



# Intimate mixtures of Scots pine and Sitka spruce do not increase resilience to spring drought

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## ABSTRACT

Understanding how we can increase the resilience of forest systems to future extreme drought events is increasingly important as these events become more frequent and intense. Diversifying production forests using intimate mixtures of trees with complementary functional traits is considered as one promising silvicultural approach that may increase drought resilience. However, the direction and magnitude of the drought response of mixed-species stands relative to monospecific stands of the same species can vary with species identity, relative abundance and levels of competition in a focal tree's immediate neighbourhood. Using a long-term experiment where tree-level mortality and the neighbourhood composition of each tree was known, we assessed the radial growth response of 24-year-old Scots pine (*Pinus sylvestris*) and Sitka spruce (*Picea sitchensis*) trees in intimately mixed and monospecific stands to a short-duration, high-intensity spring drought in Scotland. Mixing proportions included 25:75, 50:50 and 75:25 of *P. sylvestris* and *P. sitchensis*. At the species level, Scots pine was more drought resistant and resilient than Sitka spruce, while Sitka spruce showed higher recovery. Surprisingly, neither pre-drought tree size nor neighbourhood competition were significantly associated with resistance or resilience to drought, and trees of both species within monospecific stands showed higher recovery and resilience than trees growing in mixed stands. Our study suggests intimate mixtures of these two species may not be an effective way to mitigate the negative impacts of future extreme spring drought events. Given that these two species comprise almost 70% of coniferous forests in the UK, our results highlight the pressing need to better understand their vulnerability to drought and the conditions under which intimate mixtures of these species could be beneficial or detrimental. Such knowledge is essential if we are to enable forest managers to effectively plan how to adapt these forests to the challenges of a changing climate.

## 1. Introduction

With the intensity, duration and frequency of extreme drought events expected to increase in the coming decades across many parts of the world (Dai, 2013; McDowell et al., 2018; Trenberth et al., 2014), understanding how forest managers can increase the resilience of forest systems to future extreme drought events is critically important (Field et al., 2020; Sohn et al., 2016). Diversifying species composition at a range of scales has been proposed as a promising approach to increase the drought resilience of planted forests (Bauhus et al., 2017a; Messier

et al., 2021) and reduce drought-linked losses in biomass accumulation. This approach includes the use of intimate mixtures, where the term 'intimate' indicates that some or all of a given tree's immediate neighbours are of a different species. However, a growing body of evidence is highlighting that the existence and nature of any mixing effects on both forest growth and drought resilience are both species and context-dependent (Gillerot et al., 2021; Grossiord, 2019; Grossiord et al., 2014; Jactel et al., 2017; Van de Peer et al., 2018). For example, Muñoz-Gálvez et al. (2020) demonstrated higher growth for *Pinus sylvestris* in mixtures with *Quercus pyrenaica* under drought conditions compared to

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monospecific stands, but also observed a resistance/recovery trade-off in both these species. Such trade-offs between the different components of tree resilience (Lloret et al., 2011) have now been documented across gymnosperm species both spatially (Gazol et al., 2017) and temporally (Li et al., 2020) in some of the most abundant and economically important tree species in Europe (Vitasse et al., 2019), possibly reflecting different ecophysiological strategies for dealing with drought (Gazol et al., 2020; Li et al., 2020).

The ecological theory proposing better performance of mixed-species forests under drought relative to monospecific stands of the same species relates in part to processes such as niche differentiation or facilitation, collectively referred to as ‘complementarity’ (Loreau and Hector, 2001). Niche differentiation can occur when differences in the physiological or morphological traits of admixed species increases access to, or exploitation of available resources, potentially acting to reduce direct tree-to-tree competition under stressful conditions (Bauhus et al., 2017b). Niche differentiation can result from variability in tree architecture above and below ground and vary over time. Stratification of the canopy can lead to greater total light capture and create favourable microclimates (De Frenne et al., 2021), while differences in rooting depth can increase access to water in mixed-species stands compared to monospecific stands of the same species. Facilitative processes such as hydraulic redistribution (where water is moved from deeper, moister soil layers to dryer surface soils via plant roots) has also been shown to mitigate against the negative effects of drought on individual trees (Neumann et al., 2012; Pickles and Simard, 2017).

Studies that look at the composition of individual tree neighbourhoods to understand the relationship between species diversity, competition and forest productivity highlight the importance of interactions between species and individual trees at fine spatial scales (Fichtner et al., 2020, 2018, 2017). Vitali et al. (2018) demonstrated that the drought response of Norway spruce (*Picea abies*) in mixtures could be positive or negative depending on the identity of the species in a tree’s immediate neighbourhood, while Jourdan et al. (2020) showed that the proportion of heterospecific neighbours could have a positive, negative or neutral effect on drought resilience depending on the identity of the focal species. Furthermore, Fichtner et al. (2020) provided evidence that the functional traits of the species occupying a tree’s immediate neighbourhood play a dominant role in mediating individual tree drought response, with drought sensitive species benefiting from more functionally diverse neighbourhoods. Specifically, Fichtner et al. (2020) highlighted how species with low cavitation resistance particularly stand to benefit from growing in diverse neighbourhoods. In addition to the functional characteristics of admixed species, individual tree size can be a strong predictor of tree growth response to drought, with larger trees commonly reported to be more susceptible to drought (Bennett et al., 2015; Martínez-Vilalta et al., 2012; Ovenden et al., 2021b). This pattern has been found to be particularly evident in *P. sylvestris* (Merlin et al., 2015) and is likely associated with, but not limited to differences in stomatal control on photosynthesis (Zang et al., 2012) and the fact that larger trees are often exposed to higher solar radiation and leaf-to-air vapour pressure deficit than sub-canopy trees (Bennett et al., 2015).

How processes at the level of individual trees and their neighbourhoods interact and scale up to patterns of drought resistance and resilience at the stand level is an equally important but under-explored aspect of forest drought studies, often due to sampling designs that fail to record the full range of tree sizes or capture the influence of tree mortality (Bottero et al., 2021). However, understanding how different species, trees growing in different species mixtures, mixing proportions or pre-drought tree and stand characteristics influence drought response is particularly important for informing forest management decisions targeted at increasing the drought resilience of both economically and ecologically important tree species (Thurm et al., 2016).

In the UK, Sitka spruce (*Picea sitchensis* Bong. Carr.) and Scots pine (*Pinus sylvestris* L.) are the two most economically important timber

species, collectively making up > 68 % of all coniferous forest area, with *P. sitchensis* alone comprising 51 % (Forest Research, 2020). *P. sitchensis* is considered to be a drought-susceptible species (Grant et al., 2018; Green et al., 2008; Huang et al., 2017) and often has a shallow rooting architecture in Scotland on upland sites (Coutts and Philipson, 1987), sometimes due to planting on seasonally waterlogged soils (Quine and Gardiner, 2007). In contrast, *P. sylvestris* is a widely distributed (Matías and Jump, 2012), more drought resistant species due to its ability to root deeper and access deeper water sources (Faulkner and Malcolm, 1972; Mickovski and Ennos, 2002), its higher cavitation resistance than *P. sitchensis* (Jackson et al., 1995) and ability to increase both fine root biomass of absorptive fine roots in mixed- relative to monospecific stands (Wambsganss et al., 2021). Similarly, differences in growth rates and the nutritional requirements of *P. sylvestris* and *P. sitchensis* has meant that these two species are sometimes planted in nursing mixtures where the pine facilitates the growth of the spruce through improved nitrogen availability on nutrient poor soils (Mason et al., 2021; Mason and Connolly, 2018). This in turn means that intimate mixtures of these two species likely result in structural variability, canopy stratification and differences in site microclimate (e.g. through shading). Consequently, these two species potentially express complementary functional traits that may also act to reduce drought stress when planted in intimate mixtures. However, little is known about the radial growth response of mature trees of either species to drought and to our knowledge, no study has yet compared the relative performance of these two species under drought conditions in both monospecific and mixed-species stands.

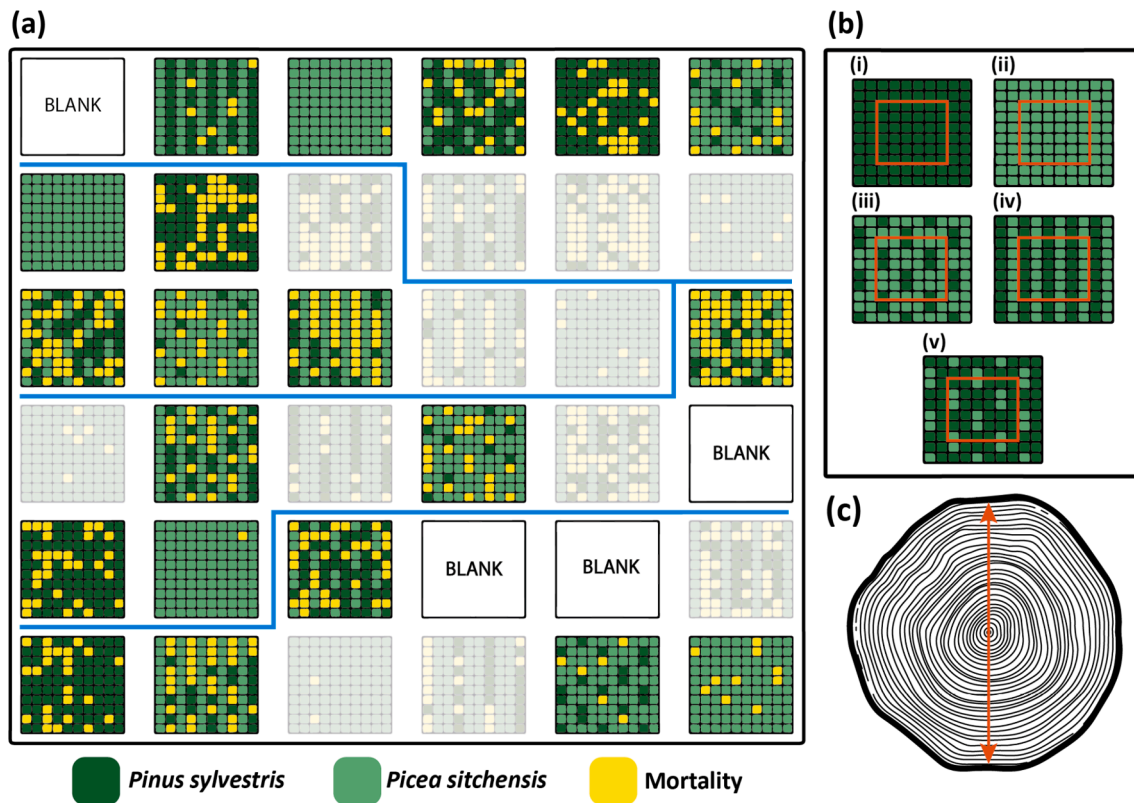
In this study, we set out to determine whether *P. sitchensis* and *P. sylvestris* differed in their resistance, recovery, and resilience to an extreme spring drought event in 2012 using an experimental forest of these two species containing both mixed and monospecific stands. We examined whether pre-drought tree size modulated individual drought response and how patterns at the tree level change depending on the species, neighbourhood composition at establishment and proportion of each species in intimate mixtures. Specifically, we aimed to test the following hypotheses:

1. *P. sitchensis* will exhibit lower resistance but higher recovery and resilience than *P. sylvestris* to a commonly experienced extreme drought event, reflecting the greater drought susceptibility of *P. sitchensis* and the observed trade-off in the components of tree resilience noted in other gymnosperms.
2. As more drought-susceptible species have been shown to benefit from the presence of more drought adapted species (Fichtner et al., 2020), *P. sitchensis* resistance and resilience will increase with the numbers of *P. sylvestris* trees in their immediate neighbourhood. In turn, this difference is expected to result in the highest drought resistance and resilience in those mixtures with the highest pine-to-spruce ratio.
3. Larger trees will show lower resistance and resilience to drought than smaller trees, reflecting the findings of other recent work across a range of species (Bennett et al., 2015).

## 2. Materials and methods

### 2.1. Site description and management history

Our study site was established in 1988 as a nursing experiment to investigate the long-term differences in growth and yield between intimate mixtures of *Pinus sylvestris* and *Picea sitchensis*. Trees were planted in different proportions alongside monospecific stands of the same two species (Fig. 1, Table 1) (Mason et al., 2021). The experiment is located in the north of Scotland (57°47′05.0″N, 4°08′53.5″W) at an elevation of 213 m a.s.l. with the soil classified as a podzolic ironpan with a peaty surface horizon (i.e. a peaty layer of 15–45 cm across much of the site). The site was cultivated to 60 cm with a double mould-board plough and tine to break the ironpan at the time of establishment. The planting



**Fig. 1.** Experimental layout depicting the location of every tree and whether each tree was dead or alive in 2018. (a) Dark and light green squares indicate live *P. sylvestris* (SP) and *P. sitchensis* (SS) trees respectively, yellow squares indicate trees recorded as ‘dead’ during the 2018 survey and blue lines delineate the four blocks of the randomised block design. Plots labelled as “Blank” indicate filler plots with non-experimental trees established at the same time, while translucent plots are additional treatments which were not included in the present study. (b) Indicates the mixing proportions at establishment and resultant tree neighbourhoods used in the present study, with (i) = pure SP, (ii) = pure SS, (iii) = 75 % SS with 25 % SP, (iv) = 50 % SS and 50 % SP and (v) = 25 % SS with 75 % SP. Orange squares in (b) indicate the internal 6x6 sample plots from which dendrochronological data were collected from all live trees. (c) Indicates the north/south direction that tree-cores were collected. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**

Proportions of *P. sylvestris* (SP) and *P. sitchensis* (SS) in the three intimate mixtures (SS25, SS50 and SS75) used in this study along with a description of the conspecific and heterospecific neighbourhoods produced by each mixture (or monoculture – SP and SS).

Treatment code	Treatment details	Neighbourhoods
SP	Pure SP	Each SP neighboured by 8 other SP
SS	Pure SS	Each SS neighboured by 8 other SS
SS75	A 75:25 SS and SP mixture. Mixture created by a pattern of one row of pure SS followed by one row with alternating pairs of SS and SP.	SS surrounded by 5 other SS and 3 SP SS surrounded by 7 other SS and 1 SP SP surrounded by 7 SS and 1 other SP
SS50	A 50:50 SS and SP mixture. Mixture created by a pattern of alternate rows of each species	SS surrounded by 2 other SS and 6 SP SP surrounded by 2 other SP and 6 SS
SS25	A 25:75 SS and SP mixture. Mixture created by a pattern of one row of pure SP followed by one row with alternating pairs of SS and SP.	SP surrounded by 5 other SP and 3 SS SP surrounded by 7 other SP and 1 SS SS surrounded by 7 SP and 1 other SS

Parts of this table have been modified with permission from [Mason et al., \(2021\)](#).

scheme resulted in monospecific stands of *Pinus sylvestris* and *Picea sitchensis* and five intimate mixtures of the two species (mixed in 25:75, 33:66, 50:50, 66:33 and 75:25 proportions), so that the eight trees immediately surrounding each focal tree characterised its neighbourhood (Fig. 1). In this present study, we focused on the monospecific stands and the 25:75, 50:50 and 75:25 mixtures only. Four replicate plots of each treatment were established in a randomised block design, with each plot consisting of 100 trees in a 10x10 tree grid at 1.9–2.0 m spacing (Fig. 1) surrounded by a two- to three-deep tree buffer on all sides (buffer trees are not shown in Fig. 1). A small amount of post-planting mortality was replaced with the original species across the experiment in 1989 and 1990 to ensure all plots were fully stocked. No fertilisers were applied to the treatments used in this study, but the site was known to be nitrogen deficient ([Mason et al., 2021](#)). No thinning had been conducted in the stand since it was established and no wind-throw has been recorded historically or at the time of sampling. An experiment-wide mortality assessment was conducted visually between October and December 2018, during which the status of each tree (dead or alive) (Fig. 1 and Table 2) and its diameter at breast height (DBH – 1.3 m) was recorded. While all mixtures had > 99 % survival in 2000 ([Mason et al., 2021](#)), a considerable amount of mortality (predominantly *P. sylvestris*) was present across many of the treatments by 2018. We quantified neighbourhood composition based on planted species proportions, not post-mortality species proportions, because the former did not require additional assumptions to calculate, they represent a large proportion of the lifetime of the experiment (prior to the 2012 drought) and managers are less likely to modify tree neighbourhoods (e.g. due to economic constraints of selective thinning in short-rotation forestry), making the planted species proportions the treatment of more interest in



**Table 2**

Total number of trees noted as dead during the 2018 mortality assessment for each species (SP = *P. sylvestris* and SS = *P. sitchensis*) in pure (SP and SS) and mixed (SS25, SS50 and SS75) stands, summed across all four replicates in the wider 10x10 tree plots (Total mortality) and within the internal 6x6 tree sample plots (Total sample plot mortality). The Total number of sample trees refers to the number trees from which undamaged dendrochronological samples were used in the analysis. Values in parentheses indicate the percentage mortality of each species in each treatment across the wider experiment and in the sample plots.

Mixture	Species	Total mortality	Total sample plot mortality	Total number of sample trees
SP	SP	113 (28 %)	36 (25 %)	40
SS	SS	12 (3 %)	4 (3 %)	40
SS25	SP	153 (51 %)	49 (45 %)	50
SS25	SS	0 (0 %)	0 (0 %)	27
SS50	SP	96 (48 %)	41 (57 %)	31
SS50	SS	0 (0 %)	0 (0 %)	72
SS75	SP	54 (54 %)	20 (56 %)	15
SS75	SS	7 (2 %)	3 (3 %)	78
		435	153	353

this study. For a more detailed description of the site and tree establishment, see [Mason et al., \(2021\)](#).

## 2.2. Dendrochronological data

In November 2019, internal 6x6 tree plots were established centrally in each of the wider 10x10 tree plots, within which dendrochronological samples were collected for the following mixing proportions: SP, SS, SS25, SS50 and SS75 ([Fig. 1](#) and [Table 1](#)). Two cores were collected using 5.15 mm Hagl f increment borers from each live tree in the north and south direction (parallel with the direction of the plough lines) at 1.3 m high in each of the four replicates of each mixture. In the pure *P. sitchensis* and *P. sylvestris* plots, 10 trees of each species were randomly selected for coring from each of the four replicates. This sampling design resulted in 706 useable cores (a small number of cores were damaged) from 353 sample trees. Additionally, the DBH at 1.3 m high of all live trees from inside each internal 6x6 tree sample plot was measured. No samples were collected from dead trees. Sampling these mixing proportions produced a mirrored design, meaning that both *P. sitchensis* and *P. sylvestris* were represented by individual trees for which the eight-tree neighbourhood at establishment consisted of one, two, five, seven or eight conspecific and corresponding seven, six, three, one and zero heterospecific neighbours.

Each tree core was mounted, sanded with progressively finer sandpaper to ensure each ring boundary could be readily identified and then scanned at a resolution of 1600dpi. The width of each ring was subsequently calculated for each tree core using WinDENDRO image analysis software (Regents Instruments, Quebec). Each core was then crossdated, both visually and using the *dplR* package in R version 3.6.1 (R Core Team, 2019), resulting in 321 confidently dated trees (of the original 353 useable samples). These 321 trees were then detrended using an autoregressive detrending method using the *dplR* package to produce a Ring Width Index (RWI) ([Bunn et al., 2019](#)) ([Fig. S1](#)). We used an autoregressive detrending method over other methods such as cubic smoothing splines as the use of splines did not adequately remove age related trends in our data, likely linked to the young age of our samples. We also calculated annual tree growth rate in terms of basal area increments (BAI) following [Eq. \(1\)](#),

$$BAI = \pi(R_t^2 - R_{t-1}^2) \quad (1)$$

where  $R$  is the radius of the tree in year  $t$ . Tree size in terms of basal area (BA) was subsequently calculated for each year by summing annual BAI over time for each tree ([Table S1](#)).

## 2.3. Pointer year detection and climate analysis

We used the Standardised Growth Change (SGC) method to identify negative pointer years (PYs) in the tree-ring record (representing years of abnormally low growth) as this method has been shown to outperform other common PY detection methods ([Buras et al., 2020](#)). PY analysis was conducted using detrended RWI values for all trees across the common overlap period (2001 – 2019) and considered extreme if they lie outside the 95 % confidence interval, meaning that only abnormally low growth episodes with a probability of occurring <0.025 are considered as negative PYs ([Buras et al., 2020](#)).

To identify any short term (monthly), seasonal (3 months), or multi-seasonal (6 months) droughts in the climate record, we calculated the Standardised Precipitation Evapotranspiration Index (SPEI) ([Vicente-Serrano et al., 2010](#)) using the *SPEI* package in R ([Begueria and Vicente-Serrano, 2017](#)). The SPEI uses a standardised climatic water balance calculated as the difference between precipitation and evapotranspiration over different timescales to give a relative measure of drought severity ([Begueria et al., 2014](#); [Vicente-Serrano et al., 2010](#)). We calculated the SPEI for every month and year, integrated over one, two, three and six months from 1988 to 2019, reflecting the dates of tree establishment and sampling. The SPEI was calculated using interpolated climate data at 1 km resolution, obtained from the Climate Hydrology and Ecology Research Support System (CHESS) meteorology dataset for Great Britain ([Robinson et al., 2017](#)). Only 2012 was identified as an extreme drought year between 1988 and 2019 (see section 3.1 – *Drought year detection*) in both the climate and tree-ring record (when the experiment was 24 years old) and so this year became the focus of our analysis.

## 2.4. Neighbourhood competition

To assess the influence of neighbourhood competition on tree-level drought response, we calculated a distance-dependent index of neighbourhood competition in the year before drought (2011) following [Eq. \(2\)](#),

$$TotNID_i = \sum_{j=1}^8 \frac{BA_j}{distance_{ij}} \quad (2)$$

where  $TotNID_i$  is the neighbourhood index for each tree ( $i$ ), with eight neighbours ( $j$ ),  $BA$  is the basal area of the  $j$ th competitor (cm) and  $distance$  is the distance between tree  $i$  and the  $j$ th neighbour (m) ([Forrester et al., 2013](#); [Vitali et al., 2018](#)). Due to the sampling design and the way in which  $TotNID_i$  is calculated (requiring the  $BA$  of all eight trees in each tree's immediate neighbourhood),  $TotNID_i$  could only be calculated for live trees forming the central 4x4 trees inside the 6x6 tree sample plots. Any trees noted as dead during an experiment-wide mortality assessment carried out by Forest Research Technical Support Staff in 2018 were also considered to have been dead or exerting no competitive influence in 2011 and so had their  $BA$  set to zero for the purposes of calculating the  $TotNID_i$  for live trees in the year before drought. Any sample trees that could not be confidently crossdated were excluded from this analysis, as were any trees for which an undatable tree would have formed part of the immediate eight tree neighbourhood (as the presence of an undatable tree in a focal tree's neighbourhood meant  $TotNID_i$  could not be derived), resulting in 108 trees for which  $TotNID_i$  in 2011 was calculated (34 % of the crossdated trees).

## 2.5. Resistance, recovery and resilience

To quantify the impact of the 2012 drought, we calculated the Resistance ( $R_t$ ), Recovery ( $R_c$ ) and Resilience ( $R_s$ ) indices proposed by ([Lloret et al., 2011](#)) for each tree using RWI values. Resistance is commonly calculated as the ratio of growth in the drought year relative to a pre-drought growth average ( $Dr/PreDr$ ), recovery as the ratio of a

post-drought growth average to growth in the drought year (PostDr/Dr), and resilience as the ratio of a post-drought growth average to a pre-drought growth average (PostDr/PreDr). For these calculations, Dr, PreDr and PostDr are growth in the drought year and the pre- and post-drought growth averages respectively. Pre- and post-drought growth averages are normally calculated using between two- and four-years growth before and after the drought year (Rubio-Cuadrado et al., 2018; Steckel et al., 2020; Vitasse et al., 2019), however recent work has demonstrated how the choice of the number of years over which growth averages are calculated can influence estimates of these indices (Ovensen et al., 2021b; Schwarz et al., 2020). To check our results were robust to the choice of pre- and post-drought period, we calculated multiple values of  $R_t$  for each tree using pre-drought growth averages derived from two, three and four years before the 2012 drought and calculated  $R_c$  for each tree one, two, three and four years after drought, instead of using a post-drought growth average. Calculating  $R_c$  in this way (as opposed to using post-drought growth averages) allowed recovery to be assessed annually throughout the post-drought period (where climate likely varied from year to year). We calculated  $R_s$  for each tree in the first, second, third and fourth years after drought using pre-drought growth averages derived from two, three and four years before drought, resulting in 12 estimates of  $R_s$  for each tree.

## 2.6. Statistical analysis

We initially fit three separate linear mixed-effects models using the *lme4* package in R (Bates et al., 2015) following Eq. (3) to assess whether Resistance ( $R_t$ ), Recovery ( $R_c$ ) or Resilience ( $R_s$ ) to the 2012 drought differed between species, neighbourhood composition and tree size in the year before drought ( $BA_{2011}$ ). These models also allowed us to test whether our results were sensitive to the timescales used to calculate each index using all 321 confidently dated sample trees.  $R_t$ ,  $R_c$  and  $R_s$  (response variables) were log-transformed prior to analysis to satisfy assumptions of normally distributed residuals.

$$Index_{ij} = X_{ij}\beta + b_{0ij} + \varepsilon_{ij} \quad (3)$$

In Eq. (3),  $Index_{ij}$  refers to either Resistance ( $R_t$ ), Recovery ( $R_c$ ) or Resilience ( $R_s$ ) for the  $j$ th tree in the  $i$ th plot,  $X$  is an  $n \times p$  matrix of  $p$  fixed effect variables (including *Species*, *Conspecific Neighbourhood*, *Index calculation* and  $BA_{2011}$  fixed effects) across the  $n$  measured trees,  $\beta$  is a  $p \times 1$  column vector of regression estimates,  $b_{0ij}$  represents the random effect of  $TreeID_{ij}$ , where  $b_{ij} \sim N(0, \sigma_{b0}^2)$  and  $\varepsilon_{ij}$  represents error term, where  $\varepsilon_{ij} \sim N(0, \sigma_e^2)$ .  $\sigma_{b0}^2$  and  $\sigma_e^2$  are estimates of variance of random effects and residual error, respectively. *Conspecific Neighbourhood* stands for the number of conspecifics in a focal tree's immediate neighbourhood of eight surrounding trees at establishment, with five treatment levels (one, two, five, seven and eight). *Index calculation* stands for the different combinations of the pre-drought and post-drought period lengths used to define the three indices.  $BA_{2011}$  was globally standardised across all trees (by subtracting the mean and dividing by the standard deviation) and represents tree size in the year before drought. Two-way interactions between *Species*  $\times$  *Neighbourhood*, *Neighbourhood*  $\times$  *Index calculation* and *Species*  $\times$  *Index calculation* were included in all models.

We subsequently re-fit the same three mixed-effects models for  $R_t$ ,  $R_c$  and  $R_s$  detailed in Eq. (3) with the restricted dataset of 108 trees for which the 2011 neighbourhood competition index ( $TotNID_i$ ) could be calculated but including  $TotNID_i$  as an additional predictor variable to test for the influence of neighbourhood competition on  $R_t$ ,  $R_c$  and  $R_s$ . No significant interactions between *Species*  $\times$   $TotNID_i$  and *Neighbourhood*  $\times$   $TotNID_i$  were found for any of the three models and so these interactions were dropped from the final models that included  $TotNID_i$ .

Finally, we fit three mixed effect models, again following Eq.3, to investigate the differences in all three indices between the different mixtures (SS, SP, SS25, SS50 and SS75, Table 1, Fig. 1), rather than

between neighbourhoods. In this case, each index ( $R_t$ ,  $R_c$  and  $R_s$ ) was the response variable and *Species*, *Mixture*, *Index calculation* and  $BA_{2011}$  were fixed effects and *Tree ID* was a random effect. For all models, we checked for multicollinearity between predictor variables using the Variance Inflation Factor ( $VIF < 3$  in all cases). We subsequently used the *emmeans* package in R (Lenth, 2016) to conduct post-hoc pairwise comparisons on all fitted mixed-effects models, and corrected for multiple comparisons using the Tukey method.

## 3. Results

### 3.1. Drought year detection

Standardised Growth Change analysis identified a single negative pointer year in the tree-ring record in 2012 ( $p = 0.015$ ) and so this year became the focus of our analysis. The 1-month (SPEI of  $-2.22$ ) and 2-month (SPEI of  $-2.41$ ) SPEI analysis showed that March 2012 corresponded to an extreme drought event (where extreme is defined as an  $SPEI < -2$  (Hoffmann et al., 2018; Potop et al., 2014)). In contrast, SPEI values for April with a one-, two-, three- or six-month integration period in 2012 ranged from  $-0.63$  to  $1.96$ , suggesting that drought conditions did not persist into April 2012. These SPEI values indicate that the extreme drought of 2012 at our study site can be characterised as a short duration, high intensity event in early spring. This assessment is reflected in the raw climate data which shows a combination of both abnormally low precipitation and abnormally high temperatures in March 2012, which in turn corresponds to the start of the growing season for the two study species in Scotland (Adams, 2014; Grace and Norton, 1990). March 2012 precipitation was  $> 2SD$  below the 1988 – 2011 average while the mean monthly temperature in March 2012 was  $> 2SD$  above the 1988 – 2011 average. In contrast, January 2012 was relatively wet with above average precipitation ( $2012 = 130$  mm compared with a 1988 – 2011 mean of  $82 \pm 43$  mm (1SD)) and average temperatures ( $2012 = 2.5$  °C compared with a 1988 – 2011 mean of  $3 \pm 1.3$  °C (1SD)) while both November and December 2011 were not abnormally dry (within 2SD of the 1988 – 2010 average). Collectively, this analysis suggests that it is unlikely that any growth depression in 2012 was due to an abnormally dry winter of 2011/12. Similarly, mean daily temperatures did not drop below zero during March, April, or May 2012, suggesting there were no late spring frosts in 2012 at this site that might have impacted tree growth.

### 3.2. Resistance, recovery, and resilience

Results from the mixed-effects modelling and *post-hoc* analysis using estimated marginal means revealed a significant difference in resistance ( $R_t$ ), recovery ( $R_c$ ) and resilience ( $R_s$ ) between *P. sitchensis* and *P. sylvestris* in response to the 2012 drought event (Fig. 2 and Table 3). *Pinus sylvestris* displayed significantly higher  $R_t$  ( $P. sylvestris = 0.924 \pm 0.032$  (1SE),  $P. sitchensis = 0.687 \pm 0.020$  (1SE),  $p < 0.001$ ; Fig. 2a), while *P. sitchensis* displayed higher  $R_c$  ( $P. sylvestris = 1.06 \pm 0.034$  (1SE),  $P. sitchensis = 1.32 \pm 0.036$  (1SE),  $p < 0.001$ ; Fig. 2b) regardless of the years used to calculate each index (Fig. 2b), though the existence of significant interactions between *Species* and *Index calculation* (Table 3) indicated that the relationships between *Species* and  $R_t$ ,  $R_c$  and  $R_s$  varied depending on the method used to calculate these indices. The interaction between *Species* and the *Index calculation* was more complex for  $R_s$ . The significant differences in resilience observed between *P. sylvestris* and *P. sitchensis* were dependent on the number of years used to calculate the pre-growth average (Fig. 2c). For example, when using a two-year pre-drought growth average to calculate  $R_s$ , we found evidence that *P. sylvestris* had significantly higher  $R_s$  than *P. sitchensis* in the first, second, third and fourth years after the 2012 drought (Fig. 2c). However, if pre-drought growth averages were calculated using four pre-drought years rather than two pre-drought years, *P. sylvestris* was only significantly more resilient than *P. sitchensis* in the second year after

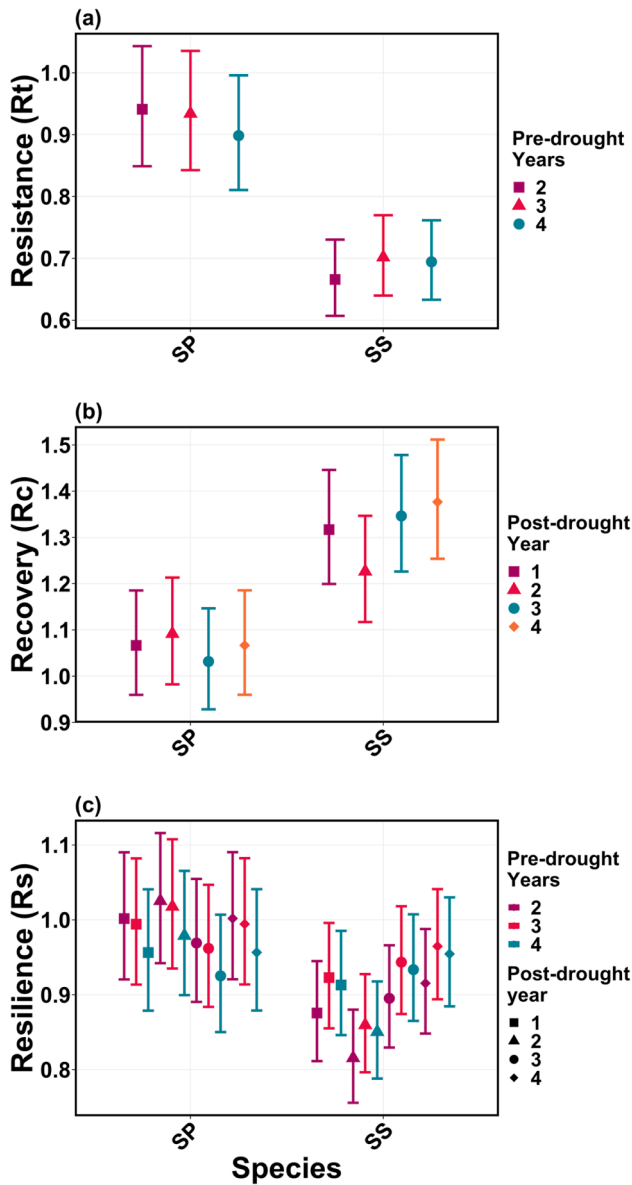


Fig. 2. Differences in Resistance (a), Recovery (b) and Resilience (c) between *P. sylvestris* (SP) and *P. sitchensis* (SS) to the 2012 drought averaged across all conspecific neighbourhoods. Pre- or post-drought year(s) reflect the number of years used to calculate each index. Error bars represent 95% unadjusted confidence intervals and values were back-transformed onto the original scale.

drought. We found no evidence that *P. sitchensis* was ever more resilient to drought than *P. sylvestris*, regardless of the approach to calculating  $R_s$  (Fig. 2c).

Estimated marginal means indicated that monospecific stands (eight conspecific neighbours) had significantly higher  $R_c$  ( $p < 0.04$ ) than neighbourhoods consisting of one or five conspecifics in the second year after drought only (Fig. 3b), but these differences between neighbourhoods were not significant in the first or third year after drought. No other pairwise comparisons between other neighbourhood combinations were significant for  $R_c$  (Fig. 3b). No significant interaction between *Species* and *Neighbourhood* was documented for  $R_c$ ,  $R_t$  or  $R_s$  ( $p > 0.07$  in all cases) (Table 3). Comparing estimated marginal means between neighbourhoods for each species separately showed that the only significant differences in  $R_s$  for both *P. sylvestris* and *P. sitchensis* were between the monospecific neighbourhoods and other neighbourhood types considered. Monospecific neighbourhoods were always associated with higher  $R_s$  compared to all other conspecific neighbourhoods or mixtures

Table 3

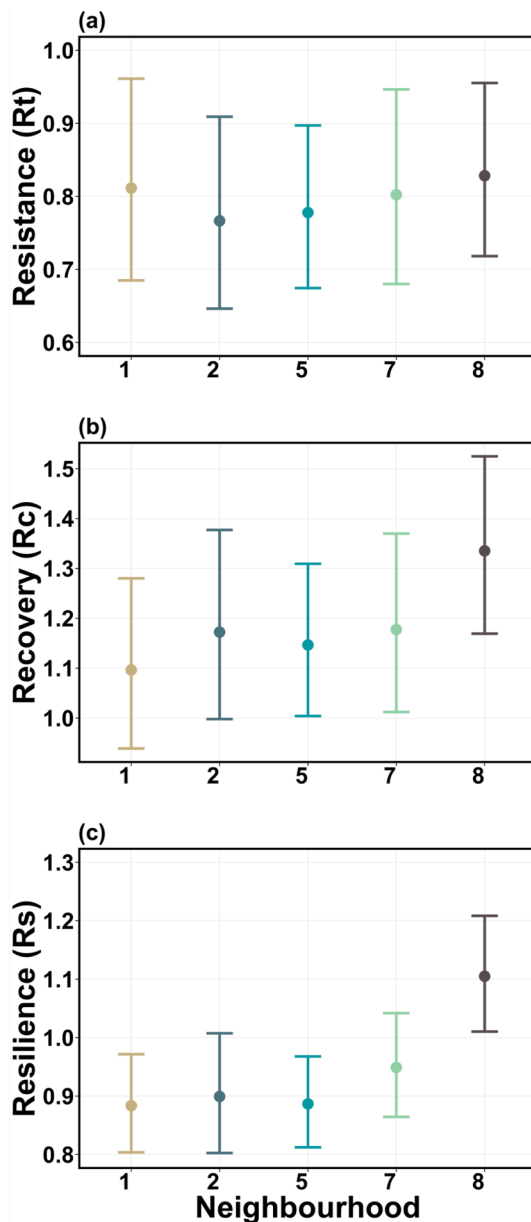
Type 2 ANOVA for the mixed-effects models of Resistance ( $R_t$ ), Recovery ( $R_c$ ) and Resilience ( $R_s$ ) for all 321 sample trees.  $Df$  = degrees of freedom, interactions are denoted by a  $\times$  and significant effects ( $p < 0.05$ ) are highlighted in bold. *Species* was either *P. sitchensis* or *P. sylvestris* while *Neighbourhood* indicates the number of conspecifics (one, two, five, seven or eight) in the immediate eight tree neighbourhood of every tree while  $BA_{2011}$  represents tree size (basal area) in the pre-drought year (2011).

Resistance ( $R_t$ )			
	Chisq	df	p-value
<b>Species</b>	<b>64.033</b>	<b>1</b>	<b>&lt;0.001</b>
Neighbourhood	2.821	4	0.588
<b>Index calculation</b>	<b>65.632</b>	<b>2</b>	<b>&lt;0.001</b>
$BA_{2011}$	1.140	1	0.286
Species $\times$ Neighbourhood	2.071	4	0.722
<b>Species <math>\times</math> Index calculation</b>	<b>100.929</b>	<b>2</b>	<b>&lt;0.001</b>
<b>Neighbourhood <math>\times</math> Index calculation</b>	<b>32.452</b>	<b>8</b>	<b>&lt;0.001</b>
Recovery ( $R_c$ )			
<b>Species</b>	<b>42.558</b>	<b>1</b>	<b>&lt;0.001</b>
Neighbourhood	10.304	4	0.356
<b>Index calculation</b>	<b>25.181</b>	<b>3</b>	<b>&lt;0.001</b>
$BA_{2011}$	4.297	1	0.038
Species $\times$ Neighbourhood	6.300	4	0.178
<b>Species <math>\times</math> Index calculation</b>	<b>32.443</b>	<b>3</b>	<b>&lt;0.001</b>
<b>Neighbourhood <math>\times</math> Index calculation</b>	<b>25.411</b>	<b>12</b>	<b>0.013</b>
Resilience ( $R_s$ )			
<b>Species</b>	<b>22.992</b>	<b>1</b>	<b>&lt;0.001</b>
<b>Neighbourhood</b>	<b>44.464</b>	<b>4</b>	<b>&lt;0.001</b>
<b>Index calculation</b>	<b>113.030</b>	<b>11</b>	<b>&lt;0.001</b>
$BA_{2011}$	3.355	1	0.670
Species $\times$ Neighbourhood	8.526	4	0.074
<b>Species <math>\times</math> Index calculation</b>	<b>152.565</b>	<b>11</b>	<b>&lt;0.001</b>
<b>Neighbourhood <math>\times</math> Index calculation</b>	<b>99.749</b>	<b>44</b>	<b>&lt;0.001</b>

for *P. sitchensis* (Fig. 3c and Fig. 4c). In addition, *P. sylvestris* had significantly higher  $R_s$  than *P. sitchensis* when focal tree neighbourhoods contained one or two conspecifics ( $p = < 0.005$  in both cases), but *P. sitchensis* never displayed higher  $R_s$  than *P. sylvestris* in any of the considered neighbourhood compositions. No other significant differences in  $R_s$  between species based on neighbourhood composition were detected.

Significant two-way interactions were identified between the approach used to calculate all three indices (*Index calculation*) and the conspecific *Neighbourhood* (Table 3 and Fig. 3), indicating that the relationship between neighbourhood composition and all three indices varied depending on the post-drought year and/or the number of years used to calculate each index. *Post-hoc* analysis using estimated marginal means found no significant differences in  $R_t$  between different neighbourhood compositions, regardless of the number of years used to calculate pre-drought growth averages and  $R_t$  (Fig. 3a). Significant differences within neighbourhoods for  $R_c$  were only detected between methods that used two and four post-drought years to calculate post-drought growth averages in neighbourhoods consisting of one or two conspecifics, with a similar pattern found for  $R_s$ .

When considering average tree response in the different mixtures, a similar pattern emerged. No significant differences in  $R_t$  were found between any combinations of pure or mixed stands (Table 4 and Fig. 4a) but significant differences between monospecific and mixed stands were detected for both  $R_c$  and  $R_s$  ( $p < 0.002$  in both cases, Table 4, and Fig. 4b and 4c). For  $R_c$ , pairwise comparisons of estimated marginal means show that monospecific stands of *P. sylvestris* and *P. sitchensis* were not significantly different from one another ( $p = 0.246$ , Table 4) and pure stands of *P. sylvestris* did not display significantly different values for  $R_c$  than any of the other mixtures (SS25, SS50 and SS75,  $p > 0.417$  in all three cases). However, pure stands of *P. sitchensis* displayed significantly higher  $R_c$  than all three mixed stands ( $p < 0.006$  in all three cases) (Fig. 4b). Pairwise comparisons also showed that monospecific stands of both *P. sitchensis* and *P. sylvestris* displayed significantly higher  $R_s$  than all three mixed stands ( $p < 0.006$  in all cases) but were not significantly



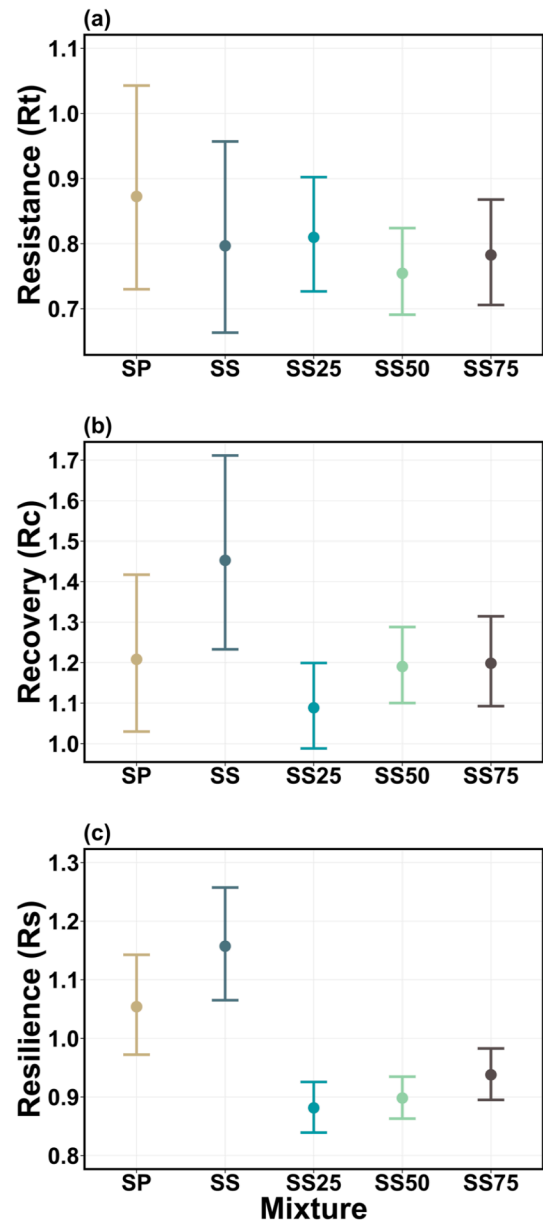
**Fig. 3.** Differences in Resistance (a), Recovery (b) and Resilience (c) between conspecific neighbourhoods (one, two, five, seven or eight conspecifics) to the 2012 drought, averaged across species (*P. sylvestris* and *P. sitchensis*) and the number of years used to calculate each index. Error bars represent 95% unadjusted confidence intervals.

different from each other ( $p = 0.204$ ) (Fig. 4c).

Finally, pre-drought tree size ( $BA_{2011}$ ) was not a significant predictor of  $R_t$  or  $R_s$  (but marginally significant for  $R_c$ ) (Table 3) and neither was  $TotNID_i$  (Tables S2,  $p > 0.21$  in all cases), indicating that neither tree size nor neighbourhood competition were likely associated with differences in the resistance or resilience of the trees in this experiment to the spring drought of 2012.

#### 4. Discussion

In this study, we investigated whether the number of conspecifics in a focal tree's immediate neighbourhood, the degree of neighbourhood competition or species identity was associated with differences in the resistance ( $R_t$ ), recovery ( $R_c$ ) or resilience ( $R_s$ ) of *P. sylvestris* and *P. sitchensis* to a short-duration, but high-intensity spring drought.



**Fig. 4.** Differences in Resistance (a), Recovery (b) and Resilience (c) between the different monospecific and mixed species stands (SP = pure *P. sylvestris*, SS = pure *P. sitchensis*, SS25 = 25 % *P. sitchensis* and 75 % *P. sylvestris*, SS50 = 50 % *P. sitchensis* and 50 % *P. sylvestris* and SS75 = 75 % *P. sitchensis* and 25 % *P. sylvestris*, see Fig. 1 and Table 1 for a more detailed description) to the 2012 drought, averaged across Species and Index calculation. Error bars represent 95 % unadjusted confidence intervals.

Additionally, we investigated whether any relationship between neighbourhood composition and these three indices varied between the two species or with pre-drought tree size, whether any trade-off between these indices existed and how average tree response varied based on the mixing proportions at establishment. We found evidence that *P. sylvestris* was significantly more resistant and resilient to spring drought than *P. sitchensis*, but *P. sitchensis* exhibited greater recovery. In contrast to our expectations, monospecific neighbourhoods of both species displayed higher recovery and resilience than other neighbourhood compositions we considered. Pure stands of both species were also associated with greater levels of resilience than all mixed species stands, and pre-drought tree size and neighbourhood competition had little effect on drought resistance or resilience.

In support of our first hypothesis, we found evidence for a trade-off



**Table 4**

Type 2 ANOVA for the mixed-effects models of Resistance ( $R_t$ ), Recovery ( $R_c$ ) and Resilience ( $R_s$ ) for all 321 sample trees in the different mixtures.  $Df$  = degrees of freedom, *Species* was either *P. sitchensis* (SS) or *P. sylvestris* (SP), *Mixture* indicates the mixing proportions of the two species (SP, SS, SS25, SS50 and SS75) while  $BA_{2011}$  represents tree size (basal area) in the pre-drought year (2011). Significant results ( $p < 0.05$ ) are highlighted in bold.

	Resistance ( $R_t$ )		
	Chisq	df	p-value
<b>Species</b>	<b>32.39</b>	<b>1</b>	<b>&lt;0.001</b>
Mixture	5.43	4	0.246
<b>Index calculation</b>	<b>54.60</b>	<b>2</b>	<b>&lt;0.001</b>
$BA_{2011}$	0.58	1	0.448
Recovery ( $R_c$ )			
<b>Species</b>	<b>14.49</b>	<b>1</b>	<b>&lt;0.001</b>
Mixture	19.37	4	0.001
<b>Index calculation</b>	<b>24.01</b>	<b>3</b>	<b>&lt;0.001</b>
$BA_{2011}$	2.37	1	0.124
Resilience ( $R_s$ )			
<b>Species</b>	<b>25.43</b>	<b>1</b>	<b>&lt;0.001</b>
Mixture	118.86	4	<0.001
<b>Index calculation</b>	<b>106.57</b>	<b>11</b>	<b>&lt;0.001</b>
$BA_{2011}$	1.87	1	0.172

between resistance and resilience with recovery in *P. sitchensis* and *P. sylvestris* (Fig. 2). Resistance ( $R_t$ ) values for *P. sylvestris* were consistently higher than *P. sitchensis* across all neighbourhoods, reflecting the relatively greater drought resistance of *P. sylvestris*. In contrast to  $R_t$  and as expected, *P. sitchensis* displayed higher recovery ( $R_c$ ) than *P. sylvestris* in each of the four post-drought years considered (Fig. 2), in keeping with our first hypothesis and the trade-off reported by Gazol et al. (2017). However, in contrast to Gazol et al. (2017) and the analysis of gymnosperm responses to wet season droughts by Li et al. (2020), we did not find evidence of a resistance ( $R_t$ )/resilience ( $R_s$ ) trade-off between the two species, as *P. sylvestris* was both more resistant and resilient than *P. sitchensis*. It is worth noting that trade-offs between resistance and recovery might be expected due to the way in which these indices are calculated. Resistance is a measure of growth reduction in the drought year relative to a pre-drought growth average, but recovery is a measure of post-drought growth relative to growth in the drought year. As a result, trees that show the greatest growth reductions in the drought year (i.e. least resistance) might also be expected to display the highest recovery values when recovery is rapid, resulting in an apparent trade-off while actually reflecting differences in initial drought resistance.

The high  $R_t$  of *P. sylvestris* to the early spring drought of March 2012 is in keeping with the findings of Merlin et al. (2015) who also found high resistance in this species to spring drought. However, Castagneri et al. (2015) found that successive periods of low precipitation in late spring (May) were associated with multi-year growth declines in *P. sylvestris* growing in north-western Italy. While the multidimensionality of drought (timing, duration, intensity, frequency, etc.) and other site factors (e.g. soil type) complicates the direct comparison of tree response to different events in different locations, a growing body of work is highlighting how species-specific vulnerabilities to drought are intimately linked to the timing of a given event (D'Orangeville et al., 2018; Forner et al., 2018; Huang et al., 2018; Kannenberg et al., 2019; Vanhellemont et al., 2018). This differential response of *P. sylvestris* to early and late spring droughts might indicate that the drought susceptibility of *P. sylvestris* is more temporally specific than previously thought, implying the need to explore drought vulnerability at an intra-seasonal resolution.

Despite its importance as a commercial timber species, very little research has assessed the growth response of *P. sitchensis* to drought using the resilience framework of Lloret et al. (2011) employed here. Huang et al. (2017) also noted *P. sitchensis* as having relatively low drought resilience but slightly higher drought resistance than found in our study, however Huang et al. (2017) focused on summer drought and

did not consider the influence of neighbourhood composition. In a study of five major European tree species, Vitasse et al. (2019) found low resistance to extreme spring drought events in Norway spruce (*Picea abies* (L.)), a similarly drought-susceptible spruce species to *P. sitchensis*. However, Vitali et al. (2017) showed that the impact of drought on *P. abies* in Germany differed between drought events, being least resistant and resilient to the summer drought of 2003. Collectively, this evidence demonstrates the pressing need to understand the historic drought response of *P. sitchensis* under a range of both drought and site conditions and highlights the need to consider the interactions between the various dimensions of drought when making cross-study comparisons. Understanding these interactions will be key to ensuring forest managers can make informed decisions on how to increase the resilience of this commercially important species under global change.

While the between-species comparison of all three indices ( $R_t$ ,  $R_c$  and  $R_s$ ) in our study was often robust to the number of years used in the calculation (e.g. *P. sylvestris* consistently had higher  $R_t$  than *P. sitchensis*, regardless of the method used to calculate  $R_t$ ), in many cases the absolute value for each index changed significantly depending on the pre- or post-drought period considered. Significant two-way interactions were observed for both *Neighbourhood* and *Species* with *Index calculation* for all three indices (Table 3) and through post-hoc comparisons using estimated marginal means (Fig. 2). These findings echo other recent studies which demonstrate the risks of the often subjective *a priori* selection of a single pre- and post-drought period over which growth is averaged and these indices calculated (Ovenden et al., 2021b; Schwarz et al., 2020), whilst also highlighting how the lack of consistency in the choice of these periods seriously hampers cross-study comparability. In turn, these issues mean that we should be cautious in the use of meta-analytical approaches that attempt to synthesise studies on forest resilience (Castagneri et al., 2021), as the values for these indices may not be directly comparable where different approaches to calculating them have been used.

In contrast to our second hypothesis, we found that monospecific neighbourhoods exhibited both higher  $R_c$  than individuals with one or five conspecifics in their immediate neighbourhood (in the second year after drought only) and higher  $R_s$  than all other considered neighbourhoods, while no differences in  $R_t$  were detected between any of the neighbourhoods (Fig. 3). Similarly, average tree response in monospecific plots of both species was consistently more resilient than any of the mixed-species plots we considered, while none of these mixtures were significantly different from one another for any of the three indices (Fig. 4). We therefore found no evidence that increasing the proportion of *P. sylvestris* in the neighbourhood of *P. sitchensis* increased the resistance, recovery, or resilience of *P. sitchensis* to spring drought (or *vice versa*). Whilst we cannot rule out that some *P. sylvestris* mortality occurred due to drought, the relatively small impact of the 2012 drought on sampled *P. sylvestris* trees compared to *P. sitchensis* suggests this is unlikely. Similarly, we did not find any evidence that mixed-species stands of these two species displayed higher  $R_t$ ,  $R_c$  or  $R_s$  than pure stands under drought, reflecting findings of no positive mixing effect for the  $R_c$  or  $R_s$  of *P. abies* to drought in similar studies (Gillerot et al., 2021; Vitali et al., 2018). Our findings appear to contrast with the proposal by Fichtner et al. (2020), that drought sensitive species with lower cavitation resistance (e.g. *P. sitchensis*) may benefit from more diverse neighbourhoods that include less drought sensitive species (e.g. *P. sylvestris*). However, our study was limited to comparisons of only one and two species mixtures and only considered the radial growth under a short but intense spring drought. Similarly, we acknowledge that while our study focused on the relative response to spring drought between these two species, the absolute impact on tree growth was small for *P. sylvestris*, suggesting the 2012 drought conditions may not have been severe enough to cross any threshold in this species (Ovenden et al., 2021a). Future research should investigate how intimate mixtures of these two species respond to different types of drought (i.e. differences in timing, duration or intensity) across a range of sites to build a more



comprehensive understanding of the conditions under which these mixtures might be beneficial or detrimental.

That monospecific stands were more resilient to drought than intimate mixtures of two species which potentially exhibit complementary functional traits (e.g. rooting depths) reflects other recent work showing negligible neighbourhood diversity effects on drought resilience (Gillerot et al., 2021). While our results agree with Bello et al. (2019), who documented faster growth in *P. sylvestris* monocultures than when mixed with *Quercus petraea*, they contrast with our second and third hypotheses as well as other work on both *P. sylvestris* (Merlin et al., 2015; Steckel et al., 2020) and other spruce species (*P. abies*) (Ding et al., 2017). This difference between studies is unlikely to be linked to differences in tree age, as both Ding et al. (2017) and Merlin et al. (2015) examined the drought response of *P. sylvestris* and *P. abies* trees that were of a similar age to those used in this present study when drought occurred.

At the stand level, the lowest total stand basal area observed in the year before the 2012 drought was in the pure stands of *P. sitchensis*, with the second lowest total basal area being in the pure stands of *P. sylvestris*. These results reflect the findings of Mason et al. (2021), who present evidence of significant overyielding in all mixtures relative to the monocultures at this same site both 15 and 30 years after they were planted in 1988. Mason et al. (2021) suggest that the overyielding of these mixtures is due to the initial facilitation of spruce growth due to the nutritional benefits of being mixed with pine on nitrogen deficient soils. As the canopy closes, Mason et al. (2021) suggests that these facilitative mechanisms then give way to intense competition, with the faster-growing spruce outcompeting the light-demanding pine, causing pine mortality and subsequently a reduction in inter-tree competition. Neighbourhood competition was not a significant predictor of  $R_t$ ,  $R_c$  or  $R_s$ , suggesting that these stands might have been in a developmental phase where facilitative processes rather than competitive ones were still dominant when the 2012 drought occurred, or that sufficient pine mortality had already occurred for inter-tree competition to be of minimal importance for regulating tree drought response. While it is possible that neighbourhood composition and competition were confounded in our analysis, VIF values  $< 3$  suggested low collinearity between predictor variables.

In our study, the SS25 and SS50 mixtures (Table 1) had both the lowest mean resilience values (Fig. 4c) and the highest levels of mortality (all of which was *P. sylvestris*) in both the internal 6x6 tree sample plots and the wider 10x10 tree plots (Fig. 1 and Table 2). As we calculated neighbourhood competition using only those eight trees in a focal tree's immediate neighbourhood, such high levels of *P. sylvestris* mortality would likely result in an index of low neighbourhood competition but need not necessarily be reflected by a low stand basal area, as those remaining live trees grow larger due to competitive release following the mortality (or heavy suppression) of their neighbours. Indeed, when the experiment was 30 years old, Mason et al. (2021) estimated the largest mean *P. sitchensis* DBH (28.7 cm) to be in the mixture with the lowest proportion of *P. sitchensis* (SS25). These results may indicate that, while individual tree basal area or estimates of competition derived from the basal area of local neighbourhoods were not significant predictors of any of  $R_t$ ,  $R_c$  or  $R_s$  (Table S2), higher total stand basal area might influence recovery and resilience at both the tree and stand level, reflecting the hypothesis that mixtures may require more resources to sustain above-ground productivity (Wambsganss et al., 2021). This result is particularly interesting as tree size itself was not a significant predictor of tree level resistance or resilience, highlighting the need to consider the influence of tree mortality and facilitative/competitive processes at both the tree and stand scales when assessing forest drought response (Bottero et al., 2021).

Collectively, our results demonstrate the importance of inter-species differences in drought tolerance and how intimate two-species mixtures do not automatically confer greater drought resistance or resilience. Instead, our findings suggest there is a need to more precisely understand the drought conditions, species composition, tree age and

developmental stage at which species mixtures might become beneficial if we are to increase forest resilience to drought.

## 5. Conclusion

Understanding how to adapt our planted forests to deal with the challenges of a changing climate is of critical importance if we are to ensure the continuity of these habitats and the products and services we derive from them. Despite the call by Messier et al., (2021) to diversify the species composition of our planted forests to increase their resilience, these authors also suggest that the strength of evidence regarding the susceptibility of monospecific vs mixed-species plantations to drought is low. In our study, we found that monospecific neighbourhoods of both *P. sitchensis* and *P. sylvestris* were more resilient to spring drought than any of the intimate mixtures we considered, highlighting the need to better understand the complexity of diversity-resilience relationships.

To our knowledge, this is the first study to assess both the historic drought response of *P. sitchensis* in the UK and the first study to evaluate the relative drought response of intimate mixtures of key commercial UK species. Considering the economic and ecological importance of these two species alongside the overyielding in these species mixtures reported by Mason et al., (2021), developing a more comprehensive understanding of how these (and other) species have responded to a range of historic drought conditions in both mixed and monospecific stands will be essential if we are to inform effective management decisions that balance a range of objectives.

## Declaration of Competing Interest

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

## Data availability

Data will be made available on request.

## Acknowledgements

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## Author Contributions

TO led the conceptual development, methodological approach, analysis and writing of the manuscript, MP contributed to the concept development, data collection and writing of the manuscript, DF contributed to the concept development, methodological approach and writing of the manuscript, MM contributed to the conceptual development and writing of the manuscript, JR contributed to the data collection and writing of the manuscript, DT contributed to the data collection and writing of the manuscript, VS contributed to the conceptual development, methodological approach and writing of the manuscript and AJ contributed to the conceptual development and writing of the manuscript.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120448>.

## References

- Adams, S.H., 2014. The Impact of Changing Climate on Tree Growth and Wood Quality of Sitka spruce. PhD Thesis - Univ. Glas.
- Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67. <https://doi.org/10.18637/jss.v067.i01>.
- Bauhus, J., Forrester, D.I., Gardiner, B., Jactel, H., Vallejo, R., Pretzsch, H., 2017a. Ecological Stability of Mixed-Species Forests, in: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), *Mixed-Species Forests*. pp. 337–382. <https://doi.org/10.1007/978-3-662-54553-9>.
- Bauhus, J., Forrester, D.I., Pretzsch, H., 2017b. From observations to evidence about effects of mixed-species stands. *Mixed-Species Forests*. 27–71.
- Beguieria, S., Vicente-Serrano, S.M., 2017. SPEI: Calculation of the standardised precipitation evapotranspiration index. R package version 1.7. Vienna, Austria: CRAN.
- Beguieria, S., Vicente-Serrano, S.M., Reig, F., Latorre, B., 2014. Standardized precipitation evapotranspiration index (SPEI) revisited: Parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *Int. J. Climatol.* 34, 3001–3023. <https://doi.org/10.1002/joc.3887>.
- Bello, J., Vallet, P., Perot, T., Balandier, P., Seigner, V., Perret, S., Couteau, C., Korboulevsky, N., 2019. How do mixing tree species and stand density affect seasonal radial growth during drought events? *For. Ecol. Manage.* 432, 436–445. <https://doi.org/10.1016/j.foreco.2018.09.044>.
- Bennett, A.C., McDowell, N.G., Allen, C.D., Anderson-Teixeira, K.J., 2015. Larger trees suffer most during drought in forests worldwide. *Nat. Plants* 1, 1–5. <https://doi.org/10.1038/nplants.2015.139>.
- Bottero, A., Forrester, D.I., Cailleret, M., Kohnle, U., Gessler, A., Michel, D., Bose, A.K., Bauhus, J., Bugmann, H., Cuntz, M., Gillerot, L., Schwarz, J., Youssef, R., Carlos, J., Rigling, A., 2021. Growth resistance and resilience of mixed silver fir and Norway spruce forests in central Europe: Contrasting responses to mild and severe droughts. *Glob. Chang. Biol.* 1–17. <https://doi.org/10.1111/gcb.15737>.
- Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., 2019. dplR: Dendrochronology Program Library in R. R package version 1 (7).
- Buras, A., Rammig, A., Zang, C.S., 2020. A novel approach for the identification of pointer years. *Dendrochronologia* 63, 125746. <https://doi.org/10.1016/j.dendro.2020.125746>.
- Castagneri, D., Bottero, A., Motta, R., Vacchiano, G., 2015. Repeated spring precipitation shortage alters individual growth patterns in Scots pine forests in the Western Alps. *Trees - Struct. Funct.* 29, 1699–1712. <https://doi.org/10.1007/s00468-015-1250-z>.
- Castagneri, D., Vacchiano, G., Hackett-pain, A., Deroose, R.J., Klein, T., Bottero, A., 2021. Meta-analysis Reveals Different Competition Effects on Tree Growth Resistance and Resilience to Drought. *Ecosystems*. <https://doi.org/10.1007/s10021-021-00638-4>.
- Coutts, M.P., Philipson, J.J., 1987. Structure and physiology of Sitka spruce roots. *Proc. R. Soc. Edinburgh. Sect. B. Biol. Sci.* 93, 131–144. <https://doi.org/10.1017/s0269727000006345>.
- D'Orangeville, L., Maxwell, J., Kneeshaw, D., Pederson, N., Duchesne, L., Logan, T., Houle, D., Arseneault, D., Beier, C.M., Bishop, D.A., Druckenbrod, D., Fraver, S., Girard, F., Halman, J., Hansen, C., Hart, J.L., Hartmann, H., Kaye, M., Leblanc, D., Manzoni, S., Ouimet, R., Rayback, S., Rollinson, C.R., Phillips, R.P., 2018. Drought timing and local climate determine the sensitivity of eastern temperate forests to drought. *Glob. Chang. Biol.* 24, 2339–2351. <https://doi.org/10.1111/gcb.14096>.
- Dai, A., 2013. Increasing drought under global warming in observations and models. *Nat. Clim. Chang.* 3, 52–58. <https://doi.org/10.1038/nclimate1633>.
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D.M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klimes, D.H., Koelmeijer, I.A., Lembrechts, J.J., Marrec, R., Meeussen, C., Ogée, J., Tyystjärvi, V., Vangansbeke, P., Hylander, K., 2021. Forest microclimates and climate change: Importance, drivers and future research agenda. *Glob. Chang. Biol.* 27, 2279–2297. <https://doi.org/10.1111/gcb.15569>.
- Ding, H., Pretzsch, H., Schütze, G., Rötzer, T., 2017. Size-dependence of tree growth response to drought for Norway spruce and European beech individuals in monospecific and mixed-species stands. *Plant Biol.* 19, 709–719. <https://doi.org/10.1111/plb.12596>.
- Faulkner, M.E., Malcolm, D.C., 1972. Soil physical factors affecting root morphology and stability of scots pine on upland heaths. *Forestry* 45, 23–36. <https://doi.org/10.1093/forestry/45.1.23>.
- Fichtner, A., Härdtle, W., Li, Y., Bruehlheide, H., Kunz, M., von Oheimb, G., 2017. From competition to facilitation: how tree species respond to neighbourhood diversity. *Ecol. Lett.* 20, 892–900. <https://doi.org/10.1111/ele.12786>.
- Fichtner, A., Härdtle, W., Bruehlheide, H., Kunz, M., Li, Y., Von Oheimb, G., 2018. Neighbourhood interactions drive overyielding in mixed-species tree communities. *Nat. Commun.* 9. <https://doi.org/10.1038/s41467-018-03529-w>.
- Fichtner, A., Schnabel, F., Bruehlheide, H., Kunz, M., Li, Y., Von Oheimb, G., 2020. Neighbourhood diversity mitigates drought impacts on tree growth. *J. Ecol.* 108, 865–875. <https://doi.org/10.1111/1365-2745.13353>.
- Field, J.P., Breshears, D.D., Bradford, J.B., Law, D.J., Feng, X., Allen, C.D., 2020. Forest Management Under Megadrought: Urgent Needs at Finer-Scale and Higher-Intensity. *Front. For. Glob. Chang.* 3, 1–10. <https://doi.org/10.3389/ffgc.2020.502669>.
- Forest Research, 2020. *Forestry Statistics 2020 - A compendium of statistics about woodland, forestry and primary wood processing in the United Kingdom. Forest Research*.
- Forner, A., Valladares, F., Bonal, D., Granier, A., Grossiord, C., Aranda, I., 2018. Extreme droughts affecting Mediterranean tree species' growth and water-use efficiency: The importance of timing. *Tree Physiol.* 38, 1127–1137. <https://doi.org/10.1093/treephys/tpy022>.
- Forrester, D.I., Kohnle, U., Albrecht, A.T., Bauhus, J., 2013. Complementarity in mixed-species stands of Abies alba and Picea abies varies with climate, site quality and stand density. *For. Ecol. Manage.* 304, 233–242. <https://doi.org/10.1016/j.foreco.2013.04.038>.
- Gazol, A., Camarero, J.J., Anderegg, W.R.L., Vicente-Serrano, S.M., 2017. Impacts of droughts on the growth resilience of Northern Hemisphere forests. *Glob. Ecol. Biogeogr.* 26, 166–176. <https://doi.org/10.1111/gcb.12526>.
- Gazol, A., Camarero, J.J., Sangüesa-barreda, G., Serra-Maluquer, X., Sánchez-Salguero, R., Coll, L., Casals, P., 2020. Tree Species Are Differently Impacted by Cumulative Drought Stress and Present Higher Growth Synchrony in Dry Places. *Front. For. Glob. Chang.* 3. <https://doi.org/10.3389/ffgc.2020.573346>.
- Gillerot, L., Forrester, D.I., Bottero, A., Rigling, A., Lévesque, M., 2021. Tree Neighbourhood Diversity Has Negligible Effects on Drought Resilience of European Beech, Silver Fir and Norway Spruce. *Ecosystems* 24, 20–36. <https://doi.org/10.1007/s10021-020-00501-y>.
- Grace, J., Norton, D.A., 1990. Climate and Growth of Pinus Sylvestris at Its Upper Altitudinal Limit in Scotland: Evidence from Tree Growth-Rings. *J. Ecol.* 78, 601. <https://doi.org/10.2307/2260887>.
- Grant, O.M., Montero Ribeiro, A.F., Glombik, P., O'Reilly, C., 2018. Impact of limited water availability on growth and biomass production of a range of full-sibling Sitka spruce (Picea sitchensis (Bong.) Carr.) families. *Forestry* 91, 83–97. <https://doi.org/10.1093/forestry/cpx034>.
- Green, S., Hendry, S.J., Redfern, D.B., 2008. Drought damage to pole-stage Sitka spruce and other conifers in north-east Scotland. *Scottish For.* 62, 10–18.
- Grossiord, C., 2019. Having the right neighbors: how tree species diversity modulates drought impacts on forests. *New Phytol.* <https://doi.org/10.1111/nph.15667>.
- Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruehlheide, H., Checko, E., Forrester, D.I., Dawud, S.M., Finer, L., Pollastrini, M., Scherer-Lorenzen, M., Valladares, F., Bonal, D., Gessler, A., 2014. Tree diversity does not always improve resistance of forest ecosystems to drought. *Proc. Natl. Acad. Sci.* 111, 14812–14815. <https://doi.org/10.1073/pnas.1411970111>.
- Hoffmann, N., Schall, P., Ammer, C., Leder, B., Vor, T., 2018. Drought sensitivity and stem growth variation of nine alien and native tree species on a productive forest site in Germany. *Agric. For. Meteorol.* 256–257, 431–444. <https://doi.org/10.1016/j.agrformet.2018.03.008>.
- Huang, W., Fonti, P., Larsen, J.B., Rørbild, A., Callesen, I., Pedersen, N.B., Hansen, J.K., 2017. Projecting tree-growth responses into future climate: A study case from a Danish-wide common garden. *Agric. For. Meteorol.* 247, 240–251. <https://doi.org/10.1016/j.agrformet.2017.07.016>.
- Huang, M., Wang, X., Keenan, T.F., Piao, S., 2018. Drought timing influences the legacy of tree growth recovery. *Glob. Chang. Biol.* 24, 3546–3559. <https://doi.org/10.1111/gcb.14294>.
- Jackson, G.E., Irvine, J., Grace, J., 1995. Xylem cavitation in Scots pine and Sitka spruce saplings during water stress. *Tree Physiol.* 15, 783–790. <https://doi.org/10.1093/treephys/15.12.783>.
- Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J.R., Koricheva, J., Meurisse, N., Brockerhoff, E.G., 2017. Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. *Curr. For. Reports* 3, 223–243. <https://doi.org/10.1007/s40725-017-0064-1>.
- Jourdan, M., Kunstler, G., Morin, X., 2020. How neighbourhood interactions control the temporal stability and resilience to drought of trees in mountain forests. *J. Ecol.* 108, 666–677. <https://doi.org/10.1111/1365-2745.13294>.
- Kannenberg, S.A., Maxwell, J.T., Pederson, N., D'Orangeville, L., Ficklin, D.L., Phillips, R.P., 2019. Drought legacies are dependent on water table depth, wood anatomy and drought timing across the eastern US. *Ecol. Lett.* 22, 119–127. <https://doi.org/10.1111/ele.13173>.
- Lenth, R.V., 2016. Least-squares means: The R package lsmeans. *J. Stat. Softw.* 69. <https://doi.org/10.18637/jss.v069.i01>.
- Li, X., Piao, S., Wang, K., Wang, X., Wang, T., Ciais, P., Chen, A., Lian, X., Peng, S., Peñuelas, J., 2020. Temporal trade-off between gymnosperm resistance and resilience increases forest sensitivity to extreme drought. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-020-1217-3>.

- Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: Effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* 120, 1909–1920. <https://doi.org/10.1111/j.1600-0706.2011.19372.x>.
- Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412, 72–76.
- Martínez-Vilalta, J., López, B.C., Loepfe, L., Lloret, F., 2012. Stand- and tree-level determinants of the drought response of Scots pine radial growth. *Oecologia* 168, 877–888. <https://doi.org/10.1007/s00442-011-2132-8>.
- Mason, W.L., Connolly, T., 2018. Nursing mixtures can enhance long-term productivity of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) stands on nutrient-poor soils. *Forestry* 91, 165–176. <https://doi.org/10.1093/forestry/cpx051>.
- Mason, W.L., Stokes, V., Forster, J., 2021. Proportions of a pine nurse influences overyielding in planted spruce forests of Atlantic Europe. *For. Ecol. Manage.* 482, 118836 <https://doi.org/10.1016/j.foreco.2020.118836>.
- Matías, L., Jump, A.S., 2012. Interactions between growth, demography and biotic determinants in determining species range limits in a warming world: The case of *Pinus sylvestris*. *For. Ecol. Manage.* 282, 10–22. <https://doi.org/10.1016/j.foreco.2012.06.053>.
- McDowell, N.G., Michaletz, S.T., Bennett, K.E., Solander, K.C., Xu, C., Maxwell, R.M., Middleton, R.S., 2018. Predicting Chronic Climate-Driven Disturbances and Their Mitigation. *Trends Ecol. Evol.* 33, 15–27. <https://doi.org/10.1016/j.tree.2017.10.002>.
- Merlin, M., Perot, T., Perret, S., Korboulewsky, N., Vallet, P., 2015. Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. *For. Ecol. Manage.* 339, 22–33. <https://doi.org/10.1016/j.foreco.2014.11.032>.
- Messier, C., Baeten, L., Bauhus, J., Barsoum, N., Sousa-silva, R., Auge, H., Bruehlheide, H., Caldwell, B., Hall, J.S., Hector, A., Paquette, A., Parker, J.D., Scherer-lorenzen, M., Schnabel, F., Verheyen, K., Zemp, D.C., 2021. For the sake of resilience and multifunctionality, let's diversify planted forests! *Conserv. Lett.* 1–8 <https://doi.org/10.1111/conl.12829>.
- Mickovski, S.B., Ennos, R.A., 2002. A morphological and mechanical study of the root systems of suppressed crown Scots pine *Pinus sylvestris*. *Trees - Struct. Funct.* 16, 274–280. <https://doi.org/10.1007/s00468-002-0177-3>.
- Muñoz-Gálvez, F., Herrero, A., Pérez-Corona, M.E., Andivia, E., 2020. Are pine-oak mixed stands in Mediterranean mountains more resilient to drought than their monospecific counterparts? *For. Ecol. Manage.* 484 <https://doi.org/10.1016/j.foreco.2021.118955>.
- Neumann, R.B., Gardon, Z.G., Cardon, Z.G., Gardon, Z.G., 2012. The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. *New Phytol.* 194, 337–352. <https://doi.org/10.1111/j.1469-8137.2010.03195.x>.
- Ovenden, T.S., Perks, M.P., Clarke, T.-K., Mencuccini, M., Jump, A.S., 2021a. Threshold Response to Extreme Drought Shifts Inter-Tree Growth Dominance in *Pinus sylvestris*. *Front. For. Glob. Chang.* 4, 1–12. <https://doi.org/10.3389/ffgc.2021.737342>.
- Ovenden, T.S., Perks, M.P., Clarke, T., Mencuccini, M., Jump, A.S., 2021b. Life after recovery: Increased resolution of forest resilience assessment sheds new light on post-drought compensatory growth and recovery dynamics. *J. Ecol.* 1–14 <https://doi.org/10.1111/1365-2745.13576>.
- Pickles, B.J., Simard, S.W., 2017. Mycorrhizal Networks and Forest Resilience to Drought, Mycorrhizal Mediation of Soil: Fertility, Structure, and Carbon Storage. Elsevier Inc. <https://doi.org/10.1016/B978-0-12-804312-7.00018-8>.
- Potop, V., Boroneanț, C., Možný, M., Štěpánek, P., Skalák, P., 2014. Observed spatiotemporal characteristics of drought on various time scales over the Czech Republic. *Theor. Appl. Climatol.* 115, 563–581. <https://doi.org/10.1007/s00704-013-0908-y>.
- Quine, C.P., Gardiner, B.A., 2007. Understanding how the Interaction of Wind and Trees Results in Wind-Throw, Stem Break-Age, and Canopy Gap Formation, *Plant Disturbance Ecology*. Elsevier Inc. <https://doi.org/10.1016/B978-0-12088778-1/50006-6>.
- Robinson, E.L., Blyth, E., Clark, D.B., Comyn-Platt, E., Finch, J., Rudd, A.C., 2017. Climate hydrology and ecology research support system meteorology dataset for Great Britain (1961–2015) [CHESS-met] v1.2. NERC Environmental Information Data Centre.
- Rubio-Cuadrado, Á., Camarero, J.J., Aspizua, R., Sánchez-González, M., Gil, L., Montes, F., 2018. Abiotic factors modulate post-drought growth resilience of Scots pine plantations and rear-edge Scots pine and oak forests. *Dendrochronologia* 51, 54–65. <https://doi.org/10.1016/J.DENDRO.2018.08.001>.
- Schwarz, J.A., Skiadaresis, G., Kohler, M., K., J., Schnabel, F., Vitali, V., Bauhus, J., 2020. Quantifying growth responses of trees to drought - a critique of the Lloret-indicators and recommendations for future studies. *Curr. For. Reports* 185–200. <https://doi.org/https://doi.org/10.32942/osf.io/5ke4f>.
- Sohn, J.A., Saha, S., Bauhus, J., 2016. Potential of forest thinning to mitigate drought stress: A meta-analysis. *For. Ecol. Manage.* 380, 261–273. <https://doi.org/10.1016/j.foreco.2016.07.046>.
- Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., Černý, J., Coll, L., Collet, C., Ehbrecht, M., Jansons, A., Nothdurft, A., Pach, M., Pardos, M., Ponette, Q., Reventlow, D.O.J., Sitko, R., Svoboda, M., Vallet, P., Wolff, B., Pretzsch, H., 2020. Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – Site water supply and fertility modify the mixing effect. *For. Ecol. Manage.* 461, 117908. <https://doi.org/10.1016/j.foreco.2020.117908>.
- Thurm, E.A., Uhl, E., Pretzsch, H., 2016. Mixture reduces climate sensitivity of Douglas-fir stem growth. *For. Ecol. Manage.* 376, 205–220. <https://doi.org/10.1016/j.foreco.2016.06.020>.
- Trenberth, K.E., Dai, A., Van Der Schrier, G., Jones, P.D., Barichivich, J., Briffa, K.R., Sheffield, J., 2014. Global warming and changes in drought. *Nat. Clim. Chang.* 4, 17–22. <https://doi.org/10.1038/nclimate2067>.
- Van de Peer, T., Verheyen, K., Ponette, Q., Setiawan, N.N., Muys, B., 2018. Overyielding in young tree plantations is driven by local complementarity and selection effects related to shade tolerance. *J. Ecol.* 106, 1096–1105. <https://doi.org/10.1111/1365-2745.12839>.
- Vanhellemont, M., Sousa-Silva, R., Maes, S.L., Van den Bulcke, J., Hertzog, L., De Groote, S.R.E., Van Acker, J., Bonte, D., Martel, A., Lens, L., Verheyen, K., 2018. Distinct growth responses to drought for oak and beech in temperate mixed forests. *Sci. Total Environ.* 650, 3017–3026. <https://doi.org/10.1016/J.SCIOTOTENV.2018.10.054>.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index. *J. Clim.* 23, 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>.
- Vitali, V., Büntgen, U., Bauhus, J., 2017. Silver fir and Douglas fir are more tolerant to extreme droughts than Norway spruce in south-western Germany. *Glob. Chang. Biol.* 23, 5108–5119. <https://doi.org/10.1111/gcb.13774>.
- Vitali, V., Forrester, D.I., Bauhus, J., 2018. Know Your Neighbours: Drought Response of Norway Spruce, Silver Fir and Douglas Fir in Mixed Forests Depends on Species Identity and Diversity of Tree Neighbourhoods. *Ecosystems* 21, 1215–1229. <https://doi.org/10.1007/s10021-017-0214-0>.
- Vitasse, Y., Bottero, A., Cailleret, M., Bigler, C., Fonti, P., Gessler, A., Lévesque, M., Rohner, B., Weber, P., Rigling, A., Wohlgemuth, T., 2019. Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. *Glob. Chang. Biol.* 25, 3781–3792. <https://doi.org/10.1111/gcb.14803>.
- Wambsganss, J., Beyer, F., Freschet, G.T., Scherer-Lorenzen, M., Bauhus, J., 2021. Tree species mixing reduces biomass but increases length of absorptive fine roots in European forests. *J. Ecol.* 2678–2691 <https://doi.org/10.1111/1365-2745.13675>.
- Zang, C., Pretzsch, H., Rothe, A., 2012. Size-dependent responses to summer drought in Scots pine, Norway spruce and common oak. *Trees - Struct. Funct.* 26, 557–569. <https://doi.org/10.1007/s00468-011-0617-z>.