



Stability of tree increment in relation to episodic drought in uneven-structured, mixed stands in southwestern Germany



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ABSTRACT

Future increases in temperature and changes in precipitation patterns may negatively affect the growth performance of economically important tree species such as Norway spruce, which in the past have often been established and managed in monocultures. Structural diversity has been advocated as a silvicultural approach to increase resistance and resilience of forests to climate change extremes. Whether it promotes growth stability during and following drought years has not yet been analyzed.

We investigated stem growth reactions to the extreme drought of 2003 in 23 uneven-structured, mixed Norway spruce and Silver fir stands in southwestern Germany. Using linear mixed-effects models we analyzed the resistance and resilience of basal area increment in relation to species identity, drought intensity, tree size, competition, density and diversity.

Structural diversity, measured as variation in tree diameter at breast height, had no influence on increment stability during the extreme summer drought of 2003. Likewise, the effect of species diversity was weak and inconclusive. However, a higher presence of Silver fir in the mixture appeared to reduce increment stability in 2003 for both fir and spruce. Reducing competition through thinning counteracted this effect and promoted increment stability. Our findings indicate that the species identity of competitors in mixtures is a better predictor of stem growth reactions to drought than diversity. They support the conclusion that diversity does not generally increase stability to drought stress.

Silver fir consistently showed a substantially higher increment resistance and resilience than spruce. Its resistance increased with diminishing drought intensity, yet spruce reacted uniformly, manifesting a low resistance across the whole drought intensity gradient. Spruce did not regain pre-drought growth levels within the first three years after drought, whereas fir did. We conclude that fir may be able to act as a silvicultural alternative to spruce under changing climatic conditions, given appropriate sites and thinning regimes.

Considering the expected increase in drought intensity and frequency in the 21st century, understanding species interactions at the local scale emerges as an essential prerequisite for developing resilient forest stands.

1. Introduction

The late 20th and early 21st century represents probably the warmest period since 1500 or longer (Luterbacher et al., 2004). Looking ahead, the 21st century is expected to bring a rise in average temperatures, as well as an increase in the frequency and duration of drought events (IPCC, 2013). As a result, the adaptation potential of existing forests, as well as the risks of large-scale forest mortality and substantial shifts in species' distribution ranges have increasingly attracted the attention of the scientific community (Allen et al., 2010; McDowell and Allen, 2015). The long-term character of the expected

climatic changes has prompted discussions regarding silvicultural pathways towards more resistant and resilient forest ecosystems in the future (Puettmann, 2011; O'Hara and Ramage, 2013; Brang et al., 2014; Puettmann et al., 2015; Pretzsch et al., 2017).

In the context of climate change adaptation, it is essential to gauge the current drought vulnerability of different forest types and species. For example, given its fast growth and favorable wood properties, Norway spruce (*Picea abies* (L.) H. Karst.; “spruce”) is an economically important tree species in Europe which has often been managed in monocultures. In Germany spruce covers 25% of the forest area, represents 33% of the growing stock volume and is the staple species in

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forestry and the timber industry (BMEL, 2014). However, spruce has been found to be rather sensitive to drought (van der Maaten-Theunissen et al., 2012; Zang et al., 2012; Boden et al., 2014; Zang et al., 2014; Vitali et al., 2017) and drought-related pest risks such as bark beetles. Additionally, spruce has often been planted outside its natural distribution range, a factor which most likely increases its vulnerability to environmental stress (Boden et al., 2014). In consequence, future increases in temperature and changes in precipitation patterns may severely impact spruce stands by reducing growth and increasing mortality. It is expected that even under moderate climate change scenarios spruce may become unsuitable in large areas of its current, human-influenced distribution range (Hanewinkel et al., 2013).

There appears to be a relatively narrow range of silvicultural options that may help mitigate drought vulnerability of existing forests. Among them, heavy thinning has been found to reduce drought sensitivity in general – and in spruce stands in particular (Kohler et al., 2010; Sohn et al., 2013; Sohn et al., 2016b). Thinning appears to stabilize stem growth reactions especially by promoting increment recovery immediately after drought (Kohler et al., 2010; Sohn et al., 2013; Sohn et al., 2016b). Nevertheless, heavy thinning has been found to stabilize drought responses in the short-term, yet little is known about its long-term benefits and risks in relation to severe episodic droughts (D'Amato et al., 2013; Sohn et al., 2016a).

Mixing tree species with complementary traits has been suggested to promote ecological and economic resilience (Brang et al., 2014; Pretzsch et al., 2014). Both silvicultural approaches, reducing stand density through thinning and increasing species diversity, represent areas of active research, yet their track record for effectively mitigating drought sensitivity of trees and forests is rather inconsistent. In fact, there seems to be no general pattern for the interaction between tree species diversity and the drought response of trees and forests (Forrester et al., 2016; Bauhus et al., 2017). Empirical studies have found different results in this respect, with the mixing of species leading to positive (Lebourgeois et al., 2013; Pretzsch et al., 2013; Río et al., 2014; Gazol and Camarero, 2016), negative (Martínez-Vilalta et al., 2012; Grossiord et al., 2014; Jucker et al., 2014) or no effects (Klos et al., 2009; Merlin et al., 2015) on growth stability. Furthermore, many appraisals are based on experiments with a restricted spatial extent, which limits the transferability of observed patterns to a larger population (Bauhus et al., 2017).

While recognizing that compositional diversity and structural diversity are intertwined, increasing the latter has also been recommended as a potential long-term approach to promote ecological resilience (O'Hara and Ramage, 2013; Brang et al., 2014). In contrast to the steadily growing number of drought sensitivity assessments in mixed forests (Lebourgeois et al., 2013; Jucker et al., 2014; Forrester et al., 2016; Metz et al., 2016; Thurm et al., 2016; Vitali et al., 2017), few studies have tested the relationship between structural diversity and drought sensitivity so far (Gazol and Camarero, 2016).

In the current study, we used a data set displaying wide diversity gradients in managed, conifer-dominated mixed stands to investigate to which extent stem growth responses might be influenced by variations in structural diversity, species diversity and composition (i.e. the latter based on the relative representation of fir or spruce). Mainly admixed with spruce in these stands, Silver fir (*Abies alba* Mill.; “fir”) is a species known to be more tolerant to shade and drought than spruce (Hartl-Meier et al., 2014; Zang et al., 2014; Vitali et al., 2017). As a result, we expected different species responses to drought.

Recent studies revealed that when trees with different sizes co-occur within a stand, large trees tend to be more severely affected by drought in terms of stem growth and mortality than smaller trees (McDowell et al., 2011; Bennett et al., 2015; McDowell and Allen, 2015). Given the high variability of tree sizes in our study stands, we expected to also detect such a size-related sensitivity to drought.

Our leading hypothesis (i) was that diversity promotes stem growth

Table 1

General site and stand information for the experimental plots used in the current analysis. STS and GS stand for the single-tree selection and group shelterwood management treatments, respectively. Stand basal area values refer to residual basal area after the last thinning intervention preceding 2003. The attributes tree age in 2003 and tree diameter under bark in 2003 are based on a subset of tree ring chronologies originating from stem disks (N = 183).

Attribute	STS	GS
Number of sites/plots	2/2	6/21
Plot area (ha), Mean	0.8	0.25
Elevation (m), Min-Max	745–1003	518–1042
Mean annual temperature 1910–2010 (°C), Min-Max	5.4–6.2	4.9–7.8
Annual precipitation sum 1910–2010 (mm), Min-Max	1688–1755	922–1977
Mean annual temperature 2003 (°C), Min-Max	6.5–7.3	6.1–8.9
Annual precipitation sum 2003 (mm), Min-Max	1254–1262	728–1462
Stand basal area (m ² ·ha ⁻¹) preceding 2003, Min-Max	29–31	12–56
No. of tree ring chronologies from disks/cores	14/0	169/42
Tree age in 2003, Min-Max	62–156	93–155
Tree diameter under bark in 2003 (cm), Min-Max	22.0–71.4	24.2–73.8

stability during and following drought. In other words, with other things being equal, we expected higher structural diversity and species diversity to stabilize stem responses to drought. We also tested the following hypotheses: (ii) fir and spruce differ in their average stem growth sensitivity to drought, and their responses are mediated by drought intensity; (iii) larger trees show larger relative stem growth reductions during drought; (iv) diminishing competition through thinning reduces stem growth sensitivity to drought.

2. Material and methods

2.1. Study sites

Our study sites are located in southwestern Germany and are dominated by fir and spruce. Other species present in the stands are European beech (*Fagus sylvatica*), sycamore maple (*Acer pseudoplatanus*), and, less frequently, European ash, Norway maple, Scots pine and pioneer species. The eight study sites originate from two long-term experiments managed by the Forest Research Institute of Baden-Württemberg (Table 1): ‘single-tree selection’ and ‘group shelterwood’, which have already been described elsewhere (Puettmann et al., 2009; Forrester et al., 2013; Dănescu et al., 2016; Dănescu et al., 2017). Although the study sites are located along an elevational gradient, most stands can be classified as mixed-mountain forests. Across sites, annual precipitation sums range from 900 to 2000 mm, and a temperate to cool-temperate climate is characteristic.

Long-term programs for thinning interventions, with a large variation in thinning intensities across plots, have led to a wide range of growing conditions and structural heterogeneity. The plots have been surveyed repeatedly at intervals of usually five years and harvesting operations were always synchronized with the survey schedule in order to obtain accurate information about pre-harvest and post-harvest stand conditions. Tree diameter at breast height (*dbh*) was recorded on two perpendicular directions to the nearest 1 mm for all trees larger than 5 cm. Only trees with *dbh* > 6.5 cm were considered for variable calculation. If trees died or disappeared between subsequent surveys, only their last recorded living dimensions were taken into account. In summary, plots belonging to these particular experiments were selected for several reasons: (i) they offer an excellent information base owing to long-term monitoring; (ii) they cover a wide range of vertical and horizontal stand structures due to the application of different harvesting regimes; (iii) they cover a relatively wide environmental gradient.

Table 2

Summary of a subset of variables tested when modeling resistance and resilience (analysis with distance-independent predictors: 8 sites, 23 plots, 225 observations – from which 80 pertained to spruce and 145 to fir). SD indicates standard deviation and *bai* stands for basal area increment. Values for *PDSI*, *Relwat_{we}* and *Tratio* represent averages over the growing season (May–September).

Attribute name and description	Spruce				Fir			
	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
Relative increment responses (response variables)								
<i>resistance</i> = <i>bai_{drought}</i> / <i>bai_{predrought}</i>	0.62	0.18	0.28	1.16	0.89	0.2	0.48	1.48
<i>resilience</i> = <i>bai_{postdrought}</i> / <i>bai_{predrought}</i>	0.75	0.24	0.37	1.58	0.95	0.26	0.41	1.79
Absolute tree increment								
<i>bai_{predrought}</i> = pre-drought <i>bai</i> (cm ² ·yr ⁻¹)	31.6	18.06	1.4	79.3	43.2	25.8	6.5	150
<i>bai_{drought}</i> = <i>bai</i> in 2003 (cm ² ·yr ⁻¹)	18.8	11.37	1	53.4	36.7	20.0	3.4	113.9
<i>bai_{postdrought}</i> = post-drought <i>bai</i> (m ² ·yr ⁻¹)	23.4	14.25	0.9	58.9	40.5	24.6	3.6	121.7
Drought stress level								
<i>Elevation</i> (m)	789	181	518	1042	794	183	518	1042
<i>Slope</i> = slope (%)	21.9	14.92	4.67	52	21.3	14.6	4.67	52
<i>PDSI</i> = Palmer Drought Severity Index	-2.62	0.5	-3.41	-2	-2.62	0.51	-3.41	-2
<i>Relwat_{we}</i> = rel. plant-available water in the root area	0.45	0.22	0.09	0.78	0.45	0.21	0.09	0.78
<i>Tratio</i> = transpiration (<i>T</i>) ratio (current <i>T</i> /potential <i>T</i>)	0.79	0.18	0.5	1	0.78	0.17	0.5	1
Tree size and competitive status								
<i>sd</i>								
<i>d_{ub}</i> = tree diameter under bark (cm)	45.8	10.15	22.0	71.4	45.8	9.5	19.7	73.8
<i>dom</i> = tree dominance index	0.52	0.29	0.01	1	0.53	0.29	0.02	1
<i>dom_{fir}</i> = tree dominance relative to fir individuals	0.49	0.32	0	1	0.52	0.29	0.02	1
Stocking and thinning								
<i>BA</i> = total stand basal area after thinning (m ² ·ha ⁻¹)	29.2	9.63	12.3	44.1	30.9	11.5	12.3	55.6
<i>BA_{rem_5_per}</i> = % removed basal area in the last 5 years	18.9	11.17	0	53.3	18.2	11.7	0	53.3
<i>BA_{fir}</i> = absolute fir basal area at the stand level (m ² ·ha ⁻¹)	14.4	6.25	4.7	28.8	16.3	9.73	4.7	47.8
<i>pBA_{fir}</i> = proportion of fir basal area from <i>BA</i>	0.5	0.16	0.24	0.8	0.51	0.17	0.24	0.86
Species diversity								
<i>H_{species}</i> = Shannon diversity index	0.84	0.15	0.55	1.09	0.83	0.17	0.48	1.09
<i>E_{species}</i> = standardized <i>H_{species}</i> (evenness)	77.1	17.66	37.0	99.8	76.3	19.0	38.0	99.8
<i>R_{species}</i> = number of species (richness)	3.38	1.36	2	7	3.38	1.36	2	7
Structural diversity								
<i>Gini_{dbh}</i> = Gini coefficient of dbh	0.44	0.22	0.18	0.78	0.42	0.22	0.18	0.78
<i>Like_J</i> = index of similarity to a J – shaped dbh distribution curve	3.14	1.75	0	6.4	2.82	1.7	0	5.6
<i>Skew_{dbh}</i> = skewness of dbh distribution	0.38	0.97	-1.84	1.81	0.24	0.99	-1.84	1.81
<i>VarCoef_{dbh}</i> = coefficient of variation of dbh distribution	51.0	32.73	17.3	111.65	47.7	32.4	17.3	111.7

2.2. Tree ring data

Tree ring data were derived from stem disks and increment cores collected at breast height (1.3 m) (Table 1). Stem disks were obtained destructively at different points in time from trees harvested during the experiment treatments, whereas all increment cores were collected in 2014. For each tree, two cores were extracted in perpendicular directions (N, W).

Ring-widths were measured to the closest 0.1 mm (on eight radii for stem disks) and resulting chronologies were cross-dated based on known pointer years and averaged using a quadratic mean for each tree and year. Ring-width values were transformed to basal area increment (*bai* in cm²) assuming concentric annual growth-rings. Since chronologies originating from stem disks were complete in their vast majority, tree ring widths could be used to reconstruct tree diameter when calculating *bai*. In contrast, for incomplete chronologies (tree rings closest to the stem center missing for three stem disks and possibly all increment cores) we applied a backward *bai* calculation from measured *dbh* values, while also considering bark thickness (Appendix A in Supplementary Material).

Different approaches for detrending or standardizing tree ring chronologies are commonly used in dendroecological studies (Speer, 2010), as they serve to remove the influence of low-frequency patterns in tree ring series (age- and size-related trends). However, such detrending techniques carry the risk of unintentionally removing valuable environmental signals (Yue et al., 2011) and introduce more uncertainty into the final models. Although we analyzed trees from different canopy positions, sufficient data were available to explicitly

account for the past competitive status of individual trees. Furthermore, considering the minimum tree ages in our data (Table 1), there is little risk of confounding with juvenile trends. Finally, other drought analyses carried out in the same region found similar results when comparing raw and detrended data (Vitali et al., 2017). As a result, we did not detrend or standardize tree ring chronologies in our analysis.

2.3. Selection of drought years and proxies of drought intensity

As discussed by Sohn et al. (2016a), there is no standard procedure for identifying drought events in tree-ring data and all currently available approaches involve limitations and trade-offs. A simple approach is to select drought events solely based on regional climatic records (e.g. Thurm et al., 2016), yet this bears a substantial risk of misclassifying drought years (e.g. situations when particular sites deviate from regional drought). The Palmer Drought Severity Index, a commonly used meteorological drought index, has been shown to overestimate long-term drought frequency (Sheffield et al., 2012). Such misclassification issues can lead to altering the strength and direction of key relationships, e.g. between thinning intensity and stem growth response to drought (Sohn et al., 2016a). A second approach takes into account only years with strong reductions in tree ring widths, yet bears the statistical disadvantage that the same variable is used for sample generation and as a response in the ensuing analysis (Sohn et al., 2016a). Moreover, mast years or insect defoliations can also cause growth depressions (Sohn et al., 2016a) and thus lead to misclassified drought years.

Tolerating misclassified years in a drought analysis may dilute

ecological signals that emerge only during periods with actual soil water deficit or lead to spurious results. There is evidence that short-term fluctuations in resource availability may alter the mode of plant competition by reducing competition asymmetry (Zang et al., 2012) or even shift the dominant type of plant interactions from competition towards complementarity/facilitation (Pretzsch et al., 2013). Since our study aimed to test a diversity-stability hypothesis, it was essential to gauge tree responses only to actual drought stress. Therefore, using both drought stress indices and increment data, we confirmed the presence of two major and well-known drought events in our data: 1976 and 2003 (Fig. B1 in Supplementary Material). The impacts of these two extreme drought events in central Europe have been well documented (Bréda et al., 2006; Lebourgeois et al., 2013; Metz et al., 2016; Vitali et al., 2017).

In our data set, the diversity gradients differed markedly between the two years and the information basis for 1976 was considerably weaker than for 2003 (the ‘group shelterwood’ experiment had only commenced in 1980). Furthermore, using the 1976 drought in our analysis would have increased the risk of diluting relevant ecological signals due to juvenile trends (see minimum tree ages in 2003 in Table 1). Consequently, we focused our analysis on stem growth responses to the extreme drought of 2003, which likely featured the hottest summer of the past 500 years (Luterbacher et al., 2004).

We used proxies of drought stress intensity (Table 2) that were either simple meteorological indices such as the Palmer Drought Severity index (*PDSI*) and its self-calibrated version or more complex indices obtained as output from the hydrological model LWF-Brook90 (Wilpert et al., 2016) (Appendix B in Supplementary Material). One of these indices was the transpiration ratio (*Tratio*), calculated as the ratio between current and potential evapotranspiration. All indices were calculated over a fixed period corresponding to the growing season (May to September). As several studies found growth responses to drought to be dependent on elevation (Desplanque et al., 1999; Lebourgeois et al., 2010; van der Maaten-Theunissen et al., 2012) or slope (Klos et al., 2009), we also considered these variables in our analysis. Furthermore, we tested a selection of potential solar radiation indices (intensity and duration) for the hydrological summer (May–October) (Appendices F and G in Supplementary Material), which rely heavily on local topographic information (Dănescu et al., 2017).

2.4. Indices of stem growth responses to drought

We quantified stem growth responses to drought using the indices of resistance and resilience (*sensu* Lloret et al., 2011), which were derived from basal area increments series. Resistance quantifies the magnitude of increment reduction during drought, relative to pre-drought increment levels, whereas resilience is the ratio between the post-drought and the pre-drought increment levels (Table 2). The pre-drought and post-drought periods were assigned a length of three years.

When calculating resistance and resilience it is customary to consider relatively short pre-drought and post-drought periods (e.g. 1–3 years) so as to avoid distortions that may be caused by recurrent drought events (Anderegg et al., 2015) or other anomalies such as mast years (Vitali et al., 2017). A global analysis of stem growth recovery after drought indicated a general recovery time of 1–4 years, with slightly shorter recovery intervals (1–2 years) in non-arid sites (Anderegg et al., 2015), which supports the use of these relatively short time windows. The 3-year post-drought period considered in our study may have also included a mast year in 2006 for conifers in southeastern Germany (Sohn et al., 2016b; Vitali et al., 2017). In order to gauge its influence on our results we refitted the final models using response variables based on pre-drought and post-drought periods with lengths of 1 and 2 years (i.e. which exclude 2006) and checked the significance as well as the signs and magnitudes of the estimated coefficients (Appendix C in Supplementary Material).

2.5. Data analysis

We pooled the available data for fir and spruce together and used *species* as a categorical predictor in two sets of analyses of resistance and resilience. In the main set of regressions we considered distance-independent covariates for diversity, composition and competition (i.e. plot-level estimates). In the second set of regressions we calculated distance-dependent covariates for competition, composition and diversity within a circular neighborhood of 8 m radius around each target tree. Here we excluded from the analysis 6 observations belonging to trees without neighbors. The chosen dimension of the neighborhood is not optimal (*cf.* Puettmann et al., 2009), yet it was imposed by the necessity to strike a balance between including a sufficient number of competitors around a target tree and maintaining a large enough sample size. In order to avoid edge effects in the distance-dependent analyses, trees located within 8 m distance from the plot border were allowed to act as neighbors but not as target trees. As a result, the sample sizes differed greatly between distance-independent analyses ($N = 225$) and distance-dependent ones ($N = 121$). Given the exploratory nature of the analysis with distance-dependent predictors and since its conclusions generally converged with those from our main, distance-independent analysis, the latter will be emphasized in the results and discussion sections.

In order to calculate tree and stand-level predictors of stem growth responses to drought we considered for each plot the most recent stand inventory date prior to 2003 (0–5 years). The calculated predictors of resistance and resilience were grouped into several categories: tree size and competitive status, stocking and thinning, composition, species diversity, structural diversity and drought stress intensity (Table 2; Supplementary Material Table D1). Given that inventories and thinning were synchronized, competition and stocking related candidate predictors always reflect the post-thinning stand situation.

Several proxies for tree size and competitive status were considered: diameter under bark (d_{ub}), the mean basal area increment during the pre-drought period ($bai_{predrought}$) and a tree dominance index ($dom = 1 - bal / BA$, where bal is the cumulated basal area of larger trees and BA is stand basal area). We also considered dominance in relation to only fir (dom_{fir}) or only spruce individuals: instead of bal and BA we used the cumulated basal area of only larger fir trees or only larger spruce trees and the stand basal area attributed to either fir or spruce, respectively.

Proxies of stocking and thinning intensity in the distance-independent analysis were the total stand basal area (BA) and the relative removals of basal area in the last five years ($BA_{rem_5_per}$). We also considered the absolute and relative contributions of fir and spruce to total stand basal area (abbreviations fir: BA_{fir} and pBA_{fir}). For spatially-explicit analyses, we calculated more precise competition indices, which beyond the size and species identity of competitors also consider distances between target-trees and neighbors (e.g. the Hegyi index (Hegyi, 1974)).

Measures of compositional diversity were species richness ($R_{species}$) and the Shannon indices for species diversity ($H_{species}$) and evenness ($E_{species}$). In the analysis with distance-dependent predictors only species diversity and richness within local neighborhoods were considered.

Structural diversity was quantified based on the diameter distribution. In distance-independent analyses the coefficient of variation ($VarCoef_{dbh}$), the Gini coefficient ($Gini_{dbh}$) (Weiner and Solbrig, 1984) as well as skewness ($Skew_{dbh}$) and $LikeJ$ – an index of similarity to a J-shaped dbh distribution (Hanewinkel et al., 2014) – were calculated while considering all trees in the stand as neighbors. In distance-dependent analyses, we calculated the coefficient of variation and the Gini index within tree neighborhoods.

Our data generally met the assumptions of linear regression except for the assumption of independence since multiple trees were present in a plot and plots were nested within sites. Therefore, we used the

framework of linear mixed-effects models for modeling resistance and resilience. Random effects mitigate nested data structures with inherently correlated errors. This modeling approach was implemented using the package *nlme* (Pinheiro and Bates, 2000) in R 3.1.2 (R Core Team, 2014):

$$y_{jk} = X_{jk} \cdot \beta + Z_j \cdot b_j + \varepsilon_{jk}$$

$$b_j \sim N(0, \sigma_j^2); \varepsilon_{jk} \sim N(0, \sigma_{jk}^2) \quad (1)$$

where y_{jk} is the response variable, with j indexing experimental plots and k individual tree observations. X_{jk} and Z_j are design matrices containing fixed and random effects, respectively; β , b are parameter vectors for fixed and random effects; σ are standard deviations.

In order to not overfit a model with random effects we tested different random effect specifications while maintaining a large number of non-collinear fixed predictors in the same model (results not shown). Fixed predictors tended to be highly collinear (Supplementary Material Fig. G1) within their respective groups (i.e. tree size and competitive status, stocking and thinning, species diversity, structural diversity and drought stress intensity). Therefore, we tested all of them for significance, yet from a certain group of correlated predictors we retained in the final model only the one which led to the largest reduction in the Akaike information criterion for small datasets, AICc. We tested interactions between the categorical variable *species* and all other candidate predictors. Model selection with AICc is demonstrated in Appendix F.

We tested the significance of random and fixed effects with likelihood-ratio tests and conditional F-tests, respectively, while using the “Restricted Maximum Likelihood” estimation method (Pinheiro and Bates, 2000). Effects were considered significant when $p < 0.05$. When selecting models using AICc, we used the “Maximum Likelihood” estimation method (Pinheiro and Bates, 2000). We checked model assumptions graphically using quantile-quantile plots and residual plots.

3. Results

3.1. Compositional and structural diversity did not influence stem growth stability

Structural diversity did not influence stem growth responses to drought. Furthermore, the evidence of species diversity effects on stem growth responses was weak and inconsistent. A species diversity effect was observed only in one model with distance-dependent predictors where the Shannon diversity index in the neighborhood ($H_{species_nt}$) was negatively related to resilience (Supplementary Material Table D2 and Fig. D6). However, this effect lost its significance when varying the length of the pre-drought and post-drought periods (Appendix C in Supplementary Material), and no similar effect was apparent in any of the models with distance-independent predictors.

3.2. Fir was more resistant and resilient than spruce

Irrespective of the response variable and subset of the data considered, the categorical variable *species* had the highest explanatory power across all models (results not shown). Fir consistently showed a much higher resistance and resilience than spruce (Fig. 1; Table 3). In fact, spruce did not regain pre-drought growth levels within the first three years after 2003, whereas fir did. In summary, stem growth during the 2003 drought was much more sensitive in spruce than in fir. Models with distance-dependent predictors led to identical conclusions (Supplementary Material Appendix D).

Fir and spruce showed different patterns of resistance across drought intensity gradients. Fir’s resistance increased with diminishing drought intensity (i.e. higher values of *Tratio*), whereas spruce displayed a uniformly low resistance across the whole range of the drought intensity gradient (Fig. 2). The interaction between species identity and drought intensity was an influential predictor of resistance in both

distance-dependent and independent analyses (Fig. 2 and Supplementary Material Fig. D2). In contrast, none of the considered drought intensity proxies influenced resilience (Supplementary Material Table F2).

3.3. Sensitivity to drought was size-dependent

Pre-drought (i.e. 3 years) increment was the best size-related predictor of stem growth resistance to drought (Supplementary Material Tables F1). Trees with high increment rates before drought showed a lower resistance during drought than slower growing trees (Fig. 3; Supplementary Material Fig. D3).

In contrast, when inspecting the linear relationship between absolute pre-drought increment and tree size (Fig. 4 and Supplementary Material Fig. G1), the largest trees in the stand clearly displayed the fastest growth rates both before as well as during drought. Nevertheless, the discrepancy between increment rates before and during drought increased with tree size (Fig. 4), thus leading to the same conclusion as when regressing resistance on pre-drought increment (Table 3 and Fig. 3). Drought impacts on stem growth were clearly size-dependent for both species, with larger trees showing higher increment fluctuations.

3.4. Higher (fir) competition reduced stem growth stability

Increment resistance and resilience decreased as the level of competitive pressure increased at both stand and neighborhood levels. Competition-related variables were selected in all models and consistently indicated that higher competition destabilizes stem growth during drought (Supplementary Material Tables F1 and F2). Importantly, proxies of fir competitive pressure were selected in many models as the best competition-related variables. Therefore, higher proportions of fir in the mixture appeared to have a particularly destabilizing effect for trees of both species.

3.4.1. Resistance

When using only distance-independent variables to characterize competition, both the fir proportion of stand basal area (pBA_{fir}) and the absolute basal area of fir trees (BA_{fir}) were statistically significant and negatively related to resistance for both fir and spruce. However, the proportion of fir (pBA_{fir}) led to a larger decrease in AICc (Supplementary Material Table F1) and was selected in the final model (Table 3, Fig. 5). In contrast, the Hegyi index was the best competition-related predictor of resistance in the model with distance-dependent predictors (Supplementary Material Table D2 and Fig. D4).

3.4.2. Resilience

The absolute fir basal area at the stand level (BA_{fir}) was strongly negatively related to the resilience of increment for both spruce and silver fir in the model with distance-independent competition (Fig. 5). Although other similar variables were also significant (e.g. BA , pBA_{fir}), BA_{fir} led to the largest decrease in AICc in this case (Supplementary Material Table F2). A strong negative relationship was also apparent between resilience and fir basal area in the neighborhood (BA_{fir_nt}) (Supplementary Material Table D2 and Fig. D8). Although other similar predictors were significant (e.g. pBA_{fir_nt}), the model containing BA_{fir_nt} displayed the lowest AICc (results not shown). Additionally, resilience showed a weak, yet significant negative relationship with tree dominance in relation to fir individuals (dom_{fir}) in both distance-dependent and independent analyses (Fig. 6 and Supplementary Material Fig. D7).

Variables related to stocking after thinning were consistently selected in the models for resistance and resilience. They appeared to provide more effective predictors of stem growth reactions to drought than proxies of thinning intensity (i.e. $BA_{rem_5_per}$) (Supplementary Material Tables F1 and F2). However, considering that stand basal area

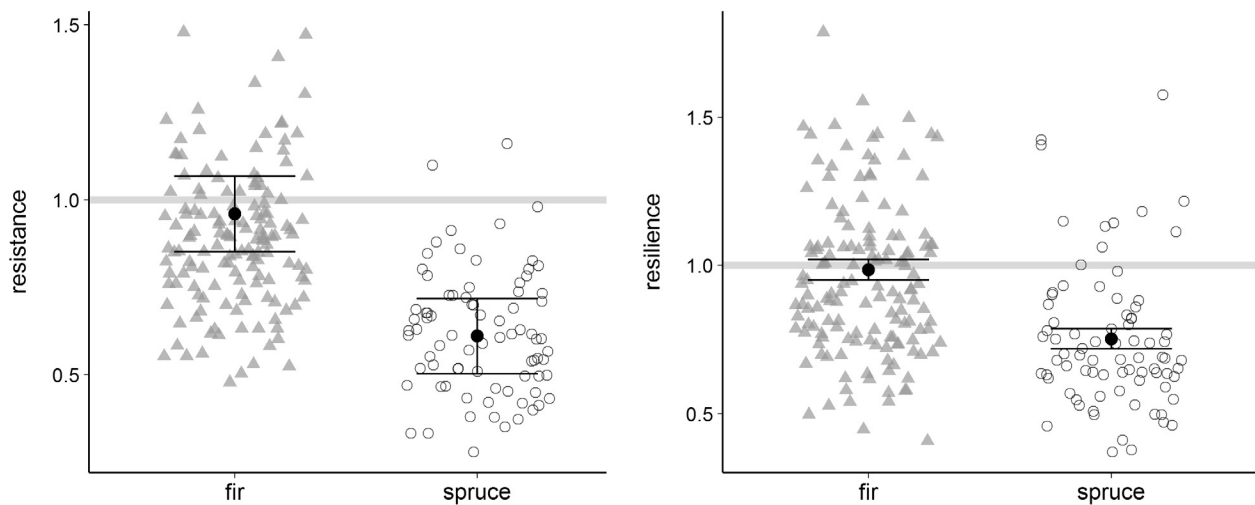


Fig. 1. Plots illustrating differences in resistance and resilience between fir and spruce in the analysis with distance-independent predictors. Other model covariates were kept fixed at their median values. Black dots indicate mean species responses (± 1 standard error). The reference gray horizontal lines indicate a situation with no tree response to drought for resistance and a situation with identical pre-drought and post-drought increments for resilience.

Table 3

Summaries of final models for resistance and resilience using distance-independent predictors (N = 225). Abbreviations: *BA_fir*, total fir basal area at the stand level; *bai_pre-drought*, absolute basal area increment in the pre-drought period; *pBA_fir*, proportion of fir in the stand basal area; *dom_fir*, tree dominance relative to fir individuals; *Tratio*, transpiration ratio. Coefficient estimates are followed by standard errors enclosed in parentheses. All displayed coefficients were statistically significant. Marginal R^2 considers only the contribution of fixed effects; conditional R^2 considers the contribution of both fixed and random effects.

	Resistance	Resilience
Estimates for fixed effects		
intercept	0.751 (0.094)	0.959 (0.064)
species (fir)	-0.115 (0.107)	0.232 (0.034)
<i>Tratio</i>	0.0734 (0.110)	-
<i>pBA_fir</i>	-0.278 (0.099)	-
<i>bai_pre-drought</i>	-0.002 (0.001)	-
species (fir): <i>Tratio</i>	0.593 (0.141)	-
<i>dom_fir</i>	-	-0.146 (0.052)
<i>BA_fir</i>	-	-0.010 (0.003)
Estimates for variance components		
Plot random effect	0.038	0.091
Residual	0.161	0.219
Explained variance		
R^2 marginal	0.50	0.21
R^2 conditional	0.53	0.32

and thinning intensity were strongly negatively correlated (Supplementary Material Fig. G1), it is safe to assume that the selected variables also act as surrogates for thinning.

3.5. Considering tree distances and shorter drought reference periods

The analyses with distance-independent and distance-dependent predictors led to similar results (Table 3 and Supplementary Material Table D2) and interpretations.

Fixed effects in the resistance and resilience models with distance-independent predictors explained respectively 50% and 21% of the variation in the responses (Table 3). In spite of the difference in sample size fixed effects in models with distance-dependent predictors explained similar amounts of variation in resistance and resilience (49% and 21%, respectively) (Supplementary Material Table D2). Our models explained a higher proportion of variation in resistance than in resilience. Furthermore, across all models the random plot effect was significant and organized 2–19% of the variation in the responses, a proportion invariably smaller than that attributed to fixed effects.

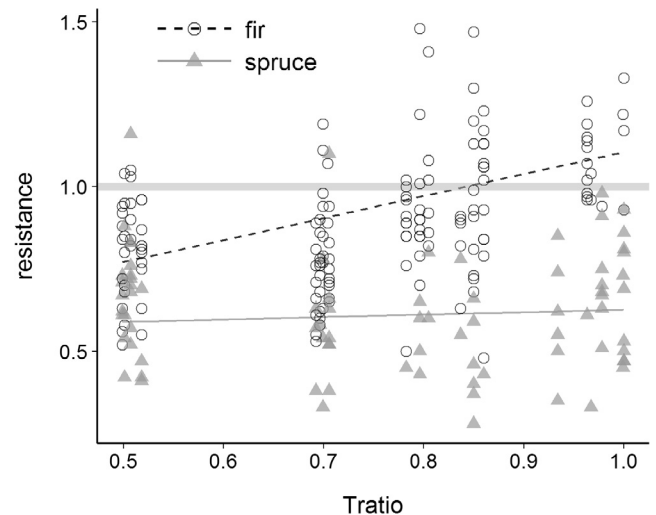


Fig. 2. Partial effect plot illustrating the relationship between resistance and the transpiration ratio (*Tratio*) in the analysis with distance-independent predictors. Other covariates were kept fixed at their median values. Higher *Tratio* values indicate higher drought intensity. The reference gray horizontal line indicates a situation with no tree response to drought.

When shortening the length of pre-drought and post-drought periods to one or two years, most variables from the final models maintained their statistical significance as well as the magnitudes and the direction of their influence (Appendix C in Supplementary Material). Shortening these reference periods appeared to slightly increase the proportion of explained variance. This outcome indicates a rather robust response pattern which was neither substantially biased by our choice of 3 years for the length of the pre- and post-drought period nor the inclusion of the mast year 2006.

4. Discussion

4.1. Composition but not diversity influences growth reactions to extreme drought

In the analyzed fir-spruce dominated mixtures we found no obvious relationships between stem growth responses to the extreme summer drought of 2003 and diversity metrics addressing either structural diversity, Shannon diversity, evenness or richness. In contrast, the

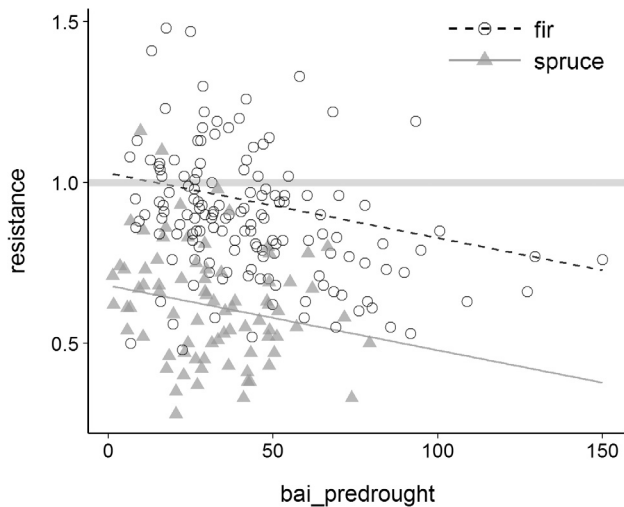


Fig. 3. Partial effect plot illustrating the relationship between resistance and pre-drought (3 years) basal area increment (*bai_predrought*) in the analysis with distance-independent predictors. Other covariates were kept fixed at their median values. The reference gray horizontal line indicates a situation with no tree response to drought.

composition of the mixture clearly influenced responses to drought: in particular, a higher proportion of fir in the mixture amplified growth sensitivity for both species (see Section 4.4 for a discussion concerning only competition effects). These findings do not support the widespread assumption of a general relationship between diversity and ecological stability, which is quite commonly voiced e.g. in close-to-nature forestry (Bauhus et al., 2013). Increasing tree species diversity may not necessarily improve drought tolerance and some authors even consider a potential trade-off between increasing tree species diversity to promote certain ecosystem functions and reducing resistance to drought stress (Bauhus et al., 2017). Our conclusions are, however, only valid for spruce-fir mixtures and their diversities.

Some studies found that mixing fir with species such as European beech (*Fagus sylvatica*; “beech”), spruce or Scots pine (*Pinus sylvestris*) increased fir stem growth stability during drought. For example, fir in the central Spanish Pyrenees showed a higher resistance to drought when located in the neighborhood of beech and Scots pine (Gazol and Camarero, 2016). Similarly, a study in the Vosges mountains (France) indicated that fir stem growth stability during drought was enhanced when fir was mixed with beech or spruce (Lebourgeois et al., 2013). This effect on fir was stronger at lower elevations and also more

poignant in mixtures with the more functionally-divergent beech than when mixed with spruce (Lebourgeois et al., 2013). However, neither of these two studies investigated the drought reactions of the other species admixed with fir. This is unfortunate as it would have helped clarify if fir was benefiting at the expense of heterospecific neighbors. A recent study in fir-spruce-Douglas-fir (*Pseudotsuga menziesii*) mixtures in the Black Forest (Germany) found that spruce resistance decreased in 2003 with increasing proportions of fir in the stand, whereas fir clearly benefitted from heterospecific neighborhoods (Vitali et al., 2018). The similar patterns revealed by our study corroborated with the information that spruce has a more superficial rooting system (Larcher, 2003) and displays a stricter stomatal control than fir during drought (Klein, 2014) give weight to the hypothesis that fir benefitted at the expense of neighboring spruce trees.

The higher productivity sometimes found in mixtures under conditions of normal water supply unfortunately appears to be also associated with higher water consumption (Forrester, 2015). Consequently, highly productive mixtures may reach higher levels of hydric stress during drought than their monospecific counterparts (Bauhus et al., 2017). However, it is not clear whether the tree community as a whole may be disadvantaged or just individual species (Bauhus et al., 2017).

As demonstrated by Forrester et al. (2016), information regarding the drought response of a single species in a mixed forest provides little information regarding the behavior of other species in the same mixture or regarding the response at the stand or community level. If the goal is to predict drought susceptibility at the community-level (i.e. a goal that we did not pursue in this study), it becomes essential to understand if all species in a mixture benefit from mixing or if only some benefit at the cost of others (Forrester et al., 2016). A further difficulty arises from the fact that the same combination of tree species can display very different responses to drought across wide spatial gradients (Forrester et al., 2016).

Therefore, it is not advisable to generalize drought reaction patterns of mixed stands observed on a fraction of species’ distribution ranges (Bauhus et al., 2017) and it seems not possible to transfer our results at the current stage as a general response pattern to other European regions where fir and spruce occur together. Nevertheless, our results do not support generalized recommendations of cultivating spruce in mixed stands in order to mitigate its drought susceptibility (Pretzsch et al., 2014). Our data provides evidence that not all admixtures to spruce would have the desired positive effect and, in particular, admixing fir with spruce may even increase the drought sensitivity of the latter.

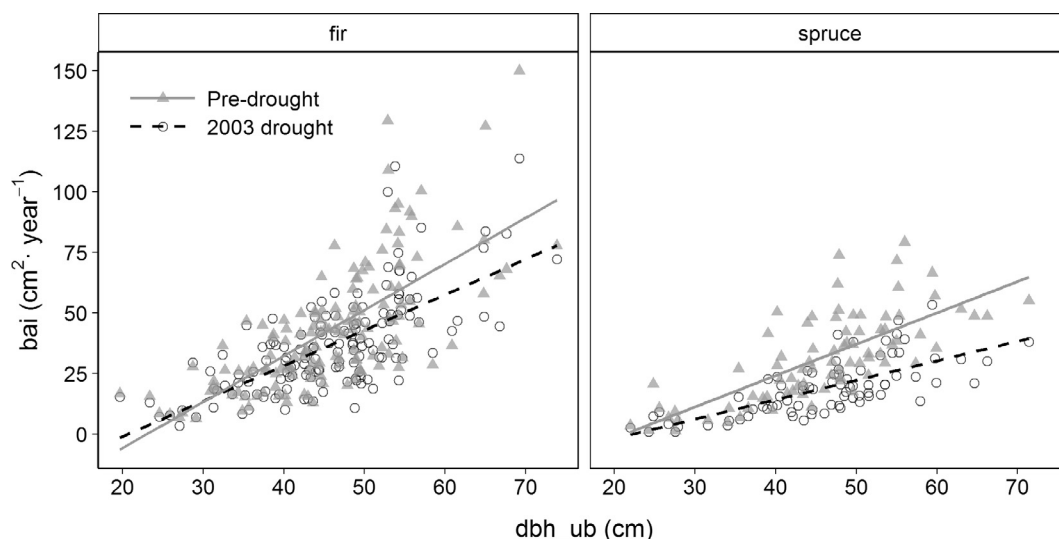


Fig. 4. Absolute basal area increment (*bai*) before (3 years) and during drought in relation to tree size (*dbh_ub*, diameter at breast height under bark) for the same set of trees.

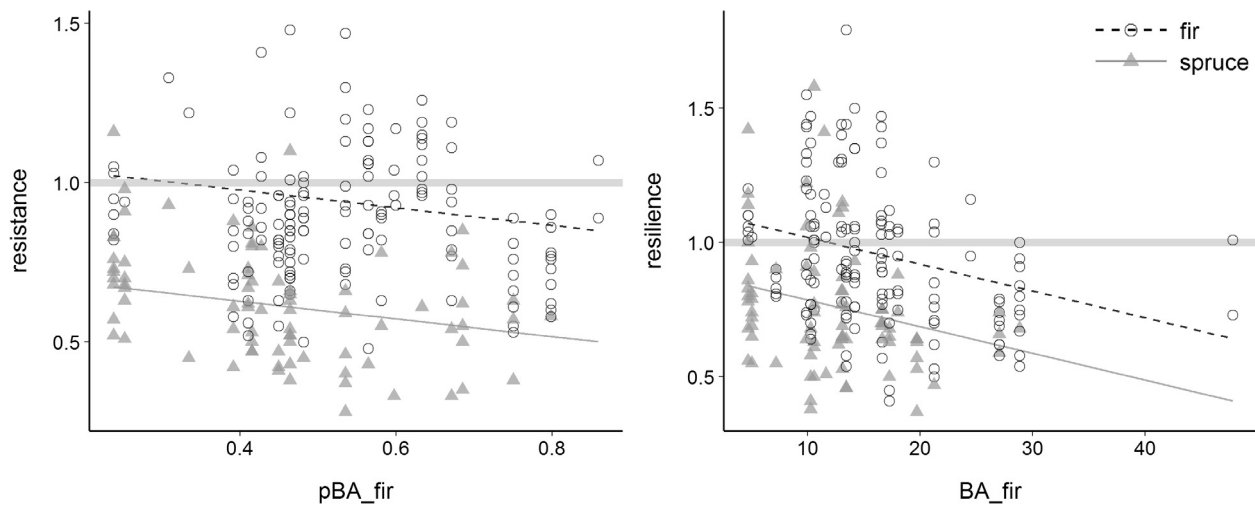


Fig. 5. Plots illustrating the relationships between stem growth responses to drought and the plot-level contribution of fir in the mixture. Left side: resistance and proportion of stand basal area attributed to fir (pBA_{fir}). Right side: resilience and the absolute fir basal area at the stand level (BA_{fir}). Other model covariates were kept fixed at their median values. The reference gray horizontal lines indicate a situation with no tree response to drought for resistance and a situation with identical pre-drought and post-drought increments for resilience.

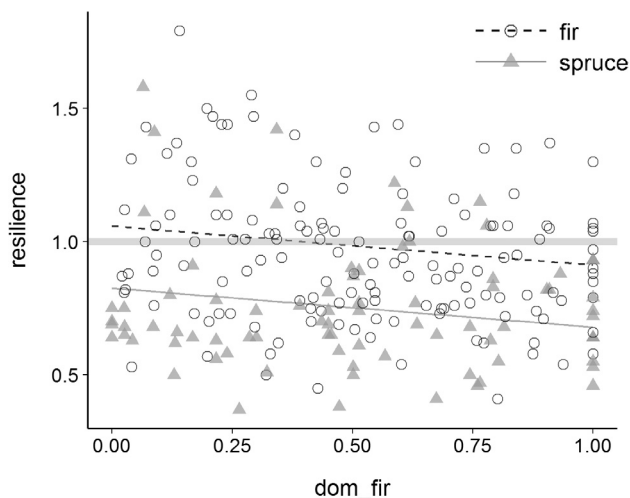


Fig. 6. Partial effect plot illustrating the relationship between resilience and tree dominance relative to fir individuals (dom_{fir}) in the analysis with distance-independent predictors. Other covariates were kept fixed at their median values. The reference gray horizontal line indicates a situation with identical pre-drought and post-drought increment levels.

4.2. Species-specific responses across a gradient of drought stress intensity

Many previous studies have classified spruce as a drought intolerant species (Zang et al., 2012; Hartl-Meier et al., 2014; Zang et al., 2014) and there is a consensus regarding its high vulnerability under a warming climate (Lu et al., 1995; Strand, 1997; van der Maaten-Theunissen et al., 2012; Boden et al., 2014; Zang et al., 2014; Vitali et al., 2017). Our analysis confirmed its high sensitivity to drought and revealed distinct patterns of response to severe drought between spruce and fir.

Spruce stem growth not only displayed a substantially stronger reaction to the 2003 summer drought (i.e. lower resistance) than fir, but it did not manage to regain pre-drought growth levels in the first three years after the 2003 drought (i.e. low resilience). In other studies spruce was found to display a low resistance but a relatively good resilience, and in some cases pre-drought growth levels were even attained within a year after drought (Zang et al., 2012). Prolonged growth depressions after drought may be triggered by twig, branch or bud dieback, xylem cavitation, changes in carbon allocation patterns from bole to roots as a result of hydric stress (Orwig and Abrams, 1997) or the depletion of

reserves of non-structural carbon during longer droughts. Since we did not measure these variables, we cannot tell why spruce resilience was so low in our study.

In contrast to spruce, fir has been described as either moderately drought tolerant (van der Maaten-Theunissen et al., 2012) or even very drought-tolerant (Elling et al., 2009; Hartl-Meier et al., 2014). There are also studies that characterize fir as vulnerable to high summer temperatures and soil water deficit, yet they tend to originate from regions where these factors generally represent major growth limiting factors: southern Italy (Battipaglia et al., 2009), southeastern Alps (Rolland et al., 2000; Maxime and Hendrik, 2010) or some regions in France (Lebourgeois et al., 2010). Additionally, in the context of the prolonged growth decline and dieback observed in fir during the 1970s and 1980s in central Europe (Elling et al., 2009) – then dubbed the “Waldsterben” (Engl. “forest dieback”) – drought sensitivity of fir was repeatedly speculated as a potential causal factor (Becker, 1989). More recent evidence suggests that exposure to high SO_2 levels was among its major driving factors (Elling et al., 2009).

The different impact of severe drought on spruce and fir stem growth may be partly explained by differences in root morphology: a deep taproot allows fir trees to explore deeper soil layers for water than the shallow root system typical for spruce (Larcher, 2003). Another relevant aspect is the species-specific seasonality of wood formation and the extent to which intense drought and seasonal cambial activity synchronize during particular years. Fir may be better able to compensate for drought periods due to its longer wood formation period (Gričar and Čufar, 2008). In Slovenia, the extreme drought in 2003 terminated ring formation in spruce prematurely by approximately one month, whereas fir continued wood formation until the regular end of the growing season (Gričar and Čufar, 2008).

Nevertheless, caution is advised when attempting to generalize species’ reactions to a singular drought event. Drawing from other past drought events, the differences in growth responses of fir and spruce to drought appear anything but consistent. E.g., in contrast to the 2003 drought, Vitali et al. (2017) found that growth responses of spruce and fir actually differed very little during the 1976 drought. The extreme drought of 2003 was characterized by high water deficits and very high summer temperatures (Merlin et al., 2015; Metz et al., 2016), whereas in 1976 a very dry spring was followed by a hot summer (Desplanque et al., 1999; Rolland et al., 2000) and resulted in prolonged water stress over the entire growing season (Merlin et al., 2015; Metz et al., 2016). Vitali et al. (2017) assumed that the 1976 drought had a less pronounced effect on spruce stem growth because trees were able to

resume growth afterwards. However, it is open to speculation whether this might have been caused by drought characteristics less unfavorable for spruce in 1976, by factors resulting in a generally decreasing growth trend of fir in the 1970s–1980s (Elling et al., 2009; Kohnle et al., 2014) or by other factors.

The literature contains reports of elevation-dependent growth reactions to drought for both spruce (Hartl-Meier et al., 2014) and fir (Desplanque et al., 1999; Lebourgeois et al., 2010; van der Maaten-Theunissen et al., 2012). Since we analyzed a single drought year, our drought intensity metrics reflect spatial variability and their ranges roughly translate to a 518–1042 m elevation range in our data (see strong positive correlation between drought intensity and elevation in Supplementary Material Fig. G1). We observed how fir resistance increased with diminishing drought intensity (i.e. increasing elevation), while spruce displayed a uniformly low resistance across the same spatial gradient. A similar pattern emerged when analyzing growth responses in 2003 in the same region in Germany but across a wider elevation range (400–1200 m a.s.l.) than in our study (Vitali et al., 2017): an elevation-dependent drought response was apparent for fir but not for spruce. Another study which considered an even wider elevation range (680–1600 m a.s.l.) finally detected a relationship between elevation and growth sensitivity of spruce in 2003, while concluding that spruce was particularly vulnerable to drought below 1200 m a.s.l. (Hartl-Meier et al., 2014). Consequently, it seems that tree ring formation in spruce was severely impacted across a much wider elevation range than in the case of fir during the exceptional drought of 2003.

4.3. Tree size and pre-drought growth rates affect growth reactions to drought

A recent meta-analysis indicated a widespread size-dependent sensitivity to drought (Bennett et al., 2015). That is, droughts were found to consistently have a more detrimental impact on stem growth and mortality rates of larger trees compared to the effect they had on smaller ones. Higher hydraulic stress in larger trees (Ryan and Yoder, 1997; Ryan et al., 2006) is believed to underpin this size-related sensitivity to drought (McDowell et al., 2011; McDowell and Allen, 2015). According to this theory, the higher solar radiation and vapor pressure deficits that crowns of larger trees are typically exposed to become a liability during drought, as soil water availability declines and evaporative demand increases. Particularly foliage in the top-canopy would need to trade-off between hydraulic safety through stomatal closure versus maintaining positive carbon balance and transpirative tissue cooling (Bennett et al., 2015). Based on this reasoning, tall trees are predicted to be more drought- and heat-susceptible than shorter trees occurring in the same stand (McDowell and Allen, 2015), while the latter should benefit from lower wind speeds, humidity deficits and direct solar radiation (Roberts et al., 1990; Aussenac, 2000).

Based on existing literature, there seems to be limited empirical support in favor of the postulated size-related sensitivity to drought. Multiple studies did find a higher stem growth stability in smaller trees (Martín-Benito et al., 2008; Martínez-Vilalta et al., 2012; Zang et al., 2012; Gazol and Camarero, 2016; Thurm et al., 2016), yet there have been also several reports of smaller trees being more severely affected by drought than larger neighbors (Orwig and Abrams, 1997; Colangelo et al., 2017). The latter result was generally explained in terms of shallower root systems in smaller trees or the typically high levels of competition experienced (Martín-Benito et al., 2008; Zang et al., 2012). Other studies found no evidence of a size-related drought sensitivity (Mérián and Lebourgeois, 2011).

On the one hand, the effects of pre-drought growth rates and size on resistance were unambiguous in our study. Large individuals of spruce and fir with high pre-drought increment rates clearly displayed a more severe relative increment reduction in 2003 than smaller, slower-growing trees. Similar relationships have been observed for spruce

(Ding et al., 2017), ponderosa pine (McDowell et al., 2006) and Scots pine (Martínez-Vilalta et al., 2012). On the other hand, considering the trees' absolute increment rates reveals a different picture. Although large trees tend to display a severe relative drop in increment during drought, they also show the highest absolute increment rates pre-drought as well as during drought (Zang et al., 2012) – a pattern that was clearly visible in our data. At the same time, since small trees tend to be more consistent in their (absolutely) slow growth, their higher increment stability more likely reflects chronic resource limitation rather than drought hardiness. In the stands of our study the most frequent and likely growth limiting resource for small trees is light. Hence, small and suppressed trees always tend to grow at their limit and have no opportunity to increase growth significantly during favorable times in terms of water availability. Accordingly, their growth cannot decline much during unfavorable conditions.

An exploratory assessment of drought-related mortality based on our data (Appendix E in Supplementary Material) suggested a substantial increase in mortality for trees in small diameter classes (and more so for fir than for spruce), in spite of their apparent increment “stability” during and after drought. Furthermore, little or no change in mortality rates was discernible for trees in larger size classes. Therefore, our results challenge the expectations that smaller trees would somehow benefit during drought (Roberts et al., 1990) or that higher drought sensitivity in larger trees should go hand-in-hand with higher mortality (Bennett et al., 2015). Nevertheless, our findings indicate that tree competition becomes more size-symmetric (*sensu* Weiner and Thomas, 1986) during dry years as compared to the more pronounced size-asymmetry typical for regularly moist years (Wichmann, 2001; Pretzsch and Biber, 2010; Zang et al., 2012; Río et al., 2014). However, despite this transient shift the principal competitive hierarchy remains fundamentally unaltered even in drought years.

4.4. Competition and thinning affect growth reactions to drought

Reducing stand density and thus competitive pressure through thinning has been often shown to effectively mitigate short-term drought impacts on tree and stand growth (Misson et al., 2003; McDowell et al., 2006; Klos et al., 2009; Kohler et al., 2010; D'Amato et al., 2013; Sohn et al., 2013; Sohn et al., 2016b; Thurm et al., 2016). Therefore, it is important to account for the level of competitive pressure when modeling growth responses to drought stress (Forrester et al., 2016). However, most of these studies have been in even-aged stands and often only the dominant and co-dominant trees have been analyzed.

When evaluating the effect of thinning on the drought response of trees, it is necessary to differentiate between an actual stress-mitigating effect of thinning during drought (e.g. by reducing competition for soil water) and its mid-term effect on post-drought tree performance (i.e. on growth recovery and resilience) (Sohn et al., 2016b). The ability to increase tree growth resilience by means of reducing competitive pressure has important practical implications, as improved post-drought growth levels through thinning may easily reduce tree susceptibility to subsequent infestations by secondary pest pathogens after drought (Sohn et al., 2016a). Previous studies in conifer monocultures have noted a positive short-term impact of thinning especially on recovery and resilience but less on resistance (Sohn et al., 2016a; Sohn et al., 2016b). Unfortunately, there is little information available regarding the long-term effects of heavy thinning on drought vulnerability (D'Amato et al., 2013; Sohn et al., 2016a). We found that reducing competition levels – in both distance dependent and independent analyses – improved resistance and resilience, which suggests that the effect of thinning may be beneficial also in uneven-structured, mixed stands (at least when the admixed species have stratified root systems, as it is the case with fir and spruce).

We expected that small trees would respond differently to a combination of release and drought impacts as compared to the taller ones

left in the stands after thinning. However, interactions between the residual stand basal area or the proportion of basal area removed through thinning and proxies of tree size, respectively, were not significant (results not shown) and did not substantially improve the resistance and resilience models (comparison of AICc values in Appendix F). This led us to conclude that although thinning did influence tree responses to drought, it did not mediate the relationship between tree size and resistance/resilience. In other words, for a given release intensity, the relative increment responses to drought of large and small trees appeared to be similar. Unfortunately, the authors are not aware of comparable studies of drought responses in mixed stands with stratified canopies where residual trees belong to different canopy layers, which could support or contradict our findings. Therefore, more research is needed on this topic.

4.5. Research and management implications

Our findings indicate that compositional and structural diversity do not generally increase stability to drought stress but that tree reactions to drought may be more dependent on the species identity of neighbors. On the one hand, the species analyzed in our study, fir and spruce, are rather functionally similar with regard to their height, growth rates, wood density, foliage, etc., except for root structure and shade tolerance, which may have contributed to the absence of results in terms of diversity. On the other hand, our data and several other studies (Forrester et al., 2016; Metz et al., 2016; Bauhus et al., 2017) suggest that the species composition of a mixed stand may be more important than diversity for predicting stem growth reactions to drought. Therefore, in view of the need to build forest ecosystems with higher resistance and resilience to drought in the future (Pretzsch et al., 2014), it will be crucial to properly mix species with demonstrated complementary behavior in relation to water consumption rather than just increase species diversity (Forrester, 2014; Forrester et al., 2016). Therefore, future studies should focus on identifying species' combinations that are optimally suited to mitigate drought impacts under given site conditions either at the community level or for certain target species.

With respect to mixing spruce and fir in central Europe, our results suggested that under the site conditions given in the study competition exerted by fir neighbors during drought was more growth limiting than competition exerted by spruce neighbors. The offshoot is that the improved drought response of fir in the vicinity of spruce neighbors comes at the price of detrimental effects on spruce. This is very unfortunate because spruce is the species more vulnerable to drought.

The fact that in fir-spruce mixtures a higher proportion of fir reduced the growth stability of both species (spruce and fir) during drought hints at an amplified competition for water with increasing fir abundance. Given the limited spatial extent of our study we cannot conclude that spruce sensitivity to drought would always be enhanced in the vicinity of fir across the two species' natural distribution ranges. However, given current climatic projections regarding an increase in the frequency and duration of extreme drought events in the future, the long-term stability of fir-spruce mixtures seems uncertain, at least for our study region.

Considering its relatively robust growth response to extreme drought and its functional traits that promote drought hardiness, we conclude that, on suitable sites and with appropriate stocking control through thinning, mixed fir stands may offer a feasible silvicultural alternative to the currently prevalent spruce stands under changing climatic conditions (Elling et al., 2009; Zang et al., 2014).

While we believe that the improved increment stability values in small trees represents a calculational artifact triggered by chronic resource limitation, further studies are needed to explore size-related drought sensitivity. Unfortunately, this phenomenon increases the complexity of upscaling growth reactions to drought from the individual tree to the stand or ecosystem levels (Zang et al., 2012).

Further challenges may be tied to variations in size-dependent drought sensitivity across environmental gradients (Orwig and Abrams, 1997; Colangelo et al., 2017) and the fact that the effects of tree size, age and growth rates on drought responses are easily confounded (Martinez-Vilalta et al., 2012).

We would like to add another note of caution with regard to generalizations from our study. Since our analysis only considered a single drought event spanning one year we cannot say how mortality rates, growth reactions, and species' responses would unfold in the case of a prolonged, multi-year drought. It is also uncertain which tree reaction patterns would emerge in case of different temporal patterns of soil water deficit and heat than experienced in 2003. Furthermore, considering that the drought response of the same mixture can fluctuate greatly across species' distribution ranges (Forrester et al., 2016), we cannot currently transfer our results and conclusions beyond the regional spatial extent of our study. Finally, the levels of explained variation in our analysis suggest that important processes and variables have remained unaccounted for and indicate potential for future model improvement.

Given the prospects of increasing drought frequency, understanding species interactions emerges as an essential prerequisite for being able to manage stable forest systems in the future. Within this context, our study has confirmed that thinning is effectively mitigating short-term stem growth sensitivity to drought. There is, nevertheless, a growing need to understand the long-term effects of thinning on tree sensitivity to drought. Together with modifying the level of neighborhood competition through thinning, species (or provenance) selection and adjusting species' proportion in mixtures may help to mitigate negative climate change impacts. In contrast, our study does not support the notion that structural diversity might also be exploited as an effective tool to attenuate detrimental impacts of drought on stand growth.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2018.02.030>.

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