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Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in south-western Germany

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Abstract

Improving our understanding of the potential of forest adaptation is an urgent task in the light of predicted climate change. Long-term alternatives for susceptible yet economically important tree species such as Norway spruce (*Picea abies*) are required, if the frequency and intensity of summer droughts will continue to increase. Although Silver fir (*Abies alba*) and Douglas fir (*Pseudotsuga menziesii*) have both been described as drought-tolerant species, our understanding of their growth responses to drought extremes is still limited. Here, we use a dendroecological approach to assess the resistance, resilience, and recovery of these important central Europe to conifer species the exceptional droughts in 1976 and 2003. A total of 270 trees per species were sampled in 18 managed mixed-species stands along an altitudinal gradient (400–1200 m a.s.l.) at the western slopes of the southern and central Black Forest in southwest Germany. While radial growth in all species responded similarly to the 1976 drought, Norway spruce was least resistant and resilient to the 2003 summer drought. Silver fir showed the overall highest resistance to drought, similarly to Douglas fir, which exhibited the widest growth rings. Silver fir trees from lower elevations were more drought prone than trees at higher elevations. Douglas fir and Norway spruce, however, revealed lower drought resilience at higher altitudes. Although the 1976 and 2003 drought extremes were quite different, Douglas fir maintained consistently the highest radial growth. Although our study did not examine population-level responses, it clearly indicates that Silver fir and Douglas fir are generally more resistant and resilient to previous drought extremes and are therefore suitable alternatives to Norway spruce; Silver fir more so at higher altitudes. Cultivating these species instead of Norway spruce will contribute to maintaining a high level of productivity across many Central European mountain forests under future climate change.

KEYWORDS
Abies alba, Central Europe, climate change, dendroecology, drought tolerance, forest management, *Picea abies*, *Pseudotsuga menziesii*

1 | INTRODUCTION

The strong need to adapt many forests to future climate conditions through changes in tree species composition is frequently in stark contrast to the dearth of information about the suitability of individual species and their provenances for these future conditions. The growth performance of economically important tree species under climatic extremes, especially extreme drought events, has been

frequently discussed in the light of ongoing and predicted climate change (IPCC 2014). In this regard, multifunctional management strategies are facing new abiotic and biotic threats on the vitality, productivity, and functioning of forests ecosystems (Albert, Hansen, Nagel, Schmidt, & Spellmann, 2015; IPCC 2014). Forests will inevitably adapt to new conditions adjusting to climate change through changes in tree species composition (Köhl et al., 2010), tree morphology, rooting depth (Brassard, Chen, Bergeron, & Paré, 2011), or leaf gas exchange (Bauerle, Hinckley, Cermak, Kucera, & Bible, 1999; Lu, Biron, Granier, & Cochard, 1996). However, this might lead to a loss of biodiversity, productivity, and ecosystem services where the climatic conditions will become less favourable, as an increase in the frequency and severity of climatic extremes has been projected (Field, Barros, Stocker, & Dahe, 2012; IPCC 2014).

In southern Europe, the length and intensity of summer droughts have doubled over the last decades (EEA 2012), making drought extremes one of the major challenges that forestry will have to adapt to in the near to mid-term future (Albert et al., 2015; Ciais et al., 2005). In order to ensure productive and functional ecosystems, forest management needs to adapt forest structure and composition to the expected increase in frequency of extreme events (Bolte et al., 2009). Resilient forests are one of the keys to face climate change. In addition, forestry has a large potential to mitigate the effects of climate change through storage of carbon in forest ecosystems, increase in forest area, and woody products (Körner, 2017; Nabuurs et al., 2007). The mitigation potential of central European forests currently depends to a large extent on productive conifer species that provide timber for long-term use (Weingarten et al., 2016).

Norway spruce (*Picea abies*) has been extensively cultivated under a wide range of climatic conditions (Caudullo, Tinner, & de Rigo, 2016), making it the second-most widespread tree species, accounting for 21% of the European forest cover (Köble & Seufert, 2001). With a coverage of 26%, it is the most important tree species in Germany by area and economic benefit (BWI 2014; Möhring & Wilhelm, 2015). However, it is well known that spruce is sensitive to extreme drought events, which affect growth rates and overall vitality (Boden, Kahle, Kv, & Spiecker, 2014; Kahle, Spiecker, Aldinger, & Michiels, 2008; Lebourgeois, 2007; van der Maaten-Theunissen, Kahle, & van der Maaten, 2013). This vulnerability is linked to a drought-related increased susceptibility to barkbeetle attacks (*Coleoptera: Scolytidae*) (Bentz et al., 2010; Christiansen & Bakke, 1988; Dutilleul, Nef, & Frigon, 2000). In southern Germany, a major loss of spruce from the colline to submontane forests has been projected (Hanewinkel, 2010; Hanewinkel, Cullmann, & Michiels, 2010). A remarkable loss of this species is already taking place, as the forest cover of Norway spruce in Germany has declined by 8% between 2002 and 2012 (BWI 2014).

As this decline could have drastic financial implications, Silver fir (*Abies alba*) and Douglas fir *(Pseudotsuga menziesii)* have been considered as possible replacement species. The last German national forest inventory recorded 1.7% and 2.0% of forest cover for Silver fir and Douglas fir, respectively (BWI 2014). Expanding the cultivation of the exotic Douglas fir is being strongly criticized by nature conservation advocates, while this is not the case for the native Silver fir (Höltermann, Klingenstein, & Ssymank, 2008). For this reason, it is also important to find out, how these possible alternative species compare under different growing conditions. This may indicate where in the landscape the native species performs better than the exotic one and vice versa. Although there is some evidence, especially for silver fir, that these species might be more drought tolerant than spruce (Bouriaud & Popa, 2009; Chen, Welsh, & Hamann, 2010; Desplanque, Rolland, & Schweingruber, 1999; Kowalik, Borghetti, Busoni, Sanesi, & Vendramin, 1988; Lebourgeois, Rathgeber, & Ulrich, 2010; Nothdurft, Wolf, Ringeler, Böhner, & Saborowski, 2012; van der Maaten-Theunissen et al., 2013), few studies compare drought tolerance of these three conifer species in Europe (Boden et al., 2014; Bouriaud & Popa, 2009; Feliksik & Wilczyński, 2009; Kantor, 2008; Podrázský, 2015; van der Maaten-Theunissen et al., 2013). Moreover, these studies have been carried out mostly at small spatial scales (individual stands, or sites with extreme climatic conditions), and are thus not suitable to extrapolate the results larger scales. Moreover, the growth reactions of these conifers to drought extremes have not yet been investigated in a framework that allows the direct comparison of all three species for the same site and management conditions using the accuracy of annual growth rates obtained from dendroecological methods. The use of "standard" indices to quantify the resistance, recovery, and resilience of radial tree growth in relation to drought years (Lloret, Keeling, & Sala, 2011) provides standardized and comparable results that can also be used as reference for future studies.

Here, we aim at assessing the drought response of *P. abies*, *A. alba*, and *P. menziesii* in south-western Germany. More specifically, we address the reactions of these three species to the central European drought extremes of 1976 and 2003 using a dendroecological analysis of managed forests covering the majority of growth conditions in the Black Forest. We sampled trees from the three species covering a range of growing conditions with gradients in temperature and precipitation, to test the following two hypotheses:

1. Silver fir and Douglas fir are more drought tolerant than Norway spruce across the whole range of typical site conditions,
2. Species-specific drought responses of conifers vary along a regional altitudinal gradient.

2 | MATERIALS AND METHODS

2.1 | Study sites

The radial growth of *P. abies*, *A. alba*, and *P. menziesii* and their responses to drought extremes were analysed from tree cores collected at 18 sampling sites between ca. 300 and 1100 m a.s.l. on the western slopes of the southern and central Black Forest in south-western Germany (Figure 1). Unlike other studies that have focussed on mono-specific stands of these species, we selected stands with all three species intermixed to allow for a direct
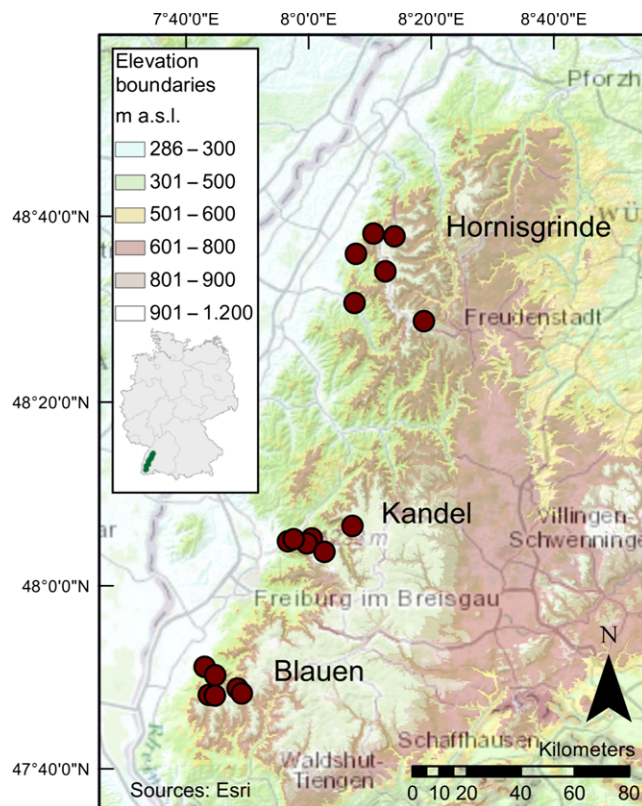
FIGURE 1 Locations of study sites along three altitudinal transects on the western slopes of three mountains (Hornisgrinde, Kandel, and Blauen). Each transect comprises six sites located at three elevations (low 300–550 m a.s.l., middle 600–800, and high 900–1200), which correspond largely to colline, submontane, and montane climatic zones, and in North and South aspect at each elevation

comparison of the climatic effect on growth of the species without having to account for site differences. To capture the variation within each population of the conifer species in the southwest, the 18 sampling sites were distributed over three main altitudinal transects (Figure 1, the Hornisgrinde in the north, the Kandel in the centre, and the Blauen in the south).

The sites comprised stands that were between 60 and 100 years old and were distributed over the altitudinal range in three main elevations (low, ranging between 300 and 550 m, middle, between 650 and 800 m, and high, between 900 and 1100 m), which represent a gradient with increasing precipitation and decreasing temperature. Differences in mean temperatures between low and high elevations were as high as differences between current temperatures and those projected for a future climate; precipitation varied by a factor of two between low and high elevation. For each elevation, two sites were chosen on north- and south-facing slopes. However, owing to the lack of a significant influence of exposition on drought response of trees, aspect was later dropped from the statistical models. We did not select extreme sites, but those that are representative of growing conditions of these species in commercial forestry (see Table 1 and S1 for details). The extensive range of growing conditions covered by this design facilitated the creation of a region-wide average tree ring chronology to remove

large part of the tree-specific variability and microsite differences (Cook & Kairiūkštis, 1990).

2.2 | Sampling design

In spring and summer of 2015, 15 healthy dominant trees per species and site were cored at diameter at breast height (DBH = 1.3 m) for a total of 270 trees per species (810 trees in total). All trees were collected in mixed stands where all three species were present, and each target tree had different combinations of neighbouring species, owing to the intimate mixture. Dominant trees were selected to minimize the effects of competition among trees on the growth signals (Cook & Kairiūkštis, 1990). The tree selection was carried out through adaptive sampling, where each target tree was selected after the previous one (Thompson, 1990). A minimum distance of at least 10 m was set between target trees to avoid target trees of the same species as direct competitors. As the area of available mixed-species stands was limited, we could not operate with a greater minimum distance. For each tree, two cores were collected with an increment borer (400 mm Suunto, Finland) from two directions perpendicular to the slope direction, to minimize a potential bias caused by reaction wood (Grissino-Mayer, 2003). For each target tree, the height was measured with a Vertex (Haglöf, 2007), DBH and species were recorded. Our sampling design intended to capture the variation in productivity that is representative of managed forests in the region. Site quality, quantified as the mean annual stand volume increment at age 100 years (MAI100), ranged from 7 (low productivity) to 19 (high productivity) (Table S1). This range covers 97% of the growth situations of the forests in Baden-Württemberg (BWI 2014). Specific growth tables for Baden-Württemberg were used to assign the site-quality indices calculated from tree age and height (ForstBW 2016).

2.3 | Dendroecological analyses

Tree cores were air-dried and subsequently polished with sand paper down to a grit size of 400 (Schweingruber, 1988). Tree ring widths were measured with the WINDENDRO image analysis system (Regents Instruments, Quebec). The chronologies were visually cross-dated. The statistical program COFECHA (Grissino-Mayer, 2001; Holmes, 1983) and the dplR package (Bunn, 2010) was used for data quality control. The EPS "expressed population signal" and the Gleichläufigkeit were calculated to estimate the quality of correlations between the series and representative character of our chronologies (Schweingruber, 1988, 2007). All calculations have been performed on single trees mean chronology for the common period 1970–2014 (Fig. S1, S2, S3, S6). Ring width measurements were detrended with cubic splines with a 50% frequency cut-off at two third of the individual series length (Cook & Kairiūkštis, 1990), using the function "detrend" (Bunn, 2008), to emphasize the higher interannual frequency variation, and remove nonclimatic noise (Cook & Peters, 1981). Detrended chronologies minimize the ring width variation associated with age trends; however, they can also conceal some of the short year-to-year variability, and stand

TABLE 1 Geographical and climatic characteristics of individual study sites for the three transects

Site[a]	Hornisgrinde HNH	HNM	HNL	HSH	HSM	HSL
Elevation [m a.s.l.]	850–920	680–790	290–365	930–1015	550–650	320–460
Aspect [°]	330-30	355-0	350-0	100–190	180–210	120–210
DMI (2003)[b]	98.6 (62)	107.2 (71)	62.9 (44)	94.2 (63)	75.6 (52)	56.9 (39)
Mean annual temperature (T, °C)[c]	6.3	5.9	8.9	6.61	7.8	9.4
Annual precipitation (P, mm)[d]	1907	2036	1416	1864	1602	1314
Mean min/max temperature (Tmin/Tmax, °C)[e]	−11.2/25.3	−10.9/24.8	−9.1/29.2	−10.5/25.7	−9.6/27.3	−8.5/29.7
Site	Kandel KNH	KNM	KNL	KSH	KSM	KSL
Elevation [m a.s.l.]	1000–1100	680–800	300–400	1079–1127	640–810	300–370
Aspect [°]	355-5	40-0	20-0	175–270	210–270	230–270
DMI (2003)	98.3, (64)	71.4 (47)	48.6 (32)	93.6 (57)	60.2 (40)	47.3 (31)
Mean annual temperature (T, °C)	5.7	7.7	9.7	6.6	8.7	10.0
Annual precipitation (P, mm)	1836	1509	1141	1854	1344	1133
Mean min/max temperature (Tmin/Tmax, °C)	−11.6/24.0	−10.1/27.0	−9.0/29.8	−10.8/25.5	−9.5/28.3	−8.6/30.3
Site	Blauen BNH	BNM	BNL	BSH	BSM	BSL
Elevation [m a.s.l.]	945–1080	680–760	430–550	895–1060	670–780	465–550
Aspect [°]	355-0	20–50	355-0	150–240	185–265	120–250
DMI (2003)	89.6 (67)	78.2 (57)	67.5 (50)	86.7 (64)	59.8 (44)	50.5 (38)
Mean annual temperature (T, °C)	6.3	6.9	7.7	6.7	8.3	8.7
Annual precipitation (P, mm)	1744	1581	1426	1732	1305	1131
Mean min/max temperature (Tmin/Tmax, °C)	−11.1/25.0	−9.5/25.8	−9.4/26.9	−10.9/25.7	−9.5/27.8	−9.7/28.5

[a]Site abbreviations are composed of three letters to indicate Transect (K = Kandel, B = Blauen, H = Hornisgrinde), aspect (N = north, S = south), and altitudinal range (H = high, M = middle, L = low).
[b]The aridity index (DMI) calculated as $DMI = P/(T + 10)$ (de Martonne, 1926), where P is the annual sum of precipitation and T the mean annual temperature for the years 1960–2014, in parenthesis the DMI for the year 2003.
[c]Mean annual temperature 1960–2014.
[d]Total annual precipitation, mean 1960-2014.
[e]Average minimum temperature of the coldest (January) and maximum of the hottest (July) month mean 1960–2014.

dynamics (Fritts, 1976). However, as our study focuses on short periods (5 years), and our samples represented only dominant trees, which are least affected by competition, no difference was found between the analysis performed on raw and detrended data. Therefore, although both raw and detrended chronologies were used for the calculations, the results based on analyses of raw data are displayed in the results section.

2.4 | Climate sensitivity and pointer years

The years 2003 and 1976 were chosen as drought years for this study because they have been documented as the driest years in Southwest Germany in recent decades (Kahle et al., 2008; van der Maaten-Theunissen, van der Maaten, & Bouriaud, 2015; Zang, Hartl-Meier, Dittmar, Rothe, & Menzel, 2014). This choice was supported by the concurrence of extreme pointer years and low levels in the "aridity index" DMI (De Martonne Index) (Figure 2). The DMI was derived for each site and year of interest was calculated according

to Maliva & Missimer (2012) to classify the sites in aridity classes:

$$DMI = P/(T + 10) \qquad (1)$$

Climatic variables, such as precipitation and daily means and extremes of temperature, were retrieved for each site for the period from 1970 to 2014 from the interpolated data of the REGNIE project by the Deutscher Wetterdienst (2013). Site-specific climate data (temperature [T] and precipitation [P]) were obtained with a 1 km² resolution.

Pointer years were measured with the "pointRes" package (van der Maaten-Theunissen et al., 2015). The threshold for the pointer year selection was set at 20% of relative growth change compared to the average growth in the four preceding years.

Form the climate sensitivity analysis carried out in Vitali (V. Vitali, U. Büntgen, J. Bauhus, unpublished), and other studies, (Feliksik & Wilczyński, 2009; Kahle & Spiecker, 1996; Pichler & Oberhuber, 2007), it appeared that for all species, summer temperature low altitudes were strongly negatively correlated with tree ring growth between 1970
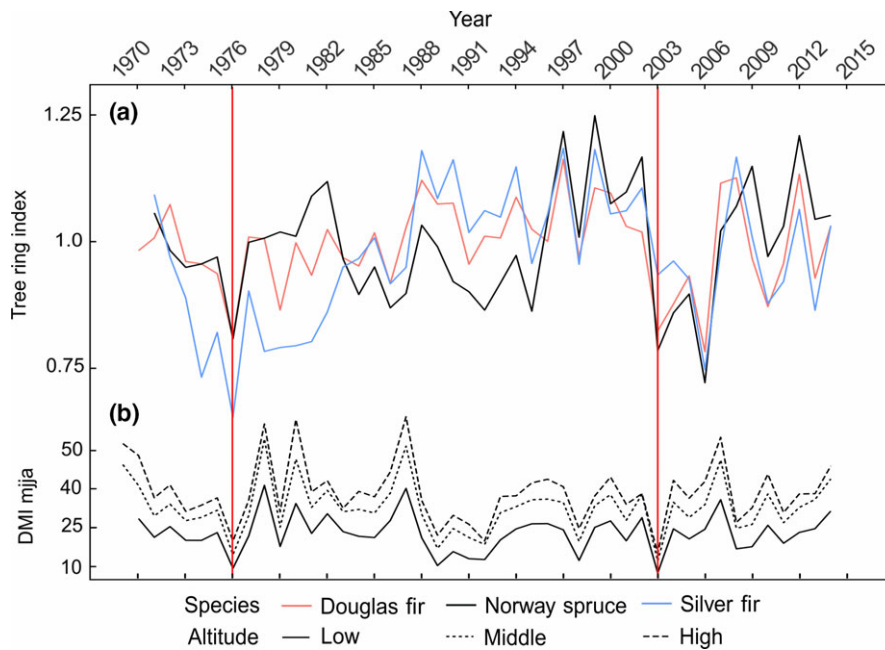
FIGURE 2 (a) Mean detrended chronologies of the three tree species. (b) Mean DMI chronology for the selected vegetation period (May to August), differentiated for the three elevation ranges. The vertical red lines mark the drought years 1976 and 2003, characterized by a clear synchronicity of dry conditions and low growth rates

and 2015, whereas summer precipitation, especially in June, showed a strong positive correlation with tree ring growth. Therefore, the vegetation period considered to derive the aridity index was calculated on an annual base for the period between May and August (DMI$_{\text{mjja}}$).

2.5 | Quantification of responses to drought

The effects of drought stress on the radial growth of the three different conifer species were quantified through three main response variables adapted from Lloret et al. (2011). Resistance (Rt), resilience (Rc), and recovery (Rs) have been calculated in relation to the drought extremes of 1976 and 2003 using the following equations:

$$\text{Resistance}(Rt) = \frac{Dr}{Pre Dr} \tag{2}$$

$$\text{Recovery}(Rc) = \frac{Post\ Dr}{Dr} \tag{3}$$

$$\text{Resilence}(Rs) = \frac{Post\ Dr}{Pre\ Dr} \tag{4}$$

"Pre dr" and "Post dr" values have been calculated as the tree ring width mean of the 2 years before and following the target event for each tree. The "Dr" variable corresponded to the tree ring width for the drought year. Resistance quantifies the magnitude of growth depression in tree rings in the drought year compared to the predrought period. Recovery expresses the growth improvement after the drought. Both measures are interconnected; i.e. high resistance (small reduction in growth) is typically followed by a low recovery as no great decline was shown in the first place. Resilience quantifies the "*capacity to reach pre-disturbance performance levels*" (Lloret et al., 2011). Postdrought periods in nonarid environments, as were our sites, have been shown to have low "legacy effect", affecting growth after the event for 1–2 years (Anderegg et al., 2015). In accordance with other studies (e.g. Sohn, Saha, & Bauhus, 2016), we restricted the length of the reference period before and after the droughts to 2 years, to avoid including other

disturbance events or growth anomalies (like the mast year in 2006) into these reference periods.

2.6 | Data analysis

The differences between drought responses in terms of resistance, recovery, and resilience of the three species were assessed through multiple regression models and analyses of variance (ANOVA). Analyses were performed for each species to identify significant correlations between responses to drought and site variables (i.e. DMI, altitude, aspect) and their interaction from 1970 onward. For multiple comparisons of variables subgroups, Tukey's post hoc test was performed. All computations for this article were performed using R version 3.1.2 (R Core Team 2014).

3 | RESULTS

3.1 | Medium-term trends in radial growth

The radial growth rates of Douglas fir were on average substantially higher than in the other two species (Figure 3; Table S1). Norway spruce showed an overall decline in growth rates over the last 30 years, whereas Silver fir radial growth increased following a growth depression in the 1970–1980s. The Gleichläufigkeit, which ranged between 60 and 85 for each species and site, and the expressed population signal (EPS) (0.93 for Douglas fir, 0.94 for Norway spruce, 0.98 for Silver fir, Fig. S4) confirmed the good correlation between the series and indicates a common climatic signal.

3.2 | Species responses to extreme droughts

All species showed a distinct growth depression in the drought years 1976 and 2003 (Figure 3a), even though the intensity of these

growth depressions differed between the species. The average chronologies for each species across sites showed a high degree of variability (Figure 3b,c). However, no single environmental variable (e.g. aspect, altitude, site quality, slope, or DMI) could explain the variability between sites.

The variability in growth responses for each species was very high in relation to the two drought extremes. There was no significant difference between the three species concerning responses to the event in 1976, except for a higher recovery rate in Silver fir (Figure 4b). The growth responses during and following the 2003 drought were significantly lower than the ones in 1976 indicating a stronger stress event. The growth responses of Douglas fir in 2003 were lower than in 1976 for all indices (Rt −7%, Rc −14%, Rs −20% compared to 1976). These reductions in growth responses were even more pronounced in Norway spruce (Rt −16%, Rs −25%). Silver fir was the only species that showed an increased resistance (+2%), even though both its recovery (−21%) and resilience (−25%) decreased.

Silver fir showed the highest resistance in relation to the drought event of 2003. In contrast, resistance and resilience were lowest in Norway spruce (Figure 4). The low recovery values of Silver fir post-2003 should not be mistaken for a low capacity to recover, but more as a lack of the need to recover owing to the high resistance expressed.

3.3 | Effects of altitude on radial growth responses

Whereas the average radial growth rates for the period 1970–2014 were not different between low, mid, and high altitudes for Norway spruce and Douglas fir, Silver fir grew at a higher rate at low-altitude sites than at higher elevations (Figure 5).

The responses to drought of the year 2003 were used to assess the potential effect of elevation across transects (Figure 6). Across species, recovery and resilience appeared to be significantly lower at high elevations (effect on Rc = −0.14 and Rs = −0.08, with $p < .05$). Looking at individual species, Douglas fir resistance to drought was not influenced by altitude, whereas resistance of Silver fir increased with altitude. Recovery of radial growth showed the highest variability in responses: Douglas fir recovery was significantly lower at high elevations, whereas that of Norway spruce was highest at mid elevations and that of Silver fir at low elevations. In contrast to Norway spruce and Douglas fir, which had the lowest resilience at high elevations, resilience of radial growth in Silver fir was highest at high elevations (Figure 6). The response to the 1976 drought showed only an altitudinal effect for spruce at low elevations (Fig. S6).

4 | DISCUSSION

4.1 | Species differences in drought responses

Silver fir and Douglas fir are consistently more resistant and resilient to drought than Norway spruce for all altitudes combined, confirming our main hypothesis. This is consistent with results from other studies in which spruce was the least drought-tolerant species when compared to Silver fir and Douglas fir (Bouriaud & Popa, 2009; Elling, Dittmar, Pfaffelmoser, & Rötzer, 2009; Feliksik & Wilczyński, 2009; van der Maaten-Theunissen et al., 2013; Zang et al., 2014). The differences in drought responses between the species may be explained by their intrinsic differences in morphology and physiology.

The root systems of the three species on free draining soils, which was also characteristic for our sites, are distinctly different. Whereas Norway spruce typically has a shallow root system (Larcher, 2003), Silver fir has a deep taproot and Douglas fir typically a heart root system with a leading taproot and extensive lateral roots (Köstler, Brückner, & Bibelriether, 1968; Mauer et al., 2012). In the case of extreme droughts, deeper root systems can exploit water from a greater soil volume and thus delay the onset of drought stress (Bréda, Huc, Granier, & Dreyer, 2006), which results in greater resistance of radial growth.

Tree ring width is directly connected to the seasonal cambial activity and resulting xylem formation. Silver fir has a significantly longer wood formation period than spruce, with the beginning in early April and the end in late October at similar elevations in the Slovenian forests (Gričar & Čufar, 2008; Swidrak, Gruber, & Oberhuber, 2014). In contrast, wood formation in Norway spruce was recorded between April and August to September, with a peak in June (Gričar & Čufar, 2008; Swidrak et al., 2014). Douglas fir cambial activity has been recorded between May and October (Beedlow, Lee, Tingey, Waschmann, & Burdick, 2013). However, in another study of the 2003 drought event, spruce cell production was recorded to stop in August to September of the drought year, while Silver fir was active until October (Gričar & Čufar, 2008). Although measurements in the Black Forest are not available, and there might be a shift in the time scale, the comparison between the species is realistic. It appears that longer wood formation periods in Silver fir and Douglas fir allow these species to partially compensate for drought periods during which cell formation ceases. This may be achieved through early or late growth during the year of the drought, and through replenishing resources to support growth in the following year, resulting in higher resistance and resilience. The temporal dynamics in wood formation may also explain the lack of differences in growth responses among species in relation to the drought of 1976, when Norway spruce was actually capable to resume radial growth after the drought (Kohler, Sohn, Nägele, & Bauhus, 2010). When considering the average response of each species across the two drought events to assess the overall reaction to droughts, spruce shows clearly the lowest resistance and resilience and Silver fir the highest (NS Rt = 0.79; Rs = 0.94; DF Rt = 0.84, Rs = 1.01; SF Rt = 0.88, Rs = 1.04).

4.2 | The influence of climatic factors on drought responses

In this study, variation in altitude provided a gradient in average temperature and precipitation, with significant differences between the three altitudinal levels. It was assumed that the effects of dry years were less pronounced at high elevations with cooler
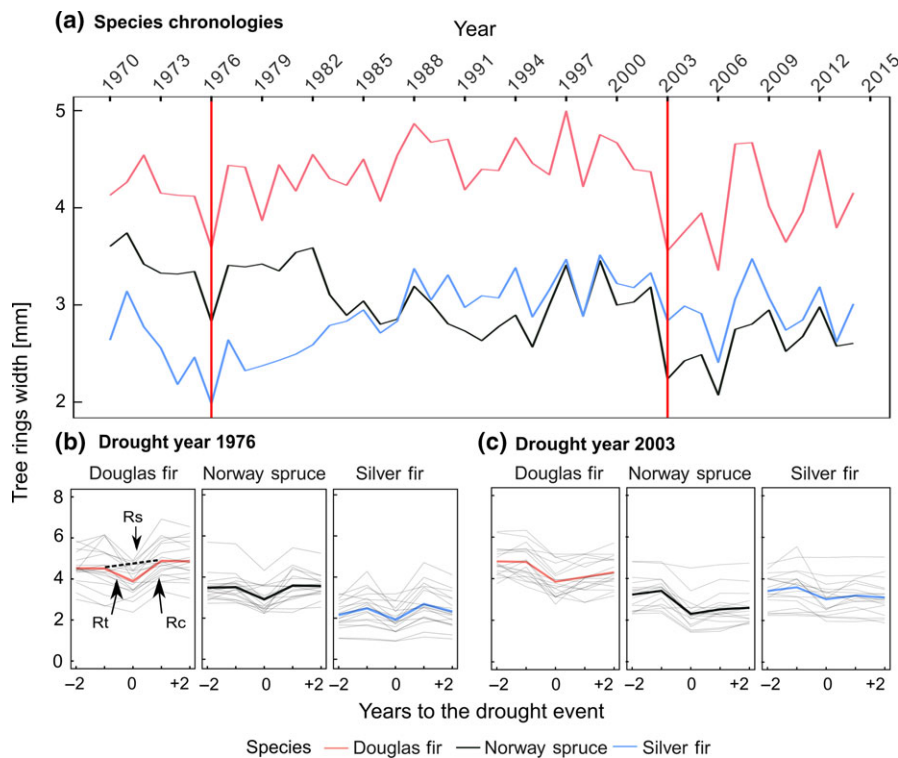
(a) Species chronologies

(b) Drought year 1976

(c) Drought year 2003

FIGURE 3 Mean chronologies of tree ring width per species (a) and magnification of ± 2 years from the drought event (b), (c). Species averages include 270 samples; site averages (grey lines) include 15 sampled trees. Full red lines in panel a. indicate the drought years 1976 and 2003. The response variables resistance (Rt), recovery (Rc), and resilience (Rs) are indicated in panel b
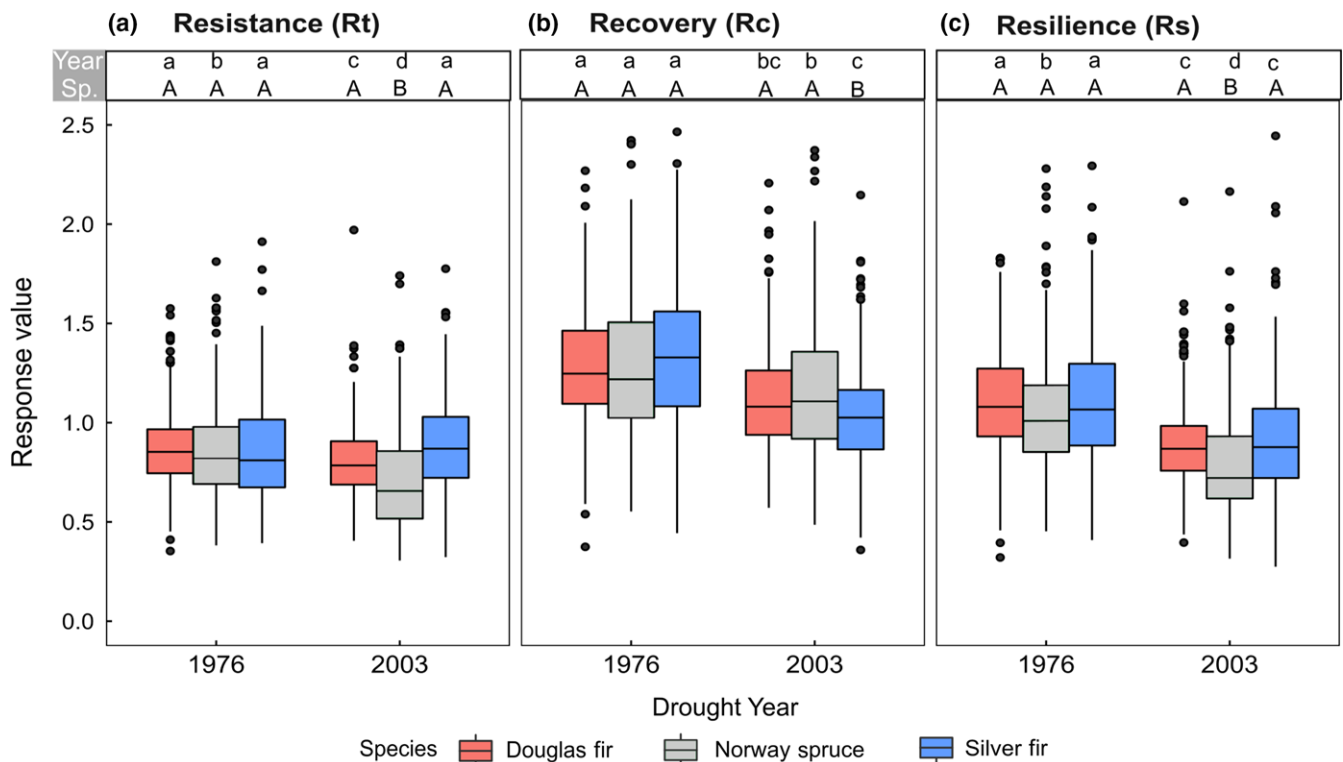

FIGURE 4 Species responses to the drought events in terms of resistance, recovery, and resilience for the years 1976 and 2003, considering ± 2 years to the event year. Capital letters indicate differences between the species for each index and year, and small letters indicate the species differences between the two drought years (ANOVA and post hoc tests, $p < .05$). The vertical lines represent the "whiskers" for the 5 and 95 percentiles of the data distribution

temperatures and higher precipitation. We further assumed that Norway spruce would benefit from increasing elevation more than the other two species.

However, this hypothesis was confirmed only for Silver fir, for which radial growth was more resistant and resilient to drought at higher than at lower sites (Desplanque et al., 1999; van der
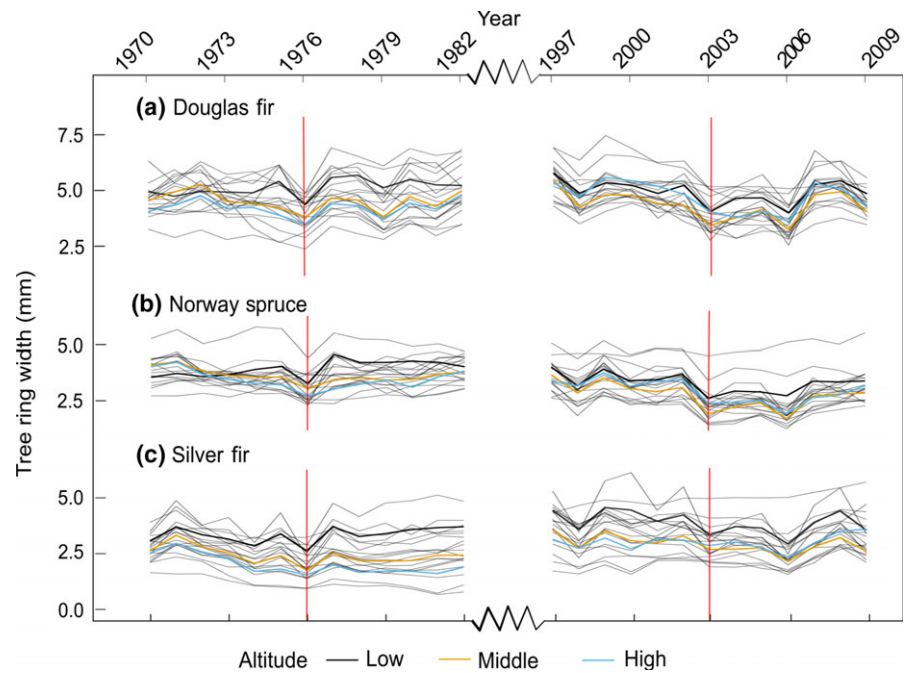
FIGURE 5 Subset of the mean chronologies of tree ring width by altitudinal ranges (Low, Middle, and High) for the years 1970–1982 and 1997–2009. The red lines highlight the drought years 1976 and 2003
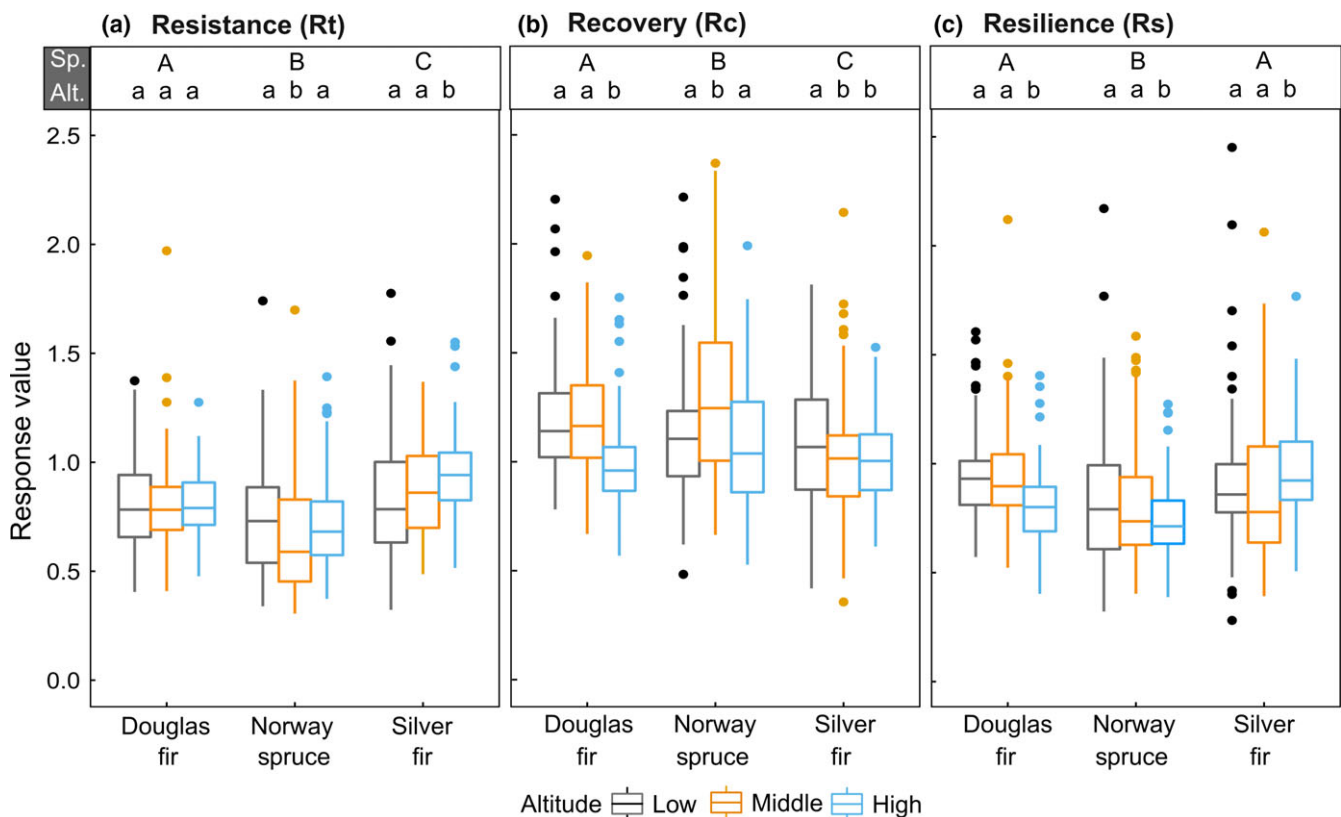

FIGURE 6 The effect of altitude on species-specific responses to the drought event of 2003 in terms of resistance, recovery, and resilience considering ± 2 years to the drought year. Different letters indicate significant differences between the altitudes (repeated ANOVA, $p < .05$)

Maaten-Theunissen et al., 2013). In contrast, radial growth of spruce and Douglas fir did not show improved growth responses to drought at higher altitudes. The differences at high elevations may be connected with winter temperature thresholds on photosynthetic activity. Winter photosynthesis has been recorded for both Silver fir and Douglas fir when temperatures were mild (~5°C, Emmingham, 1977; Bailey & Harrington, 2006), improving growth and carbohydrate storage of the following year (Guehl, Clerc, & Desjeunes,

1985; Lebourgeois, 2007). In consequence, this process, which is more likely at low and mid elevations, might aid recovery of radial growth. In contrast, photosynthesis at low temperatures is negligible in spruce, possibly an adaptation to the very cold winters of its native distribution range in subalpine and boreal forests (Guehl et al., 1985; Rossi et al., 2008). In general terms, the differences in drought responses between the three altitudinal levels were comparatively small. This reflects the relatively small altitudinal gradient (300–1100 m a.s.l). Hence results from our study should not be directly compared with results from studies carried out at more extreme sites, which showed an altitudinal effect on growth response to drought (Boden et al., 2014; van der Maaten-Theunissen et al., 2013). The altitudinal effect might also be masked by site characteristics such as soil depth, which were not quantified in this study.

4.3 | Temporal variability in drought responses

The differences in the responses between the 1976 and 2003 drought years and growth rates of the last three decades indicate the need to re-evaluate our knowledge regarding species-specific growth patterns. The improving growth of Silver fir over the last 30 years, following the growth depression related to SO_2 emissions across southern Germany in the 1970–1980s (Elling et al., 2009), and the steadily declining growth of Norway spruce show that responses to particular drought extremes are overlaid by species-specific medium- to long-term growth trends. The decline in spruce that can be observed since the beginning of the 1960s is especially disconcerting (Fig. S1). Similar growth patterns have been seen for Silver fir by Bigler, Gričar, Bugmann, and Čufar (2004), where this trend was indicative of subsequent increased tree mortality. A dramatic decline of Norway spruce in central Europe until 2100 has been projected by Hanewinkel, Cullmann, Schelhaas, Nabuurs, & Zimmermann (2012) and Hanewinkel et al. (2010).

In addition, differences between the seasonal occurrences of the two drought years must be taken into account when comparing the magnitude of the effects. The drought of 2003 was much drier and hotter, especially at high and mid elevations, than the drought in 1976, which started in early spring but with lower summer temperatures (Figure 2). Hence, growth reactions of all three species were stronger in 2003 than in 1976. The dissimilarity of wood production between the tree species makes them differently susceptible to early or late drought. The spring drought had a less pronounced effect on spruce as it could resume growth after the drought (Kohler et al., 2010). In contrast, the summer drought of 2003 stopped the ring formation in Norway spruce 1 month before the regular end of the growing season, resulting in reduced ring width and hence low resistance (Gričar & Čufar, 2008). Owing to their longer growth period, Silver fir and Douglas fir had the chance to restart wood formation in early autumn, resulting in larger rings. Moreover, during a spring drought, conifers might be able to draw upon stem water reserves, such as the elastic tissue of the bark and sapwood, to reduce the effects of soil water shortage (Cermak, Kucera, Bauerle, Phillips, & Hinckley, 2007; Swidrak et al., 2014).

4.4 | Considerations for future forest management

This is one of the few studies that compared tree growth response to drought of Norway spruce, Silver fir, and Douglas fir growing in the same stands for a large region covering a range of climatic conditions. Although, ideally, such a dendroecological study should be combined with an assessment of mortality rates and growth responses of suppressed and intermediate trees to develop a population-level response (Bigler et al., 2004; Nehrbass-Ahles et al., 2014), past studies have shown that trends in tree ring width are indicative of tree vitality or impending mortality (Bigler, Bräker, Bugmann, Dobbertin, & Rigling, 2006; Bigler et al., 2004). We would thus not expect completely different results regarding species differences, if mortality was also considered.

Our study confirmed that Norway spruce is the least drought tolerant of the three investigated conifers and thus it should be replaced or admixed with more drought-tolerant conifers such as Douglas fir and Silver fir, starting at the most drought-prone sites. Our results indicate that the native Silver fir would be a particularly suitable replacement species at higher elevations. At the moment, Douglas fir and Silver fir are also less susceptible to other disturbance factors such as bark beetles that are typically associated with dry and hot summers. However, in many cases such conversion might not be possible due to voluntary restrictions regarding the cultivation of non-native Douglas fir in public forests, or may be impractical where advanced regeneration of other tree species such as beech is already abundant. Furthermore, given the future uncertainties and the lessons that have been learned in the past, it is not advisable to replace spruce monocultures with monocultures of Silver fir or Douglas fir. An increasing mixture of conifers and broadleaves is more desirable, so to maintain the high economic performance and contribution to climate change mitigation of the former (Weingarten et al., 2016). In addition, uneven-aged mixtures might provide further benefits regarding productivity and stability (Danescu, Albrecht, & Bauhus, 2016).

Here, we analysed growth patterns of the three species from mixed-species stands, but we did not quantify the effect of mixtures, which will be the subject of subsequent analyses. Mixtures may not just help to spread the risk associated with particular species in relation to different types of disturbance and stress; they may also lead to higher productivity (Forrester & Bauhus, 2016). Even mixtures between functionally similar conifer species have shown complementarity effects (Danescu et al., 2016; Forrester, Kohnle, Albrecht, & Bauhus, 2013; Lebourgeois, Gomez, Pinto, & Mérian, 2013). However, during extreme droughts, the water stress in mixed stands may actually be increased for one or more of the participating species when compared to the respective monocultures (Forrester et al., 2016). Hence, we do not know to what extent our results are transferrable to mono-specific stands of the three species.

Finally, trees of all three species at our study sites were still capable of recovering from a single drought event. However, the effect of consecutive drought years might drastically change this capability (Lloret et al., 2011). It remains to be seen, whether the relative

differences in drought tolerance between species remain similar under such conditions.

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