et al., 2020; Steckel et al., 2020; Vospernik et al., 2023) and tree growth simulation under current climatic conditions (Engel et al., 2021). The dataset encompassed 23 triplets. By design, each triplet contains three plots, whereof two are single-species stands of *Q.* spp. and *P. sylvestris*, and one is a mixed stand of *Q.* spp. - *P. sylvestris*. The triplet data covered large geographic (Fig. 1) and environmental (Fig. 2) gradients across Europe. Mean annual temperatures at the sites varied between 5.5 °C and 11.4 °C and precipitation is 586–929 mm. Plots were established in mature stands with an interquartile age range of 55–91.5 years and an interquartile stand volume of 317–613 m^3ha^{-1} (Table 1) with median stand characteristics being comparable in both the pure and mixed stands. Even though there is variation between different triplets, the pure and mixed plots within each triplet show extremely little variation in stand characteristics, showing the plots were carefully established (Appendix: Table 1).

2.2. Climate scenarios

Historical and future climate time series were acquired from CHELSA (High Resolution Climatologies for Earth's Land Surface; https://chelsa-climate.org/), a high-resolution (30 arc *sec*) climate repository for the land surface (Karger et al., 2017). We accounted for existing variability in climate projections by simulating the data over the period 2006–2100 under four non-intercorrelated global circulation models (ACCESS1-3, CESM1-BGC, MIROC5, CMCC-CM) and two climate scenarios (RCP 4.5; RCP 8.5) following the recommendation of Sanderson et al. (2015). We retrieved time series for monthly minimum

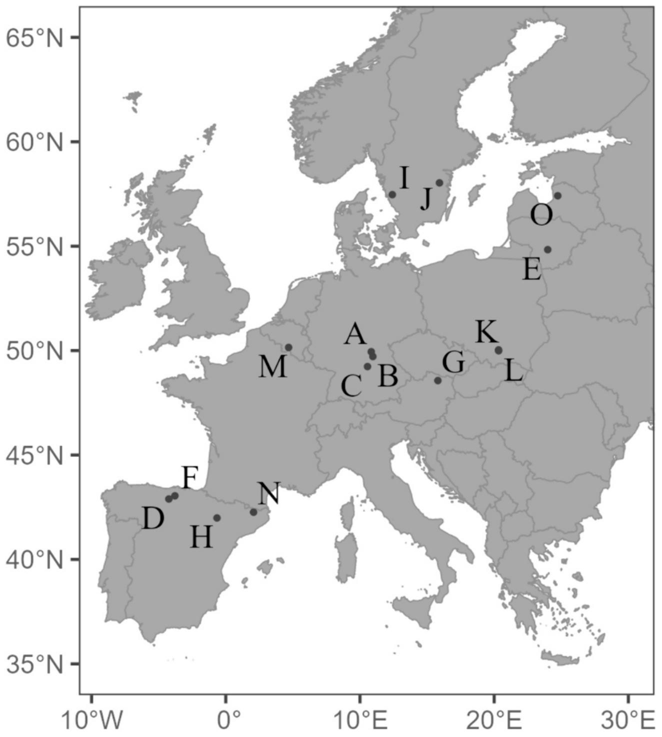

Fig. 1. Location of the study sites. Letters indicating the study site are also used in Fig. 2 and in the appendix.

temperature, monthly maximum temperature and monthly precipitation sum (Karger et al., 2020). We calculated the time series of mean temperature by averaging the minimum and maximum monthly temperature. We compared the results obtained in the context of climate change with those of a null scenario obtained from eight randomized historical climate time series (1979–2013) provided by CHELSA to determine the effects of climate change on tree growth. The time series of future climates provided by CHELSA showed stable precipitation regimes over the 21th century; For some regions an increase of precipitation was predicted, while for others there was no trend or an opposite trend. In contrast to past intra-annual precipitations recorded, the predicted precipitation sums, showed hardly any variation in precipitation sums between years. To overcome this short-coming, we replaced the precipitation forecasts with time series of randomized historical precipitation given by CHELSA. Finally, we calculated average climatic conditions per site to keep climatic conditions constant between plots of the same triplet. The climate conditions simulated in each scenario are illustrated in Fig. 2. While current mean annual temperatures varied between 5.5 °C and 11.4 °C (Appendix T1) and remain at this level in the historical scenarios, with some precipitation shifts, the scenario RCP 4.5 showed an increase in temperature up to mean annual temperatures of 12.5 °C during the study period and up to 14 °C in the RCP 8.5 scenario and little change in precipitation for the *Q.* spp. and *P. sylvestris* triplet plots.

3. Methods

3.1. Individual tree growth simulations

Simulations were carried out with the individual tree growth simulator PrognAus. The simulator consists of a basal area increment (Vospernik, 2021), a height increment (Nachtmann, 2006), a crown ratio (Hasenauer and Monserud, 1996), mortality (Monserud and Sterba, 1999) and an ingrowth model (Ledermann, 2002). The basal area increment model encompasses 22 species, which are modeled based on tree size, density and competition, climate, soil variables, harvesting and disturbances and mixture. The competition indices used are non-spatial and climate is modeled by separating climatic site effects from weather conditions by including long-term mean temperature, long-term mean precipitation and the yearly deviations thereof as input

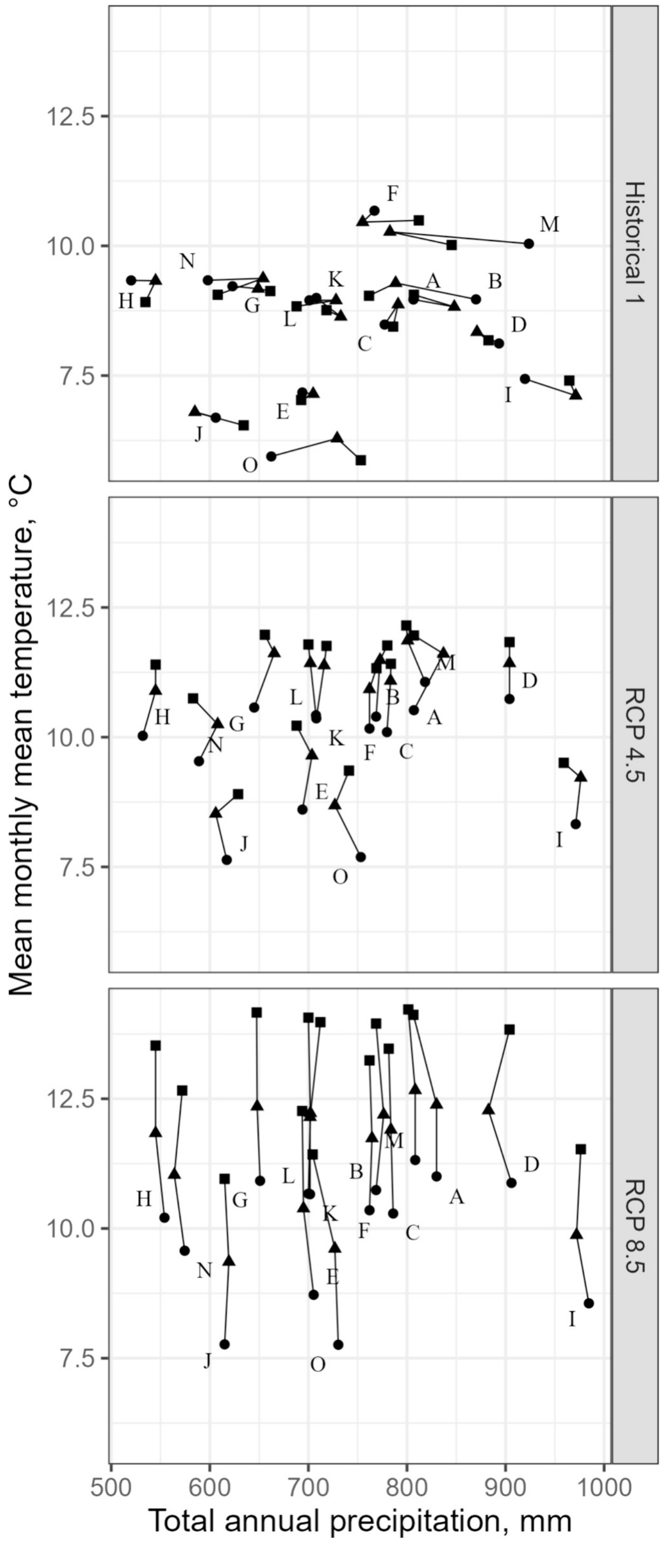

Fig. 2. Median of the mean monthly mean temperature °C and total annual precipitation (mm) during 3 periods of the simulation: 2017–2044 (circle); 2045–2072 (triangle); 2073–2100 (square). Trajectories with a shared letter denote the same site in different simulations.

Table 1
Summary (Q1: 25 % quantile, Q2: median, Q3: 75 % quantile) of mixture-wise initial stand conditions. Plot size (hectare), age (yrs), trees (ha^{-1}), basal area ($m^2\ ha^{-1}$), volume ($m^3\ ha^{-1}$).

	Q. spp.			*Q.* spp.-*P. sylv.*			*P. sylv.*		
	Q1	Q2	Q3	Q1	Q2	Q3	Q1	Q2	Q3
Plot size	0.06	0.11	0.16	0.15	0.19	0.29	0.07	0.11	0.12
Age	55	75	87	54	65.5	83	48	66	92
Trees	447	649	1493	553	779	1073	623	885	1196
Basal area	34.2	44.0	48.5	41.3	45.3	52.1	47.3	52.1	60.9
Volume	317	366	540	397	515	564	421	510	613
Basal area per species									
Q. spp.	87	93	97	35	45	48	0	3	6
P. sylvestris	0	0	3	42	52	55	86	92	97
Other	2	4	13	1	4	12	0	3	8

parameters. Mixture effects for many different species are represented by including the basal area proportion of them in the model. While the basal area increment model is climate and mixture sensitive (Vospernik, 2021), these effects are not explicitly included in the other Prognaus models (height increment: Nachtmann, 2006; crown ratio: Hasenauer and Monserud, 1996; mortality: Monserud and Sterba, 1999; or ingrowth: Ledermann, 2002) even though such effects might be implicitly reflected by the site factors used in the models (*e.g.* elevation) and stand variables (*e.g.* dominant height). All sub-models were developed based on the data of the Austrian National Forest Inventory. The data cover a large environmental gradient in temperature and precipitation (Vospernik, 2021) which because of Austria's large altitudinal (colline zone to timberline) extent and thus encompassing many climatic conditions encountered in Europe, but may not be representative for very dry Mediterranean sites. Nevertheless, the data encompass the climatic conditions encountered on triplet plots. Measurements taken on the triplet plots and climate scenarios were used as input for the individual tree growth simulations. Simulations were done at a yearly time step, without any silvicultural intervention or treatment applied during the simulation period from 2017 to 2100 and not taking into account ingrowth, thus focusing on the development of the current stand on the plots. An example of the simulation for an individual plot of a triplet is shown in Fig. 3.

3.2. *Generalization of the model output to a stand-level model*

Raw simulation results were generalized using a linear mixed model. Since the mortality model is not climate sensitive, and we do not have any information on the mortality prior to our inventory of the plots, analysis focused on the standing living volume (as opposed to the total production) at the end of the simulation (year 2100) given only information on the climatic scenario and the initial state of the stand in question. For this reason, we postulate that this relationship can be accurately assessed with a linear mixed model with readily accessible summary input terms from a forest stand.

Linear Mixed Models (LMM's) can be generally expressed as:

$$y = X\beta + Zu + \epsilon \quad (1)$$

where X is a matrix of the predictor variables, β are the fixed-effect coefficients, Z is a design matrix of the random effects, u are the random effects and ε the residuals.

To test our hypotheses H1 through H4, we designed a full best subset search (respecting the principle of marginality) of a global maximum model to select a LMM which accounts for potential differences in the scenario increments as the result of differing starting conditions in terms of standing volume and age, and any site-specific reaction. The best subset search was performed with MuMIn::dredge (v. 1.47.5, Bartoń, 2023), given a number of potential inputs (see supplementary code). All subset models included a plot-wise random effect and were fitted by maximum likelihood, ML (Laplace approximation) with `lme4::lme` (v. 1.1.33, Bates et al., 2015). The final model was that which resulted in the best (lowest) marginal Akaike's Criterion. The marginal AIC as a model selection criterion can be shown to be asymptotically related to a Leave-One-Cluster-Out Cross-Validation, which significantly cuts down on computational expense (Greven and Kneib, 2010; Fang, 2021). This is particularly suited for instances where the main interest is the prediction of previously unobserved levels.

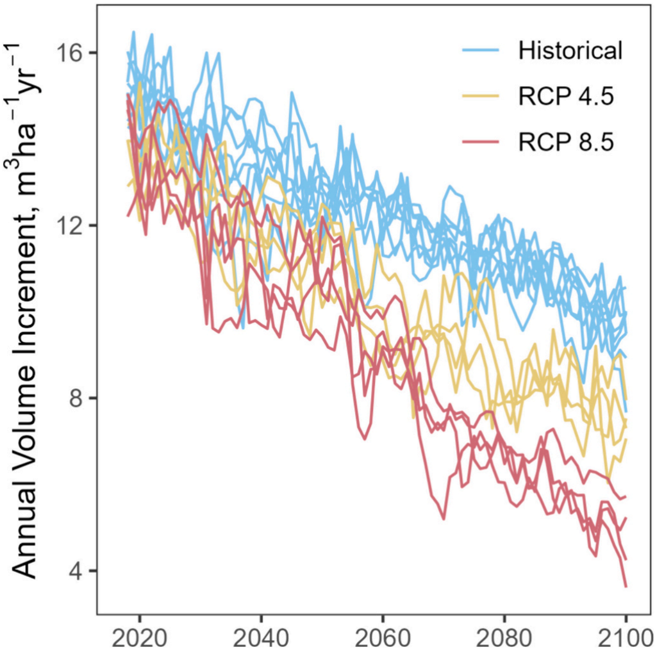

Fig. 3. Example of simulated trajectories for the German stand C-1, *P. sylvestris* (Initial conditions: volume 441 m^3ha^{-1}, basal area 50.6 m^2ha^{-1} (92.7 % *P. sylvestris*), number of trees 1750 ha^{-1}, 45 years of age). Annual volume increment decreases with age – but more rapidly so during more severe climatic scenarios.

The final model was then refitted by REML, Restricted Maximum Likelihood, to avoid the bias associated with the shrinkage property from ML estimation of random effect estimates. As the random effect estimates are then the empirical best linear unbiased predictors, which result in the minimum mean squared error given the variance components, this is particularly suitable for models mainly interested in prediction (Welham et al., 2014, p. 436). Since the (biased) estimator for the residual variance from ML is $\hat{\sigma}^2$, and the unbiased REML estimator is $\frac{n}{(n-p)}\hat{\sigma}^2$, the bias for our final model with 37 fixed-effect parameters and 648 observations would amount to $\frac{n}{(n-p)} = \frac{648}{(648-37)} = 1.06$.

Our final model with fixed-effect parameters is detailed below (Table 3). Random-effects values for the 72 plots are not presented.

The marginal mean estimates and corresponding confidence

Table 2
Simulation results for the different stand types. Volume (m^3ha^{-1}) and its standard deviation and cumulative mortality till the end of the simulation period (m^3ha^{-1}) and the standard deviation thereof.

Mixture	Climate	Volume 2100		Cumulative mortality 2100	
		Mean	SD	Mean	SD
		m^3ha^{-1}	m^3ha^{-1}	m^3ha^{-1}	m^3ha^{-1}
Oak	Historic	748.7	±61.2	420.1	±145.7
Oak	RCP 4.5	733.6	±64.8	357.3	±134.0
Oak	RCP 8.5	734.6	±66.5	370.6	±140.5
Oak-Pine	Historic	774.1	±79.7	363.1	±123.8
Oak-Pine	RCP 4.5	744.9	±85.9	315.4	±115.8
Oak-Pine	RCP 8.5	731.4	±87.7	307.2	±114.6
Pine	Historic	861.2	±101.1	374.4	±127.8
Pine	RCP 4.5	825.6	±101.7	342.4	±116.2
Pine	RCP 8.5	790.9	±100.9	324.6	±108.6

intervals for a new unobserved level were calculated with covariates set at their mixture-wise averages, longitude set at the mean of all plots, and latitude set as the median or one of the extreme values.

In order to assess the likelihood of any of the marginal estimates achieving at least the mean of another marginal estimate, confidence and prediction intervals for the 27 (3 climate scenarios, 3 latitudes, 3 stand species mixtures) marginal estimates were calculated by a bootstrapping routine (10'000 simulations), simulating the conditional distribution of the predictions, and considering the variance of the random effects. From this, comparisons of the response probabilities could be presented (Tables 4, 5 & 6). Where the tabulated values are the likelihood that a random unobserved datum from one of the marginal estimates will fall above the mean of any other marginal estimate. In text, we use the term degree of dominance (henceforth dominance) of the best performing species to signify this likelihood, *e.g.* If 78 % of *P. sylvestris* stands under a certain climate and at a certain latitude would be expected to achieve at least the mean of that of a *Q.* spp. stand, *P. sylvestris* displays a strong dominance over *Q.* spp.

4. Results

At the end of the simulation period (2100) the standing volume was highest in the historic scenario (Table 2). In this scenario also the density dependent cumulative mortality during the simulation period was highest resulting in the highest total productivity (2100).

4.1. Linear mixed model

A more detailed analysis of simulation results with the LMM gave the following results: climate (historical and future scenarios), geographical position and stand level (age, volume, stem number and mixture) variables were significant, at least when considering their interactions with other variables (Table 3, random effects not presented). In total, some 6.9 % of variance was explained by the model, whereof 79.5 % by the fixed effects, and some 17.3 % by the random-effects (Nakagawa and Schielzeth, 2013).

Where mixture (*Q.* spp., *Q.* spp. – *P. sylvestris* or *P. sylvestris*) is the species mix as a categorical variable; climate (Historical 1, RCP 4.5, RCP 8.5) is the simulated scenario; Age$_{2017}$, Volume$_{2017}$, Stems$_{2017}$ express

Table 3
Parameterised linear mixed model. Independent variable: 'Standing volume 2100'. *t*-Tests with Satterthwaite's method. Level of significance: ' ' 0.1, '.' 0.05, '*' 0.01, '**' 0.001, '***' 0.

Variable	Estimate	Std. error	Pr (>|t|)	
(Intercept)	8.126E+01	1.217E+02	0.507235	
Climate RCP 4.5	3.694E+01	2.268E+01	0.103829	
Climate RCP 8.5	2.829E+01	2.268E+01	0.212649	
Latitude	1.087E+01	2.823E+00	0.000304	***
Longitude	5.377E+00	6.423E+00	0.406091	
Mixture *Q.* spp. - *P. sylvestris*	2.272E+01	1.110E+02	0.838550	
Mixture *P. sylvestris*	−1.774E+02	1.126E+02	0.120639	
Stems$_{2017}$	6.779E−02	1.560E−02	5.92E−05	***
Age$_{2017}$	−9.396E−01	2.905E−01	0.002047	**
Volume$_{2017}$	3.474E−01	4.262E−02	4.96E−11	***
Climate RCP 4.5:Latitude	−1.367E+00	5.393E−01	0.011498	*
Climate RCP 8.5:Latitude	−1.555E+00	5.393E−01	0.004088	**
Climate RCP 4.5:Longitude	−5.784E+00	1.301E+00	1.07E−05	***
Climate RCP 8.5:Longitude	−8.659E+00	1.301E+00	6.86E−11	***
Climate RCP 4.5:Mixture *Q.* spp. - *P. sylvestris*	1.468E+00	2.923E+00	0.615741	
Climate RCP 8.5:Mixture *Q.* spp. - *P. sylvestris*	−1.193E+00	2.923E+00	0.683373	
Climate RCP 4.5:Mixture *P. sylvestris*	−1.655E+00	3.162E+00	0.600842	
Climate RCP 8.5:Mixture *P. sylvestris*	−1.068E+00	3.162E+00	0.735665	
Climate RCP 4.5:Stems$_{2017}$	8.408E−03	2.888E−03	0.003739	**
Climate RCP 8.5:Stems$_{2017}$	−3.968E−03	2.888E−03	0.169985	
Climate RCP 4.5:Age$_{2017}$	1.529E−01	5.607E−02	0.006606	**
Climate RCP 8.5:Age$_{2017}$	2.940E−01	5.607E−02	2.23E−07	***
Latitude:Mixture *Q.* spp. - *P. sylvestris*	2.238E+00	2.610E+00	0.394880	
Latitude:Mixture *P. sylvestris*	4.534E+00	2.596E+00	0.086333	.
Longitude:Mixture *Q.* spp. - *P. sylvestris*	−2.076E+00	1.388E+00	0.140418	
Longitude:Mixture *P. sylvestris*	−9.662E−01	1.323E+00	0.468259	
Mixture *Q.* spp. - *P. sylvestris*:Stems$_{2017}$	−6.888E−02	1.951E−02	0.000842	***
Mixture *P. sylvestris*:Stems$_{2017}$	−2.991E−02	2.086E−02	0.157294	
Mixture *Q.* spp. - *P. sylvestris*:Age$_{2017}$	−7.891E−01	3.778E−01	0.041375	*
Mixture *P. sylvestris*:Age$_{2017}$	−4.248E−01	3.596E−01	0.242611	
Climate RCP 4.5:Latitude:Longitude	1.958E−02	1.364E−01	0.886372	
Climate RCP 8.5:Latitude:Longitude	7.896E−02	1.364E−01	0.564897	
Historical:Latitude:Longitude	−4.069E−01	1.443E−01	0.006197	**
Climate RCP 4.5:Mixture *QP*[a]:Stems$_{2017}$	−4.834E−03	2.736E−03	0.077812	.
Climate RCP 8.5:Mixture *QP*[a]:Stems$_{2017}$	1.557E−02	2.736E−03	2.06E−08	***
Climate RCP 4.5:Mixture *P. sylvestris*:Stems$_{2017}$	7.689E−04	3.111E−03	0.804886	
Climate RCP 8.5:Mixture *P. sylvestris*:Stems$_{2017}$	2.672E−03	3.111E−03	0.390802	

[a] QP: Quercus spp. – *P. sylvestris*.

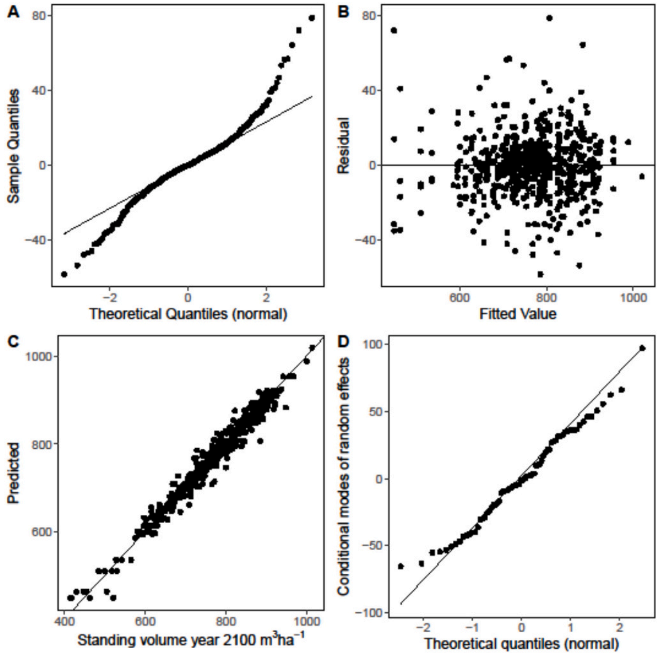

Fig. 4. Diagnostic plots of the LMM. Subplot A. QQ-plot of model residuals. Subplot B. Residuals *versus* fitted. Subplot C. Predicted *versus* actual values. Subplot D. Conditional modes *versus* normal quantiles.

the initial state of the plot in 2017 (in years, cubic meters, and stems per hectare, respectively); latitude and longitude express the location of each plot in decimal degrees. Colon (':') signifies interaction terms.

Model diagnostics (Fig. 4A) indicate model residuals are underdispersed compared to that expected from $\mathcal{N}(0,1)$ and largely homoscedastic (Fig. 4B). As can be seen in the plot of the observed *versus* predicted (Fig. 4C) overall fit is satisfactory (mean absolute percentage error: 1.49 %). The mixed model conditional modes (random effects) are close to normal (Fig. 4D).

Dimension size adjusted Generalized Variance Inflation Factor (GVIF1/(2*df)) for the different variables was, as could be expected, moderately high to high as a result of the low number of factor levels and many interactions (see supplementary documentation) and inclusion of square terms (volume). This is not perceived to be problematic in terms of prediction, given that such data could be assumed to have the same multicollinearity.

Marginal mean estimates for the mixture-wise means of the covariates at the minimum, median and maximum latitude are presented in Fig. 5. For *P. sylvestris*, an almost linear decreasing trend with increasing scenario severity is shown, with a stronger slope at low latitudes. Both the species mixture (*Q.* spp. – *P. sylvestris*) and *Q.* spp. show a demonstrable stronger decrease in volume from the historical scenario to RCP 4.5 than a subsequent shift to RCP 8.5, where reactions are more diverse. *Q.* spp. in particular, shows a maintained mean value under RCP 8.5 compared to RCP 4.5 at the highest latitude, with slightly lower values for the median and lowest latitude. *Q.* spp. – *P. sylvestris* does show a continued decrease relative to the historic scenario when moving from the RCP 4.5 to the RCP 8.5 scenario, although not as strong as the jump

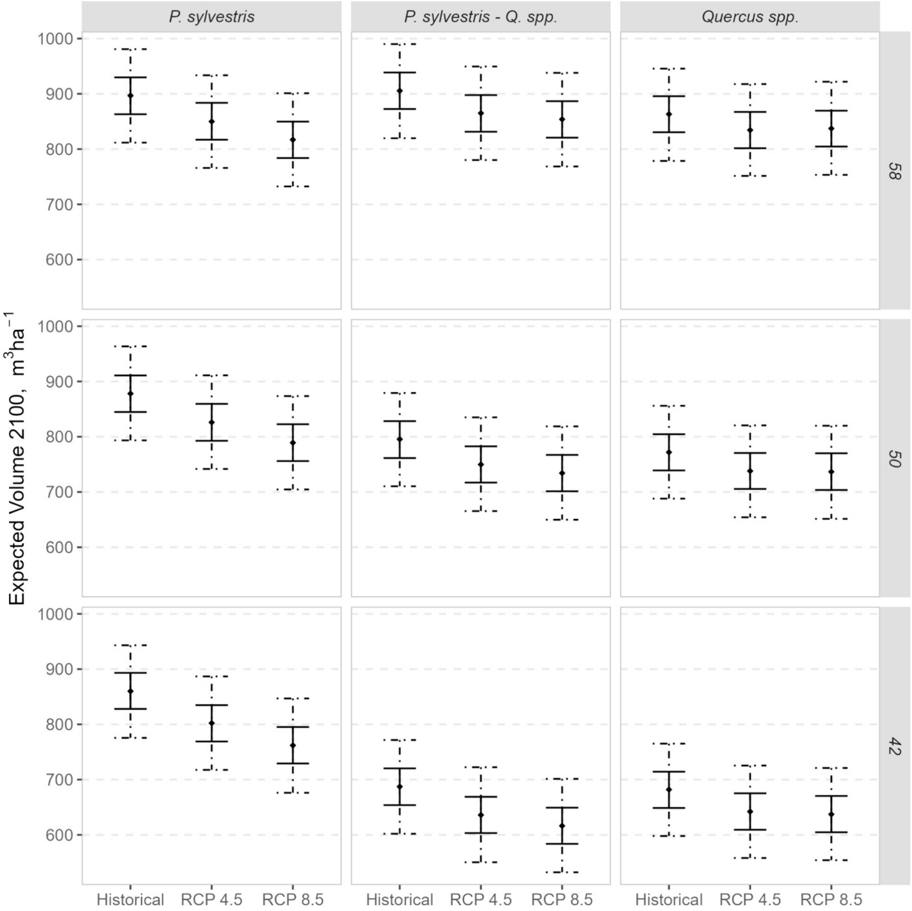

Fig. 5. Estimated marginal means (the predicted means of the response for each level, *ceteris paribus*) from the LMM. Points are the mean estimate. Solid error-bars represent the confidence interval of the estimate. Dashed error-bars represent the prediction interval of the estimate. Numbers in the panel strip text on the right refer to latitude in decimal degrees.

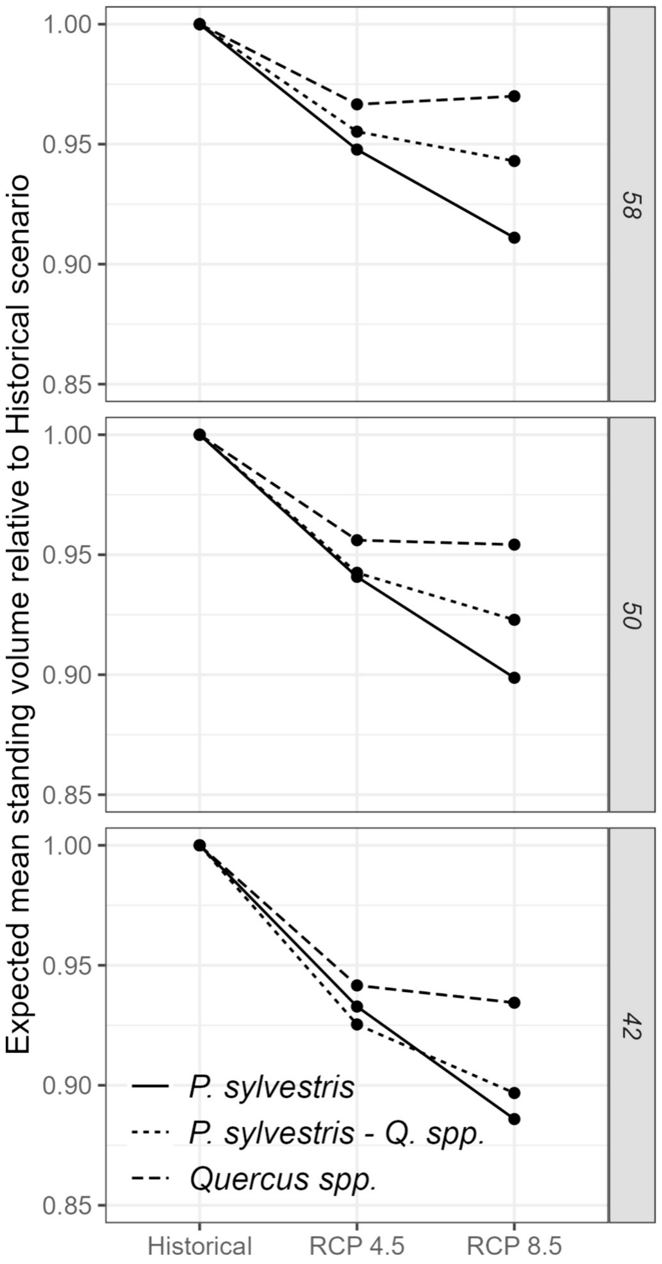

Fig. 6. Marginal mean estimates by stand composition and minimum, median and maximum latitude (values rounded in the figure only) expressed in terms of the historical scenario. Numbers in the panel strip text on the right refer to latitude in decimal degrees.

from the historic scenario to RCP 4.5 (Fig. 6).

At the three latitudes examined (58°N, 50°N, 42°N), *P. sylvestris* shows an almost linear decrease expressed relative to the historic scenario, in which the RCP 8.5 entails almost a repeat loss of standing volume (from high to low latitude, RCP 4.5: −5.2 %, −5.9 %, −6.7 %; RCP 8.5: −8.9 %, −10.1 %, −11.5 %). Q. spp. proves to be considerably more resilient than *P. sylvestris* in the RCP 4.5 – RCP 8.5 scenario comparison, where the rate of decrease observed in the Historical – RCP 4.5 shift has been stemmed completely, reversed, or only slightly continuing (RCP 4.5–3.3 %, −4.4 %, −5.8 %; RCP 8.5: −3.0 %, −4.6 %, −6.5 %). The Q. spp. – *P. sylvestris* mixture presents an intermediate resilience to increased scenario severity (RCP 4.5: −4.4 %, −5.8 %, −7.4 %; RCP 8.5: −5.7 %, −7.7 %, −10.3 %). Moving from the higher latitude towards the lower latitudes, the standing volume relative to the historical scenario rapidly encroaches on the losses experienced by the *P. sylvestris* stands, and at the lowest latitude under the RCP 4.5 scenario demonstrates an even inferior resilience.

4.2. Response probability tables

The effect of such a decrease in the mean estimate of standing volume 2100 is better expressed in terms of the response probabilities (Tables 4, 5, 6). It becomes then clear (as can also be seen from Fig. 5), that although *P. sylvestris* experiences the species-wise largest relative decrease relative to the historical scenario, the terms of its dominance (the likelihood that a given species could be expected to achieve at least the mean of a second species) is strongly related to the latitude examined. The dominance of *P. sylvestris* to *Q.* spp. under the same scenario decreases with increasing latitude and severity of the scenario. At 42°N, this dominance is close to absolute. At 50°N, this dominance has decreased to 99 %, 98 % and 89 % under the historical, RCP 4.5 and RCP 8.5 scenario, respectively. At 58°N, only 78 %, 64 % and 32 % of *P. sylvestris* stands are expected to achieve at least the mean standing volume of that of *Q.* spp. under the examined scenarios. The dominance of *Q.* spp. to the *Q.* spp. - *P. sylvestris* mixture increases with scenario severity, but *Q.* spp. - *P. sylvestris* is more strongly favored at higher latitudes. The dominance of *P. sylvestris* relative to the *Q.* spp. - *P. sylvestris* mixture decreases with latitude and scenario severity. In Tables 4, 5 and 6, bold values indicate series of scenario severities where the direction of the dominance switches. At 42°N, the relatively weak dominance of the *Q.* spp. - *P. sylvestris* mixture to *Q.* spp. is rapidly lost, such that under RCP 4.5 the dominance enjoyed by the *Q.* spp. - *P. sylvestris* mixture under the historical scenario is reversed and of the same strength. Under RCP 8.5 this dominance by *Q.* spp. has increased to almost 70 %. At the intermediate examined latitude, 50°N, a strong dominance (~71 %) of the *Q.* spp. - *P. sylvestris* mixture to *Q.* spp. is rapidly dismantled, and under the most severe scenario, RCP 8.5, switches direction, albeit very weakly. At the highest examined latitude, 58°N, a very strong dominance of *P. sylvestris* to *Q.* spp. of c. 78 % is reversed to a dominance of *Q.* spp. to *P. sylvestris* at 68 % under RCP 8.5.

Table 4
Response probabilities (probability of a new observation achieving at least the mean of the contestant) for 42°N. Read row to column. Scenario severity series (on the diagonals of the submatrices) are printed in bold if they demonstrate a directional change in dominance.

Latitude	42	*Q.* spp.			*Q.* spp. - *P. sylvestris*			*P. sylvestris*		
	%	Historical	RCP 4.5	RCP 8.5	Historical	RCP 4.5	RCP 8.5	Historical	RCP 4.5	RCP 8.5
Q. spp.	Historical	49.89	82.33	85.09	**44.91**	84.76	93.18	0.00	0.26	3.29
	RCP 4.5	17.80	49.69	54.22	14.55	**55.17**	72.10	0.00	0.01	0.30
	RCP 8.5	14.84	45.40	49.67	12.09	50.72	**68.46**	0.00	0.01	0.18
Q. spp.- *P. sylvestris*	Historical	**55.14**	85.67	88	49.79	88.02	94.82	0.00	0.37	4.40
	RCP 4.5	14.44	**44.68**	49.00	11.70	50.12	67.79	0.00	0.01	0.18
	RCP 8.5	6.32	28.33	**31.70**	5.31	32.48	49.39	0.00	0.00	0.03
P. sylvestris	Historical	99.99	100	100	100	100	100	49.72	91.16	98.76
	RCP 4.5	99.76	99.99	99.98	99.53	99.97	100	9.13	49.81	82.93
	RCP 8.5	97.00	99.64	99.80	95.52	99.79	99.92	1.21	16.87	50.31

Table 5
Response probabilities (probability of a new observation achieving at least the mean of the contestant) for 50°N. Read row to column. Scenario severity series (on the diagonals of the submatrices) are printed in bold if they demonstrate a directional change in dominance.

Latitude	50	*Q.* spp.			*Q.* spp. - *P. sylvestris*			*P. sylvestris*		
	%	Historical	RCP 4.5	RCP 8.5	Historical	RCP 4.5	RCP 8.5	Historical	RCP 4.5	RCP 8.5
Q. spp.	Historical	50.11	78.88	79.76	**28.52**	69.18	80.46	0.55	10.41	34.55
	RCP 4.5	21.65	50.14	51.41	8.91	**38.02**	52.74	0.05	1.86	12.46
	RCP 8.5	21.02	49.05	50.32	8.47	37.07	**51.73**	0.04	1.73	11.79
Q. spp.- *P. sylvestris*	Historical	**71.42**	91.35	91.90	49.99	84.99	92.46	2.90	24.35	55.85
	RCP 4.5	31.27	**61.57**	62.89	14.44	49.87	64.52	0.14	3.94	18.97
	RCP 8.5	19.79	47.01	**48.42**	7.84	35.48	50.00	0.04	1.49	10.87
P. sylvestris	Historical	99.28	99.93	99.95	97.32	99.86	99.94	49.71	88.69	98.14
	RCP 4.5	89.75	98.08	98.22	75.41	96.21	98.35	11.56	49.8	80.23
	RCP 8.5	65.29	88.59	89.14	43.43	81.23	89.79	1.91	19.50	49.19

Table 6
Response probabilities (probability of a new observation achieving at least the mean of the contestant) for 58°N. Read row to column. Scenario severity series (on the diagonals of the submatrices) are printed in bold if they demonstrate a directional change in dominance.

Latitude	58	*Q.* spp.			*Q.* spp. - *P. sylvestris*			*P. sylvestris*		
	%	Historical	RCP 4.5	RCP 8.5	Historical	RCP 4.5	RCP 8.5	Historical	RCP 4.5	RCP 8.5
Q. spp.	Historical	50.22	74.69	72.85	16.22	47.81	58.74	**21.62**	62.23	85.69
	RCP 4.5	24.75	50.28	47.14	5.20	23.68	32.51	7.49	**35.85**	65.33
	RCP 8.5	27.02	53.12	50.03	6.02	26.09	35.18	8.47	38.51	**68.10**
Q. spp.- *P. sylvestris*	Historical	83.64	94.98	94.57	49.91	82.20	88.61	58.04	89.83	98.00
	RCP 4.5	52.40	76.45	74.54	17.55	50.00	60.87	23.46	64.11	87.01
	RCP 8.5	41.43	67.51	65.32	11.63	39.61	49.91	15.94	53.88	80.36
P. sylvestris	Historical	**78.13**	92.61	91.59	41.96	76.30	83.93	49.92	86.2	96.79
	RCP 4.5	37.97	**64.16**	61.67	9.99	36.16	46.03	13.98	49.68	77.53
	RCP 8.5	14.34	34.93	**31.92**	2.10	13.22	19.66	3.33	22.73	50.11

5. Discussion

Q. spp. are predicted to be a winners of climate change increasing their current range with increasing climate warming, while the current range of *P. sylvestris* is predicted to decrease (Bombi et al., 2017; Dyderski et al., 2018). In line with these species distribution predictions, our growth simulations suggest that with increasing climatic warming, the decrease in the growth of *Q.* spp. is predicted to remain weak, whereas larger differences were found for *P. sylvestris* so that *P. sylvestris* can only be considered moderately resistant to a warming climate. The between species differences are consistent with the respective autoecologies: *Q.* spp., with its deep root system and its ability to endure very negative water potentials, is well adapted to climatic warming (Zweifel et al., 2006) because it continues sequestering carbon under drought conditions, while *P. sylvestris* closes its stomata earlier, at the cost of photosynthesis. Empirical research also shows that *Q.* spp. show less variability in ring width in comparison to other tree species (Gillner et al., 2013; Vitasse et al., 2019).

Mixture is currently beneficial for productivity at the stand level but positive mixture effects on productivity for *Q.* spp. and *P. sylvestris* are minor and only partly compensate for the decrease in growth with increasing climatic warming and the advantage of mixture is reported to decrease with drought (Aldea et al., 2022). Minor gains in productivity were also reported in empirical studies quantifying the effect of mixing on *Q.* spp. and *P. sylvestris* and improved drought response in the mixture was reported in some studies (Steckel et al., 2020) and a greater temporal stability (del Río et al., 2022), while other studies were not able to confirm a beneficial effect of mixture on drought (Bonal et al., 2017). Gains in productivity reported for *Q.* spp. and *P. sylvestris* mixed stands were 7 % and 9 %, respectively (Steckel et al., 2020; Pretzsch et al., 2020) and are thus smaller than the 8.9–11.5 % productivity loss expected for the more productive *P. sylvestris* in the RCP 8.5 scenario. Although only partly compensating for productivity losses, the mixture has also a positive effect on many ecosystem services such as provision of habitats or biodiversity (Heinrichs et al., 2019; Felton et al., 2022), and spreads the risk associated with extreme events (*e.g.* Schwarz and Bauhus, 2019) and insect outbreaks and herbivory (*e.g.* Griess and Knoke, 2011; Jactel et al., 2017; Jactel et al., 2021).

Results obtained in this study are optimistic, in that climate effects were only considered in the basal area increment model, but not yet for the height increment or mortality model. The effect of climate on height increment is, however, reported to be minor. Empirical studies on height growth of *Q.* spp. (Stimm et al., 2021) and *P. sylvestris* (Taeger et al., 2013) found no effect or small effects (<5 %) on height growth and weaker correlations with climatic variables of the current year (Taeger et al., 2013). This is because height increment is formed during a very short period in spring, and therefore only influenced by the climate in this period (Taeger et al., 2013). Shoot formation itself is a two-year process, starting with bud formation during late summer of the first year and the actual expansion occurring during spring/early summer in the second year (Bréda et al., 2006). In addition to water availability, temperature during the phase of bud formation is regarded as a trigger for shoot length (Kozlowski et al., 1991; Salminen and Jalkanen, 2005). This explains the weaker relation of annual height growth to the moisture deficit of the current year.

Climate has an important impact on individual tree mortality. Large scale mortality due to drought was reported for *P. sylvestris* (Dobbertin et al., 2005; Bigler et al., 2006; Allen et al., 2010; Cailleret et al., 2017; Brandl et al., 2020; George et al., 2022) and *Q.* spp. (Cailleret et al., 2017; Brandl et al., 2020; George et al., 2022), yet such elevated mortality effects are not explicitly included in our modelling approach, with mortality models based on the empirical data of the Austrian National Forest Inventory. Mechanisms, that lead to drought induced elevated mortality are complex and include plant physiological response to climate, climate influences on insect and pests and pathogens and their interaction (Anderegg et al., 2015). Purely physiological causes for drought induced mortality are hydraulic failure or carbon starvation (McDowell, 2011; Mantova et al., 2022), but foundational evidence of the mechanistic link has not been identified yet (Mantova et al., 2022). Susceptibility to insects and pests is driven by drought, which stresses trees but also by many characteristics of host trees, pathogens or insects (Anderegg et al., 2015), which make mortality factors difficult to disentangle. Cailleret et al. (2017), analysed radial growth patterns preceding mortality, and observed a radial growth decline in 84 % of the trees prior to mortality, but did not separate drought induced mortality from competition induced mortality. Competition induced mortality or natural thinning, results from the increasing space and resource requirement of trees with increasing size and occurs in high density stands (Pretzsch et al., 2023) and it is the mortality component most existing mortality models focus on. Climate-sensitive mortality models have been suggested by Brandl et al. (2020) who found an increased mortality risk for *Q.* spp. and *P. sylvestris* with increasing temperature but the models are not fully compatible with the PrognAus modelling framework since the study focused on dominant trees and did not include competition induced mortality. Mortality models, separating the influence of different stressors will improve climate sensitive tree growth simulation in the future. Moreover, mortality due to catastrophic events and disturbances, reported to increase with climate change (e,g, Romeiro et al., 2022) was not included in the simulations and therefore climate change will certainly cause larger economic losses than predicted by our approach. As can be seen already with other species, such as *Picea abies* in the Alps, salvaging operations constituted 39.41 % of the harvested timber volume (https://info.bml.gv.at/themen/wald/wald-in-oesterreich/wald-und-zahlen/holzeinschlagsmeldung-2022.html). In line with this, the potential range of *P. sylvestris* is predicted to decrease because of increase mortality at the dry edge of the distribution (Bombi et al., 2017; Dyderski et al., 2018).

This study shows that increasing climatic warming imposes ecological and economical threats even to relatively well drought-adapted tree species such as *Q.* spp. and *P. sylvestris* and that productivity losses for these species are higher at the dry end of the climatic gradient of their distribution. Results suggest a relative competitive advantage of *Q.* spp. over *P. sylvestris* with increasing drought frequency and severity.

Also, when analyzing growth reactions it is important to consider a different drought adaption of different provenances, as shown in the study of Taeger et al. (2013) and broadlydistributed species are optimally adapted only to a proportion of the climatic niche occupied by the species as a whole (Sáenz-Romero et al., 2019). Carefully selecting drought-resistant provenances can further mitigate climate-related risks. Stronger drought resistance of saplings is often found in saplings from drier locations (Cregg and Zhang, 2001).

In future research, the quantification of future productivity losses should be extended to other species; A limitation of this study is that it investigates the growth reactions of old stands, whereas those of younger stands may differ. More intensively investigating the more dynamic young stands is another key issue.

6. Conclusion

Climatic warming will result in severe productivity losses at dry sites or the dry end of distribution of the tree species studied here. This study suggests a competitive advantage and higher productivity of *P. sylvestris* under the current climate, the mixture of *Q.* spp. and *P. sylvestris* could be recommended with RCP 4.5, while for scenario RCP 8.5 there may be considerable loss in productivity for *P. sylvestris* and only *Q.* spp. can be recommended. Enrichment of *P. sylvestris* stands by creating mixtures with *Q.* spp., but not the opposite, might be a right silvicultural adaptive strategy, especially at lower latitudes. Tree species mixing can only partly compensate productivity losses due to climate change. This may, however, be possible in combination with other silvicultural adaptation strategies, such as thinning and uneven-aged management, which were not investigated in this study. Other options in RCP 8.5 could be assisted migration with more drought resistant species or the introduction with non-native species, although the collateral risk of such a strategy should not be minimized (Dimitrova et al., 2022).

To better understand the influence of climate on forest productivity, fitting climate and competition sensitive mortality models for a large range of species compatible with individual tree growth models is a field for future research and a next step in climate sensitive growth predictions. Equally important is the integration of the associated risk in growth predictions.

Further enhanced precipitation models in climatic predictions showing more variability would further be necessary, since predictions currently available showed too little variation in precipitation between by years. Annual precipitation, however, largely affects growth reactions.

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CRediT authorship contribution statement

Sonja Vospernik: Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Carl Vigren:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis. **Xavier Morin:** Writing – review & editing, Data curation, Conceptualization. **Maude Toïgo:** Writing – review & editing, Data curation, Conceptualization. **Kamil Bielak:** Writing – review & editing, Investigation. **Gediminas Brazaitis:** Writing – review & editing, Conceptualization. **Felipe Bravo:** Writing – review & editing, Conceptualization. **Michael Heym:** Writing – review & editing, Conceptualization. **Miren del Río:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Aris Jansons:** Writing – review & editing, Conceptualization. **Magnus Löf:** Writing – review & editing, Conceptualization. **Arne Nothdurft:** Writing – review & editing, Conceptualization. **Marta Pardos:** Writing – review & editing, Conceptualization. **Maciej Pach:** Writing – review & editing, Conceptualization. **Quentin Ponette:** Writing – review & editing, Conceptualization. **Hans Pretzsch:** Writing – review & editing, Conceptualization.

Declaration of competing interest

We have no conflicts of interest to disclose.

Data availability

Data will be made available on request.

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References

Aldea, J., Bravo, F., Vázquez-Piqué, J., Rubio-Cuadrado, A., Del Río, M., 2018. Species-specific weather response in the daily stem variation cycles of Mediterranean pine-oak mixed stands. Agric. For. Meteorol. 256–257, 220–230. https://doi.org/10.1016/j.agrformet.2018.03.013.

Aldea, J., Ruiz-Peinado, R., Del Río, M., Pretzsch, H., Heym, M., Brazaitis, G., Jansons, A., Metslaid, M., Barbeito, I., Bielak, K., Hylen, G., Holm, S., Nothdurft, A., Sitko, R., Löf, M., 2022. Timing and duration of drought modulate tree growth response in pure and mixed stands of Scots pine and Norway spruce. J. Ecol. 110, 2673–2683. https://doi.org/10.1111/1365-2745.13978.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S. W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259 (4), 660–684. https://doi.org/10.1016/j.foreco.2009.09.001.

Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J. D., Stephenson, N.L., Tague, C., Zeppel, M., 2015. Tree mortality from drought, insects, and their interactions in a changing climate. New Phytol. 208 (3), 674–683. https://doi.org/10.1111/nph.13477.

Arend, M., Link, R.M., Patthey, R., Hoch, G., Schuldt, B., Kahmen, A., 2021. Rapid hydraulic collapse as cause of drought-induced mortality in conifers. Proc. Natl. Acad. Sci. 118, e2025251118 https://doi.org/10.1073/pnas.2025251118.

Bartoń, K., 2023. MuMIn: multi-model inference. R package version 1.47.5 [WWW Document]. URL. https://CRAN.R-project.org/package=MuMIn.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using **lme4**. J. Stat. Softw. 67 https://doi.org/10.18637/jss.v067.i01.

Bayat, M., Knoke, T., Heidari, S., Hamidi, S.K., Burkhart, H., Jaafari, A., 2022. Modeling tree growth responses to climate change: a case study in natural deciduous mountain forests. Forests 13, 1816. https://doi.org/10.3390/f13111816.

Bebi, P., Kienast, F., Schönenberger, W., 2001. Assessing structures in mountain forests as a basis for investigating the forests' dynamics and protective function. For. Ecol. Manag. 12.

Benito Garzón, M., González Muñoz, N., Wigneron, J.-P., Moisy, C., Fernández-Manjarrés, J., Delzon, S., 2018. The legacy of water deficit on populations having experienced negative hydraulic safety margin. Glob. Ecol. Biogeogr. 27, 346–356. https://doi.org/10.1111/geb.12701.

Bhuyan, U., Zang, C., Menzel, A., 2017. Different responses of multispecies tree ring growth to various drought indices across Europe. Dendrochronologia 44, 1–8. https://doi.org/10.1016/j.dendro.2017.02.002.

Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an inciting mortality factor in scots pine stands of the Valais, Switzerland. Ecosystems 9, 330–343. https://doi.org/10.1007/s10021-005-0126-2.

Bombi, P., D'Andrea, E., Rezaie, N., Cammarano, M., Matteucci, G., 2017. Which climate change path are we following? Bad news from Scots pine. PLoS One 12 (12), e0189468. https://doi.org/10.1371/journal.pone.0189468.

Bonal, D., Pau, M., Toigo, M., Granier, A., Perot, T., 2017. Mixing oak and pine trees does not improve the functional response to severe drought in central French forests. Ann. For. Sci. 74 (4), 72. https://doi.org/10.1007/s13595-017-0671-9.

Bouwman, M., Forrester, D.I., Den Ouden, J., Nabuurs, G.-J., Mohren, G.M.J., 2021. Species interactions under climate change in mixed stands of Scots pine and pedunculate oak. For. Ecol. Manag. 481, 118615 https://doi.org/10.1016/j.foreco.2020.118615.

Brandl, S., Paul, C., Knoke, T., Falk, W., 2020. The influence of climate and management on survival probability for Germany's most important tree species. For. Ecol. Manag. 458, 117652 https://doi.org/10.1016/j.foreco.2019.117652.

Bréda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann. For. Sci. 63 (6), 625–644. https://doi.org/10.1051/forest:2006042.

Brus, D.J., Hengeveld, G.M., Walvoort, D.J.J., Goedhart, P.W., Heidema, A.H., Nabuurs, G.J., Gunia, K., 2012. Statistical mapping of tree species over Europe. Eur. J. Forest Res. 131 (1), 145–157. https://doi.org/10.1007/s10342-011-0513-5.

Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Čada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Čufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Hereş, A., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Linares Calderon, J.C., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., López Rodríguez, R., Mäkinen, H., Mayr, S., Mészáros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martínez-Vilalta, J., 2017. A synthesis of radial growth patterns preceding tree mortality. Glob. Chang. Biol. 23 (4), 1675–1690. https://doi.org/10.1111/gcb.13535.

Camarero, J.J., Gazol, A., Sangüesa-Barreda, G., Vergarechea, M., Alfaro-Sánchez, R., Cattaneo, N., Vicente-Serrano, S.M., 2021. Tree growth is more limited by drought in rear-edge forests most of the times. For. Ecosyst. 8, 25. https://doi.org/10.1186/s40663-021-00303-1.

Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R., Medlyn, B.E., 2018. Triggers of tree mortality under drought. Nature 558, 531–539. https://doi.org/10.1038/s41586-018-0240-x.

Cregg, B.M., Zhang, J.W., 2001. Physiology and morphology of *Pinus sylvestris* seedlings from diverse sources under cyclic drought stress. For. Ecol. Manag. 154, 131–139. https://doi.org/10.1016/S0378-1127(00)00626-5.

De Wergifosse, Louis, André, F., Goosse, H., Boczon, A., Cecchini, S., Ciceu, A., Collalti, A., Cools, N., D'Andrea, E., De Vos, B., Hamdi, R., Ingerslev, M., Knudsen, M.A., Kowalska, A., Leca, S., Matteucci, G., Nord-Larsen, T., Sanders, T.G., Schmitz, A., Termonia, P., Vanguelova, E., Van Schaeybroeck, B., Verstraeten, A., Vesterdal, L., Jonard, M., 2022. Simulating tree growth response to climate change in structurally diverse oak and beech forests. Sci. Total Environ. 806, 150422 https://doi.org/10.1016/j.scitotenv.2021.150422.

del Río, M., Pretzsch, H., Ruiz-Peinado, R., Jactel, H., Coll, L., Löf, M., Aldea, J., Ammer, C., Avdagić, A., Barbeito, I., Bielak, K., Bravo, F., Brazaitis, G., Cerný, J., Collet, C., Condés, S., Drössler, L., Fabrika, M., Heym, M., Holm, S., Hylen, G., Jansons, A., Kurylyak, V., Lombardi, F., Matović, B., Metslaid, M., Motta, R., Nord-Larsen, T., Nothdurft, A., den Ouden, J., Pach, M., Pardos, M., Poeydebat, C., Ponette, Q., Pérot, T., Reventlow, D.O.J., Sitko, R., Sramek, V., Steckel, M., Svoboda, M., Verheyen, K., Vospernik, S., Wolff, B., Zlatanov, T., Bravo-Oviedo, A., 2022. Emerging stability of forest productivity by mixing two species buffers temperature destabilizing effect. J. Appl. Ecol. 1365–2664, 14267 https://doi.org/10.1111/1365-2664.14267.

Dimitrova, A., Csilléry, K., Klisz, M., Lévesque, M., Heinrichs, S., Cailleret, M., Andivia, E., Madsen, P., Böhenius, H., Cvjetkovic, B., De Cuyper, B., De Dato, G., Ferus, P., Heinze, B., Ivetić, V., Köbölkuti, Z., Lazarević, J., Lazdina, D., Maaten, T., Makovskis, K., Milovanović, J., Monteiro, A.T., Nonić, M., Place, S., Puchalka, R., Montagnoli, A., 2022. Risks, benefits, and knowledge gaps of non-native tree species in Europe. Front. Ecol. Evol. 10, 908464 https://doi.org/10.3389/fevo.2022.908464.

Dobbertin, M., Mayer, P., Wohlgemuth, T., Feldmeyer-Christe, E., Zimmermann, N.E., Rigling, A., 2005. The decline of *Pinus sylvestris* L. forests in the Swiss Rhone Valley - a result of drought stress? https://www7.nau.edu/mpcer/direnet/publications/publications_d/files/dobbertin_decline_pinus.pdf.

Dupuy, J.L., Fargeon, H., Martin-StPaul, N., et al., 2020. Climate change impact on future wildfire danger and activity in southern Europe: a review. Ann. For. Sci. 77, 35. https://doi.org/10.1007/s13595-020-00933.

Durrant, T.H., de Rigo, D., Caudullo, G., 2016. *Pinus sylvestris* in Europe: distribution, habitat usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree Species. Publ. Off. EU. Luxembourg (e016b94++ pp.).

Dyderski, M.K., Paź, S., Frelich, L.E., Jagodziński, A.M., 2018. How much does climate change threaten European forest tree species distributions? Glob. Chang. Biol. 24 (3), 1150–1163. https://doi.org/10.1111/gcb.13925.

Eaton, E., Caudullo, G., Oliveira, S., de Rigo, D., 2016. *Quercus robur* and *Quercus petraea* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree Species. Publ. Off. EU. Luxembourg (e01c6df+ pp.).

Eilmann, B., Weber, P., Rigling, A., Eckstein, D., 2006. Growth reactions of *Pinus sylvestris* L. and *Quercus pubescens* Willd. to drought years at a xeric site in Valais, Switzerland. Dendrochronologia 23 (3), 121–132. https://doi.org/10.1016/j.dendro.2005.10.002.

Engel, M., Vospernik, S., Toïgo, M., Morin, X., Tomao, A., Trotta, C., Steckel, M., Barbati, A., Nothdurft, A., Pretzsch, H., del Rio, M., Skrzyszewski, J., Ponette, Q., Löf, M., Jansons, Ā., Brazaitis, G., 2021. 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. Ecol. Model. 442, 109406 https://doi.org/10.1016/j.ecolmodel.2020.109406.

Fang, Y., 2021. Asymptotic equivalence between cross-validations and Akaike information criteria in mixed-effects models. J. Data Sci. 15–21 https://doi.org/10.6339/JDS.201101_09(1).0002.

Felton, A., Felton, A.M., Wam, H.K., Witzell, J., Wallgren, M., Löf, M., Sonesson, J., Lindbladh, M., Björkman, C., Blennow, K., Cleary, M., Jonsell, M., Klapwijk, M.J., Niklasson, M., Petersson, L., Rönnberg, J., Sang, Å.O., Wrethling, F., Hedwall, P.-O., 2022. Forest biodiversity and ecosystem services from spruce-birch mixtures: the potential importance of tree spatial arrangement. Environ. Chall. 6, 100407 https://doi.org/10.1016/j.envc.2021.100407.

Galiano, L., Martínez-Vilalta, J., Lloret, F., 2011. Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode. New Phytol. 190, 750–759. https://doi.org/10.1111/j.1469-8137.2010.03628.x.

George, J.-P., Bürkner, P.-C., Sanders, T.G.M., Neumann, M., Cammalleri, C., Vogt, J.V., Lang, M., 2022. Long-term forest monitoring reveals constant mortality rise in European forests. Plant Biol. J. 24 (7), 1108–1119. https://doi.org/10.1111/plb.13469.

Giesecke, T., Brewer, S., Finsinger, W., Leydet, M., Bradshaw, R.H.W., 2017. Patterns and dynamics of European vegetation change over the last 15,000 years. J. Biogeogr. 44, 1441–1456. https://doi.org/10.1111/jbi.12974.

Gillner, S., Vogt, J., Roloff, A., 2013. Climatic response and impacts of drought on oaks at urban and forest sites. Urban For. Urban Green. 12, 597–605. https://doi.org/10.1016/j.ufug.2013.05.003.

Gil-Pelegrín, E., Peguero-Pina, J.J., Sancho-Knapik, D. (Eds.), 2017. Oaks Physiological Ecology. Exploring the Functional Diversity of Genus *Quercus* L., Tree Physiology. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-69099-5.

Girardin, M.P., Raulier, F., Bernier, P.Y., Tardif, J.C., 2008. Response of tree growth to a changing climate in boreal central Canada: a comparison of empirical, process-based, and hybrid modelling approaches. Ecol. Model. 213, 209–228. https://doi.org/10.1016/j.ecolmodel.2007.12.010.

Greven, S., Kneib, T., 2010. On the behaviour of marginal and conditional AIC in linear mixed models. Biometrika 97 (4), 773–789. https://doi.org/10.1093/biomet/asp042.

Griess, V.C., Knoke, T., 2011. Growth performance, windthrow, and insects: meta-analyses of parameters influencing performance of mixed-species stands in boreal and northern temperate biomes. Can. J. For. Res. 41, 1141–1159. https://doi.org/10.1139/x11-042.

Gupta, R., Sharma, L.K., 2019. The process-based forest growth model 3-PG for use in forest management: a review. Ecol. Model. 397, 55–73. https://doi.org/10.1016/j.ecolmodel.2019.01.007.

Haerdtle, W., Niemayer, T., Assman, T., Aulinger, A., Fichtner, A., Lang, A., Leuschner, C., Neuwirth, B., Pfister, L., Quante, M., Ries, C., Schuldt, A., von Oheimb, G., 2013. Climatic responses of tree-ring width and δ13C signatures of sessile oak (*Quercus petraea* Liebl.) on soils. Plant Ecol. 214, 1147–1156. https://doi.org/10.1007/s11258-013-0239-1.

Hammond, W.M., Williams, A.P., Abatzoglou, J.T., Adams, H.D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D.D., Allen, C.D., 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. Nat. Commun. 13 (1), 1761. https://doi.org/10.1038/s41467-022-29289-2.

Hartmann, H., Bastos, A., Das, A.J., Esquivel-Muelbert, A., Hammond, W.M., Martínez-Vilalta, J., McDowell, N.G., Powers, J.S., Pugh, T.A.M., Ruthrof, K.X., Allen, C.D., 2022. Climate change risks to global forest health: emergence of unexpected events of elevated tree mortality worldwide. Annu. Rev. Plant Biol. 73 (1), 673–702. https://doi.org/10.1146/annurev-arplant-102820-012804.

Hasenauer, H., Monserud, R.A., 1996. A crown ratio model for Austrian forests. For. Ecol. Manag. 84, 49–60. https://doi.org/10.1016/0378-1127(96)03768-1.

Heinrichs, S., Ammer, C., Mund, M., Boch, S., Budde, S., Fischer, M., Müller, J., Schöning, I., Schulze, E.-D., Schmidt, W., Weckesser, M., Schall, P., 2019. Landscape-scale mixtures of tree species are more effective than stand-scale mixtures for biodiversity of vascular plants, bryophytes and lichens. Forests 10, 73. https://doi.org/10.3390/f10010073.

Irvine, J., Perks, M.P., Magnani, F., Grace, J., 1998. The response of *Pinus sylvestris* to drought: stomatal control of transpiration and hydraulic conductance. Tree Physiol. 18 (6), 393–402. https://doi.org/10.1093/treephys/18.6.393.

Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O.B., Bouwer, L.M., Braun, A., Colette, A., Déqué, M., Georgievski, G., Georgopoulou, E., Gobiet, A., Menut, L., Nikulin, G., Haensler, A., Hempelmann, N., Jones, C., Keuler, K., Kovats, S., Kröner, N., Kotlarski, S., Kriegsmann, A., Martin, E., van Meijgaard, E., Moseley, C., Pfeifer, S., Preuschmann, S., Radermacher, C., Radtke, K., Rechid, D., Rounsevell, M., Samuelsson, P., Somot, S., Soussana, J.-F., Teichmann, C., Valentini, R., Vautard, R., Weber, B., Yiou, P., 2014. EURO-CORDEX: new high-resolution climate change projections for European impact research. Reg. Environ. Chang. 14, 563–578. https://doi.org/10.1007/s10113-013-0499-2.

Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J.R., Koricheva, J., Meurisse, N., Brockerhoff, E.G., 2017. Tree diversity drives forest stand resistance to natural disturbances. Curr. For. Rep. 3, 223–243. https://doi.org/10.1007/s40725-017-0064-1.

Jactel, H., Koricheva, J., Castagneyrol, B., 2019. Responses of forest insect pests to climate change: not so simple. Curr. Opin. Insect Sci. 35, 103–108. https://doi.org/10.1016/j.cois.2019.07.010.

Jactel, H., Moreira, X., Castagneyrol, B., 2021. Tree diversity and forest resistance to insect pests: patterns, mechanisms, and prospects. Annu. Rev. Entomol. 66, 277–296. https://doi.org/10.1146/annurev-ento-041720-075234.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Sci. Data 4, 170122. https://doi.org/10.1038/sdata.2017.122.

Karger, D.N., Schmatz, D.R., Dettling, G., Zimmermann, N.E., 2020. High-resolution monthly precipitation and temperature time series from 2006 to 2100. Sci. Data 7, 248. https://doi.org/10.1038/s41597-020-00587-y.

Karrer, G., Bassler-Binder, G., Willner, W., 2022. Assessment of drought-tolerant provenances of Austria's indigenous tree species. Sustainability 14, 2861. https://doi.org/10.3390/su14052861.

Körner, C., Basler, D., 2010. Phenology under global warming. Science 327, 1461–1462. https://doi.org/10.1126/science.1186473.

Kozlowski, T.T., Kramer, P.J., Pallardy, S.G., 1991. The physiological ecology of woody plants. Pallardy Academic Press, New York, Tokyo, London, Toronto, Sydney.

Ledermann, T., 2002. Ein Einwuchsmodell aus den Daten der österreichischen Waldinventur 1981–1996. Cent. Für Gesamte Forstwes. 119, 40–76.

Mantova, M., Herbette, S., Cochard, H., Torres-Ruiz, J.M., 2022. Hydraulic failure and tree mortality: from correlation to causation. Trends Plant Sci. 27 (4), 335–345. https://doi.org/10.1016/j.tplants.2021.10.003.

Martínez-Sancho, E., Gutiérrez, E., Valeriano, C., Ribas, M., Popkova, M.I., Shishov, V.V., Dorado-Liñán, I., 2021. Intra- and inter-annual growth patterns of a mixed pine-oak forest under Mediterranean climate. Forests 12, 1746. https://doi.org/10.3390/f12121746.

Maurer, S., Heinimann, H.R., 2020. Framework for assessing the windthrow risk to Norway spruce forests in Switzerland. Eur. J. Forest Res. 139 (2), 259–272. https://doi.org/10.1007/s10342-019-01251-w.

McDowell, N.G., 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. Plant Physiol. 155 (3), 1051–1059. https://doi.org/10.1104/pp.110.170704.

Menzel, A., Yuan, Y., Matiu, M., Sparks, T., Scheifinger, H., Gehrig, R., Estrella, N., 2020. Climate change fingerprints in recent European plant phenology. Glob. Chang. Biol. 26, 2599–2612. https://doi.org/10.1111/gcb.15000.

Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manag. 113, 109–123. https://doi.org/10.1016/S0378-1127(98)00419-8.

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

Müller, S., 1992. Natural acidophilous *Quercus* and *Pinus* forests in the northern Vosges, France, from a geographical perspective. J. Veg. Sci. 3, 631–636. https://doi.org/10.2307/3235830.

Nachtmann, G., 2006. Height increment models for individual trees in Austria depending on site and competition. Austrian J. For. Sci. 123, 199–222.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4 (2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.

Ozolinčius, R., Lekevičius, E., Stakėnas, V., Galvonaitė, A., Samas, A., Valiukas, D., 2014. Lithuanian forests and climate change: possible effects on tree species composition. Eur. J. For. Res. 133, 51–60. https://doi.org/10.1007/s10342-013-0735-9.

Pardos, M., Del Río, M., Pretzsch, H., Jactel, H., Bielak, K., Bravo, F., Brazaitis, G., Defossez, E., Engel, M., Godvod, K., Jacobs, K., Jansone, L., Jansons, A., Morin, X., Nothdurft, A., Oreti, L., Ponette, Q., Pach, M., Riofrío, J., Ruíz-Peinado, R., Tomao, A., Uhl, E., Calama, R., 2021. The greater resilience of mixed forests to drought mainly depends on their composition: analysis along a climate gradient across Europe. For. Ecol. Manag. 481, 118687 https://doi.org/10.1016/j.foreco.2020.118687.

Peters, R.L., Steppe, K., Pappas, C., Zweifel, R., Babst, F., Dietrich, L., Von Arx, G., Poyatos, R., Fonti, M., Fonti, P., Grossiord, C., Gharun, M., Buchmann, N., Steger, D. N., Kahmen, A., 2023. Daytime stomatal regulation in mature temperate trees prioritizes stem rehydration at night. New Phytol. 239, 533–546. https://doi.org/10.1111/nph.18964.

Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehbrecht, M., Bielak, K., Bravo, F., Ordóñez, C., Collet, C., Vast, F., Drössler, L., Brazaitis, G., Godvod, K., Jansons, A., de-Dios-García, J., 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., Ruíz-Peinado, R., del Río, M., 2020. Stand growth and structure of mixed-species and monospecific stands of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) analysed along a productivity gradient through Europe. Eur. J. For. Res. 139, 349–367. https://doi.org/10.1007/s10342-019-01233-y.

Pretzsch, H., Del Río, M., Arcangeli, C., Bielak, K., Dudzinska, M., Ian Forrester, D., Kohnle, U., Ledermann, T., Matthews, R., Nagel, R., Ningre, F., Nord-Larsen, T., Szeligowski, H., Biber, P., 2023. Competition-based mortality and tree losses. An essential component of net primary productivity. For. Ecol. Manag. 544, 121204 https://doi.org/10.1016/j.foreco.2023.121204.

Prokop, O., Kolář, T., Büntgen, U., Kyncl, J., Kyncl, T., Bošeľa, M., Choma, M., Barta, P., Rybníček, M., 2016. On the palaeoclimatic potential of a millennium-long oak ring width chronology from Slovakia. Dendrochronologia 40, 93–101. https://doi.org/10.1016/j.dendro.2016.08.001.

Puchałka, R., Koprowski, M., Gričar, J., Przybylak, R., 2017. Does tree-ring formation follow leaf phenology in Pedunculate oak (*Quercus robur* L.)? Eur. J. Forest Res. 136 (2), 259–268. https://doi.org/10.1007/s10342-017-1026-7.

Puchałka, R., Prislan, P., Klisz, M., Koprowski, M., Gričar, J., 2024. Tree-ring formation dynamics in *Fagus sylvatica* and *Quercus petraea* in a dry and a wet year. Dendrobiology 91, 1–15. https://doi.org/10.12657/denbio.091.001.

Rigling, A., Bräker, O., Schneiter, G., Schweingruber, F., 2002. Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Erico-Pinion in the Valais (Switzerland). Plant Ecol. 163 (105–121), 2002.

Roibu, C.-C., Sfecĺă, V., Mursa, A., Ionita, M., Nagavciuc, V., Chiriloaei, F., Leşan, I., Popa, I., 2020. The climatic response of tree ring width components of ash (*Fraxinus excelsior* L.) and common oak (*Quercus robur* L.) from Eastern Europe. Forests 11, 600. https://doi.org/10.3390/f11050600.

Romeiro, M.R.J., Eid, T., Antón-Fernández, C., Kangas, A., Trømborg, E., 2022. Natural disturbances risks in European Boreal and Temperate forests and their links to climate change – a review of modelling approaches. For. Ecol. Manag. 509, 120071 https://doi.org/10.1016/j.foreco.2022.120071.

Sáenz-Romero, C., Kremer, A., Nagy, L., Újvári-Jármay, É., Ducousso, A., Kóczán-Horváth, A., Hansen, J.K., Mátyás, C., 2019. Common garden comparisons confirm inherited differences in sensitivity to climate change between forest tree species. PeerJ 7, e6213. https://doi.org/10.7717/peerj.6213.

Salminen, H., Jalkanen, R., 2005. Modelling the effect of temperature on height increment of Scots pine at high latitudes. Silva Fenn. 39 (4), 497–508. https://doi.org/10.14214/sf.362.

Salomón, R.L., Peters, R.L., Zweifel, R., Sass-Klaassen, U.G.W., Stegehuis, A.I., Smiljanic, M., Poyatos, R., Babst, F., Cienciala, E., Fonti, P., Lerink, B.J.W., Lindner, M., Martinez-Vilalta, J., Mencuccini, M., Nabuurs, G.-J., van der Maaten, E., von Arx, G., Bär, A., Akhmetzyanov, L., Balanzategui, D., Bellan, M., Bendix, J., Berveiller, D., Blaženec, M., Čada, V., Carraro, V., Cecchini, S., Chan, T., Conedera, M., Delpierre, N., Delzon, S., Ditmarová, Ľ., Dolezal, J., Dufrêne, E., Edvardsson, J., Ehekircher, S., Forner, A., Frouz, J., Ganthaler, A., Gryc, V., Güney, A., Heinrich, I., Hentschel, R., Janda, P., Ježík, M., Kahle, H.-P., Knüsel, S., Krejza, J., Kuberski, Ł., Kučera, J., Lebourgeois, F., Mikoláš, M., Matula, R., Mayr, S., Oberhuber, W., Obojes, N., Osborne, B., Paljakka, T., Plichta, R., Rabbel, I., Rathgeber, C.B.K., Salmon, Y., Saunders, M., Scharnweber, T., Sitková, Z., Stangler, D.F., Stereńczak, K., Stojanović, M., Střelcová, K., Světlík, J., Svoboda, M., Tobin, B., Trotsiuk, V., Urban, J., Valladares, F., Vavrčík, H., Vejpustková, M., Walthert, L., Wilmking, M., Zin, E., Zou, J., Steppe, K., 2022. The 2018 European heatwave led to stem dehydration but not to consistent growth reductions in forests. Nat. Commun. 13, 28. https://doi.org/10.1038/s41467-021-27579-9.

Sanderson, B.M., Knutti, R., Caldwell, P., 2015. Addressing interdependency in a multimodel ensemble by interpolation of model properties. J. Clim. 28, 5150–5170. https://doi.org/10.1175/JCLI-D-14-00361.1.

Schwarz, J.A., Bauhus, J., 2019. Benefits of mixtures on growth performance of silver fir (*Abies alba*) and European beech (*Fagus sylvatica*) increase with tree size without reducing drought tolerance. Front. For. Glob. Change 2, 79. https://doi.org/10.3389/ffgc.2019.00079.

Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., Černý, J., Coll, L., Collet, C., Ehbrecht, M., Jansons, A., Nothdurft, A., Pach, M., Pardos, M., Ponette, Q., Reventlow, D.O.J., Sitko, R., Svoboda, M., Vallet, P., Wolff, B., Pretzsch, H., 2020. Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – site water supply and fertility modify the mixing effect. For. Ecol. Manag. 461, 117908 https://doi.org/10.1016/j.foreco.2020.117908.

Stimm, K., Heym, M., Uhl, E., Tretter, S., Pretzsch, H., 2021. Height growth-related competitiveness of oak (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* L.) under climate change in Central Europe. Is silvicultural assistance still required in mixed-species stands? For. Ecol. Manag. 482, 118780 https://doi.org/10.1016/j.foreco.2020.118780.

Strieder, E., Vospernik, S., 2021. Intra-annual diameter growth variation of six common European tree species in pure and mixed stands. Silva Fenn. 55 https://doi.org/10.14214/sf.10449.

Taeger, S., Zang, C., Liesebach, M., Schneck, V., Menzel, A., 2013. Impact of climate and drought events on the growth of Scots pine (*Pinus sylvestris* L.) provenances. For. Ecol. Manag. 307, 30–42. https://doi.org/10.1016/j.foreco.2013.06.053.

Thurm, E.A., Hernandez, L., Baltensweiler, A., Ayan, S., Rasztovits, E., Bielak, K., Zlatanov, T.M., Hladnik, D., Balic, B., Freudenschuss, A., Büchsenmeister, R., Falk, W., 2018. Alternative tree species under climate warming in managed European forests. For. Ecol. Manag. 430, 485–497. https://doi.org/10.1016/j.foreco.2018.08.028.

Toïgo, M., Vallet, P., Tuilleras, V., Lebourgeois, F., Rozenberg, P., Perret, S., Courbaud, B., Perot, T., 2015. 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.

Treml, V., Mašek, J., Tumajer, J., Rydval, M., Čada, V., Ledvinka, O., Svoboda, M., 2022. Trends in climatically driven extreme growth reductions of *Picea abies* and *Pinus sylvestris* in Central Europe. Glob. Chang. Biol. 28, 557–570. https://doi.org/10.1111/gcb.15922.

Venäläinen, A., Lehtonen, I., Laapas, M., Ruosteenoja, K., Tikkanen, O., Viiri, H., Ikonen, V., Peltola, H., 2020. Climate change induces multiple risks to boreal forests and forestry in Finland: a literature review. Glob. Chang. Biol. 26, 4178–4196. https://doi.org/10.1111/gcb.15183.

Vitasse, Y., Bottero, A., Cailleret, M., Bigler, C., Fonti, P., Gessler, A., Lévesque, M., Rohner, B., Weber, P., Rigling, A., Wohlgemuth, T., 2019. Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. Glob. Chang. Biol. 25, 3781–3792. https://doi.org/10.1111/gcb.14803.

Vospernik, S., 2021. Basal area increment models accounting for climate and mixture for Austrian tree species. For. Ecol. Manag. 480, 118725 https://doi.org/10.1016/j.foreco.2020.118725.

Vospernik, S., Sterba, H., 2015. Do competition-density rule and self-thinning rule agree? Ann. For. Sci. 72, 379–390. https://doi.org/10.1007/s13595-014-0433-x.

Vospernik, S., Heym, M., Pretzsch, H., Pach, M., Steckel, M., Aldea, J., Brazaitis, G., Bravo-Oviedo, A., Del Rio, M., Löf, M., Pardos, M., Bielak, K., Bravo, F., Coll, L., Černý, J., Droessler, L., Ehbrecht, M., Jansons, A., Korboulewsky, N., Jourdan, M., Nord-Larsen, T., Nothdurft, A., Ruiz-Peinado, R., Ponette, Q., Sitko, R., Svoboda, M., Wolff, B., 2023. Tree species growth response to climate in mixtures of *Quercus robur/Quercus petraea* and *Pinus sylvestris* across Europe - a dynamic, sensitive equilibrium. For. Ecol. Manag. 530, 120753 https://doi.org/10.1016/j.foreco.2022.120753.

Weiskittel, A.R., Hann, D.W., Kershaw, J.A., Vanclay, J., 2011. Forest Growth and Yield Modeling. Wiley-Blackwell, John Wiley & Sons Ltd., Oxford.

Welham, S.J., Gezan, S.A., Clark, S.J., Mead, A., 2014. Statistical Methods in Biology - Design and Analysis of Experiments and Regression. Chapman and Hall/CRC, New York.

Yuste, J.C., Konopka, B., Janssens, I.A., Coenen, K., Xiao, C.W., Ceulemans, R., 2005. Contrasting net primary productivity and carbon distribution between neighboring stands of *Quercus robur* and *Pinus sylvestris*. Tree Physiol. 25, 701–712. https://doi.org/10.1093/treephys/25.6.701.

Zweifel, R., Zimmermann, L., Zeugin, F., Newbery, D.M., 2006. Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. J. Exp. Bot. 57, 1445–1459. https://doi.org/10.1093/jxb/erj125.

Zweifel, R., Steppe, K., Sterck, F.J., 2007. Stomatal regulation by microclimate and tree water relations: interpreting ecophysiological field data with a hydraulic plant model 19. J. Exp. Bot. 58 (8), 2113–2131. https://doi.org/10.1093/jxb/erm050.

Zweifel, R., Rigling, A., Dobbertin, M., 2009. Species-specific stomatal response of trees to drought - a link to vegetation dynamics? J. Veg. Sci. 20, 442–454. https://doi.org/10.1111/j.1654-1103.2009.05701.x.