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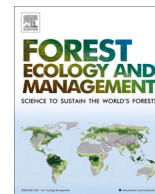


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The greater resilience of mixed forests to drought mainly depends on their composition: Analysis along a climate gradient across Europe

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ABSTRACT

Despite growing evidence that diverse forests play an important role in ecosystem functioning, ensuring the provision of different ecosystem services, whether such diversity improves their response to drought events remains unclear. In this study, we use a large tree-ring database from thirty case studies across nine European countries and eleven species, covering from Mediterranean to hemiboreal forests, to test if the growth response to site specific drought events that occurred between 1975 and 2015 varied between mixed and monospecific stands. In particular, we quantify how stands resist those specific drought events and recover after them, thus analyzing their resilience. For each drought event and forest stand we calculated resistance, recovery, resilience and relative resilience and we related the variation in these indices between monospecific and mixed stands with type of admixture, tree species identity, site aridity gradient, stand basal area and stand age. We found a large variability among case studies, even for those that share similar species composition and have similar climates. On average, mixed stands showed higher resistance, resilience and relative resilience to drought events than monospecific stands. However, the beneficial effect of mixtures could not be generalized, being greatly modulated by the type of admixture and tree species identity, and depending on site water supply and stand characteristics, such as basal area and age. The increase in resilience in mixtures compared with monocultures was greater on the conifer-broadleaved admixtures, and to a lesser extent in the broadleaved-broadleaved combinations. The observed response patterns to drought largely varied among the eleven studied species, thus

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revealing the importance of functional traits for understanding a species' response to drought across its distribution range. Along the site aridity gradient, resilience and relative resilience to drought increased in drier sites for both monospecific and mixed stands, with an observed trend towards higher resilience in mixed stands in the drier and hotter sites. Our results confirm the complexity of the relationships found of resistance, recovery, resilience and relative resilience with drought when comparing pure vs mixed stands.

1. Introduction

Mixed forests, characterized by the coexistence of at least two tree species, represent more than two thirds of the total forested areas on Earth (FAO, 2016). A similar figure was reported for European forests, where the area of monospecific forests decreased in the last years (Forest Europe, 2015, pp 28). Over the last decades there has been a widespread agreement that tree species biodiversity plays an important role in forest ecosystem functioning (Baeten et al. 2013; Grossiord et al. 2014; Grossiord 2019), ensuring the provision of a multitude of ecosystem services (Hooper et al. 2012; Gamfeldt et al. 2013; van der Plas et al. 2016; Pretzsch et al. 2019). Moreover, mixed forests can be more stable to different disturbances, both biotic (Jactel et al. 2017) and abiotic (Anderegg et al., 2018; Pretzsch et al. 2019), while they can increase the temporal stability of community productivity (Jucker et al. 2014; del Rio et al., 2017) or even increase such productivity (Jucker et al. 2014; Zhang et al. 2012; Forrester 2014; Pretzsch 2017; Jactel et al. 2018). This will result in higher amounts of carbon stored above- and below-ground in mixed forests (Forrester et al. 2006; Epron et al. 2013).

Projected climate during the twenty first century will affect forest ecosystem functioning and associated ecosystem services (Pardos et al. 2015; Ammer 2019). In particular, more intense and long-lasting drought events are expected to strongly impact forests (Bonafant et al. 2017, McDowell et al. 2020). In recent decades, a sharp decline in forest growth and survival, induced by more frequent and intense droughts, has already been observed in different types of forests and tree species (Aubin et al. 2016). The functional processes that contribute to drought resistance have been widely studied: alterations in tree allometry partitioning, rooting strategies, photosynthesis depletion, stomatal closure (McDowell et al., 2008; Calama et al. 2013; Pardos et al. 2010). These processes are both dependent on species-specific traits and on environmental conditions (Mitchell et al. 2008; Mayoral et al. 2016). In particular, tree species coexisting in a mixed forest can adopt different strategies (tolerance, avoidance and recovery) to cope with drought (Mayoral et al. 2015; Anderegg and HilleRisLambers, 2015, Aubin et al. 2016). Drought tolerance traits include higher xylem resistance to embolism, lower intrinsic water use efficiency, lower leaf water potential and higher wood density, which correspond to the anisohydric strategy. Avoidance traits are deep roots, rapid stomatal control and regulation of transpiration (to maintain a relatively constant midday leaf water potential as soil water potential and predawn leaf water potential decrease), characterizing the isohydric strategy. Species resistance to drought can be classified along a continuum between anisohydric and isohydric strategies (Martínez-Vilalta and García-Forner 2017; Fu and Meinzer, 2019). Recovery traits, which include abundant carbohydrates reserves, resprouting ability and reproductive effort, enable trees to recover following drought-induced decline. Those differential responses to drought are supposed to allow complementarity among species, therefore facilitating the co-existence of species under stressful environmental conditions (Mayoral et al. 2015).

The role of mixed forests in the improvement of individual tree resistance to and recovery from drought (Lebourgeois et al. 2013) has been widely studied in the last years. Results from different authors showed that the benefits of mixture cannot be generalized for all forest types and tree species, noting that the species' identity could be more important than the number of species in the mixture (Grossiord et al. 2014; Merlin et al. 2015; Pretzsch et al. 2019; Jourdan et al. 2019; Steckel et al. 2020). Furthermore, the benefits of mixtures may also

depend on the climatic differences between sites and biomes (Lebourgeois et al. 2013). Although there is evidence that tree diversity regulates drought impacts in forests, it is difficult to draw general conclusions on how such diversity affects the directionality (positive vs negative effects) of forest responses to drought (Grossiord 2019).

At the community level, the beneficial interactions between species in a mixed forest that result in reduced vulnerability to drought can be explained by three different mechanisms, namely resource partitioning (e.g. root stratification or differential stomatal regulation strategies), facilitation (e.g. active hydraulic redistribution, improved soil water and reduced biotic damages during drought) and selection effects (e.g. presence of particularly drought-tolerant species) (Grossiord 2019). According to Forrester and Bauhus (2016), what seems more important to better cope with drought in mixed stands compared to monospecific stands is the coexistence of species with complementary traits that improve water availability, water uptake or water use efficiency and a compatibility with the climatic and edaphic conditions of the site. However, the complementary traits that cause the effect at one site could be different to those that cause the same effect at another site (Baeten et al. 2013). Mixing tree species might on the contrary decrease drought resistance when enhanced tree growth leads to higher evapotranspiration demand (Kunert et al. 2012; Forrester et al. 2016; Grossiord 2019). To this respect, the stress gradient hypothesis postulates that facilitation is more frequent under more unfavourable conditions (Bertness and Callaway 1994; Callaway and Walker 1997). This may result in a shift from negative to positive interactions between tree species across a benign to harsh environmental gradient and interannual variations in species interactions (del Río et al. 2014). However, when analysing tree growth facilitation and competition reduction cannot be well distinguished, and only the net effect of species interactions can be observed. Thus, the broader framework proposed by Forrester (2014), which consider simultaneous occurrence of competition reduction and facilitation and different variation patterns with environmental conditions depending on the main limiting factor, is more suitable for interpreting spatio-temporal variation in tree species interactions.

Another issue to consider is whether all the species will benefit from the mixture, or one of them benefits at the expense of the other species. It has been shown that different tree species in mixed stands differ considerably in their response to drought (Pretzsch et al. 2016). While some species show a positive response to drought (i.e., less stressed in mixed stands), others show a negative response (i.e., they are affected by drought even in mixed stands) or even a neutral one, but with potentially different responses along the geographical range of the species (Aubin et al. 2016). Vulnerability to water stress for a given species may also depend on stand basal area (Forrester et al. 2016), stand density (Bottero et al. 2017) and stand age (Sohn et al. 2016). These are important issues to consider when conducting studies across large geographical scales, where local site characteristics, climate conditions, forest management, forest type, tree species assemblages (and their related functional traits) are likely to interact, making the identification of species mixture effects more complex (Grossiord, 2019; Bello et al., 2019).

In this study, we used tree ring data from thirty case studies covering from Mediterranean to hemiboreal forests and eleven tree species to test whether the response of mixed stands to drought events differed to that of monospecific stands. Furthermore, we investigated whether such differential response to drought varied with the type of admixture, tree species identity, site aridity gradient, stand basal area and stand age. For

assessing tree responses to drought, we used the three components proposed by Lloret et al. (2011): resistance (Rt), recovery (Rc), resilience (Rs) and relative resilience (RRs). More specifically we tested the following hypotheses:

Hypothesis I: tree growth response to drought events differs between mixed and monospecific stands.

Hypothesis II: The benefits of mixture to cope with drought events cannot be generalized to the three types of admixtures found (conifer-conifer, conifer-broadleaved, broadleaved-broadleaved)

Hypothesis III: Tree growth response to drought events in monospecific and mixed stands is mediated by the identity of tree species

Hypothesis IV: Tree growth response to drought events in monospecific and mixed stands vary along an aridity gradient

Hypothesis V: Tree growth response to drought events in monospecific and mixed stands depends on stand characteristics (basal area and age)

2. Material and methods

2.1. Experimental sites

This study was performed using data from 30 case studies spread over 9 countries that represent different European forest stands, including both natural forests and plantations. Stands were located along a gradient from hemiboreal to Mediterranean forests, spanning from central Spain to northern Latvia (Table A1, Fig. 1). Altogether, the case studies cover the main admixtures found across Europe, including conifer and conifer (*Pinus-Juniperus*; *Pinus-Pinus*; *Pinus-Picea*; *Picea-Abies*; *Larix-Pinus*; *Larix-Picea*), conifer and broadleaved (*Pinus-Quercus*; *Pinus-Fagus*; *Picea-Fagus*; *Larix-Quercus*, *Larix-Alnus*, *Larix-Tilia*) and broadleaved and broadleaved (oak-beech). We considered many important tree species for the bioeconomy of European forests such as *Fagus sylvatica*, *Quercus pyrenaica*, *Quercus petraea*, *Quercus robur*, *Quercus pubescens*, *Pinus sylvestris*, *Pinus pinaster*, *Pinus pinea*, *Pinus nigra*, *Picea abies*, *Abies alba* and *Larix decidua*, with most tree species occurring in several case studies. The studied species showed different functional traits that are described in Table 1.

In twenty-five case studies out of the total of thirty, plots were organized in triplets. A triplet consisted of a set of three plots that included a two-species mixed stand and the two monospecific stands of the component species of the mixed stand. In the other five case studies

(SP1, LI1, LI2, LI3, and LI4), plots were divided between monospecific and mixed stands. In these five case studies, only trees for the main species (*Pinus pinea* for SP1 and *Larix decidua* for LI1, LI2, LI3, and LI4) were cored. Mixed stands in case study SP1 are formed by *Pinus pinea*, *Quercus ilex* and *Juniperus thurifera*. *Larix decidua* plots shared the space with different conifers (*Pinus sylvestris*, *Picea abies*) and broadleaves (*Alnus glutinosa*, *Betula pendula*, *Tilia cordata*, *Quercus robur*). A total of 587 plots were sampled in closed even-aged, well or fully stocked stands according to local silvicultural guidelines that had not been thinned or at least not thinned within the last 10 years. In the mixed stands, the trees of the two species were usually arranged in small groups. Plots were located at elevations between 20 and 1400 m a.s.l. (mean = 460 m), with mean annual precipitation ranging from 435 to 1200 mm (mean = 812 mm) and mean annual temperature from 5.6 to 13.5 °C (mean = 8.6 °C) (Table A1).

2.2. Data collection and dendrochronological analyses

Two perpendicular increment cores at breast height were taken per tree. The total number of trees cored was 3,298 trees (Table A2). Annual ring widths were measured from each increment core using standardised dendrochronological techniques (Speer 2010). At the end of the growing season, when cores were taken, different dendrometric variables were measured on each plot, both at tree (diameter at breast height of all trees in each plot) and stand level (mean diameter, mean height, basal area and tree density).

To analyze the effect of drought on tree growth we calculated the tree basal area increment (BAI, cm²), using mean annual ring width of both increment cores:

$$BAI = \pi/4(d_t^2 - d_{t-1}^2) \quad (1)$$

where d_t and d_{t-1} are the tree diameter at breast height at the end (d_t) and the beginning (d_{t-1}) of a given annual ring increment corresponding to rings formed in year t and year $t-1$, respectively.

To eliminate the biological growth trends and to produce stationary and residual tree ring width chronologies (Fritts et al., 1990) we used a detrending procedure and an autocorrelation removal with the Friedman supersmoother spline (Friedman, 1984) and autocorrelation modeling. Through this procedure we obtained chronologies of dimensionless indices (CDI), preserving a common variance with interannual time scales. To assess the reliability of the chronologies, we calculated descriptive statistics using “*dplr*” R package (Bunn 2010) for each species and plot, including *Rbar* (mean interseries correlation) and *EPS* (expressed population signal of detrended BAI series) (Table A2). *Rbar* has been used to measure the strength of the common growth signal within each chronology (Wigley et al 1984), while *EPS* is used to measure the reliability of chronologies (Lindholm et al. 1999). In our study, mean *Rbar* was 0.37, indicating a medium common signal for each species and plot. Mean *EPS* was 0.88, a value above the threshold of 0.85 indicating that chronologies were reliable and well replicated.

2.3. Climate data

We used climate data on a monthly basis (precipitation, mean, maximum and minimum temperature) for each case study. Climate data were obtained from meteorological stations nearby each case study site. When data were not available, they were obtained from the CGMS database (AGRI4CAST, <http://mars.jrc.ec.europa.eu/mars>). Monthly data were used to calculate mean annual temperature (T, °C) and annual precipitation (P, mm) from 1975 to 2015 (see Figure A1 for the relationship between mean annual temperature and total annual precipitation). For characterizing the climatic water supply for each case study, we used the annual De Martonne aridity index (DMI, mm °C⁻¹) (Eq. (2)) and De Martonne aridity index for the summer months (June, July and August) (DMI_{summer}, mm °C⁻¹) (Eq. (3)), for the period 1975–2015.



Fig. 1. Location of the 30 case studies across Europe. Species studied in each case study are shown in parenthesis. Aa: *Abies alba*; Fs: *Fagus sylvatica*; Pa: *Picea abies*; Pn: *Pinus nigra*; Pp: *Pinus pinaster*; Pt: *Pinus pinaster*; Ps: *Pinus sylvestris*; Qp: *Quercus petraea*; Qpb: *Quercus pubescens*; Qpy: *Quercus pyrenaica*; Ld: *Larix decidua*.

Table 1
Environmental and functional characteristics of the studied species.

	<i>Fagus sylvatica</i>	<i>Quercus petraea</i>	<i>Quercus pubescens</i>	<i>Quercus pyrenaica</i>	<i>Pinus nigra</i>	<i>Pinus pinaster</i>	<i>Pinus sylvestris</i>	<i>Pinus pinea</i>	<i>Abies alba</i>	<i>Picea abies</i>	<i>Larix decidua</i>
Environmental preferences	shade tolerant (Pretzsch et al. 2015)	prefers more shaded environments (del Río et al. 2013; Pretzsch et al. 2019)	more light-demanding (Jourdan et al. 2019)		Light demanding (Trasobares et al. 2004) It can grow on a variety of soils and is well-adapted to rocky soils (López-Tirado and Hidalgo, 2014)	Grows preferably in sandy, stony and well drained soils (Prieto-Recio et al. 2015) Shade-intolerant (Andivia et al. 2020)	More light demanding (Ceballos and Ruiz de la Torre, 1979)	Grows mainly in sandy soils with low water retention (Pardos et al. 2010) Prefers mid-shade exposition (Calama et al. 2013)	grows better in humid conditions (Jourdan et al. 2019) capable of persisting for long periods in the forest understorey without appreciable growth, responding positively to a gradual increase in light (Grassi and Bagnaresi, 2001)	water uptake in the upper soil layers (Pretzsch, Schütze and Uhl 2013)	Light demanding (Gradeckas and Malinauska 2005)
Root system		Resprouting ability: capacity to recovery after drought (Mayoral et al. 2015) strong taproot that reaches deeper soil layers (Canadell et al. 1996)			shallower root system It does not possess a well-developed taproot (López-Tirado and Hidalgo, 2014)	preserve its taproot until maturity root architecture adapted to the soil profile (Corcuera et al. 2012)	deep root system with taproot (Köstler et al. 1968)	Multi-stratified root system (de-Dios-García et al. 2018)	Deep root system with taproot (Köstler et al. 1968)	Rather shallow root system (Puhe 2003; Filipiak, 1992)	
Sensitivity to drought	sensitive to drought, but recovers easily after a drought (Jourdan et al. 2019)	less sensitive to drought recovers more rapidly in drier sites (Nothdurft and Engel 2020)	lower sensitivity to high temperatures during drought (Sperlich et al. 2019)	moderate drought tolerance	relatively tolerant to drought although cumulative water deficit constrains their growth in the long term (Herguido et al. 2016)	dependent on access to a variable groundwater belowground competition is limiting for growth (Rozas et al. 2011 tree mortality & decline in pure stands (Prieto-Recio et al. 2015)	especially sensible to drought stops growth in harsh conditions (Merlin et al. 2015)	can profit from sporadic rain events during drought (Mutke et al. 2012)	relatively tolerant to drought for an alpine coniferous (Jourdan et al. 2020) growth decline, forest dieback & widespread mortality (Gazol and Camarero 2016)	falls back after drought, but recovers quickly (Pretzsch, Schütze and Uhl 2013)	more sensitive to drought than other conifers (Nothdurft and Engel 2020)
Physiological and morphological traits to cope with drought	Stomata opening extended much further into drought: anisohydric behaviour Maintenance of low osmotic potentials during drought (Aranda et al. 2020) genetic variability and a high degree of phenotypic plasticity to water availability (Aranda et al. 2014)	Higher SLA and lower leaf thickness early phenology (Ramírez-Valiente et al., 2020)	osmotic adjustment to increase tolerance to drought (Aranda et al. 2020)		lower transpiration rates and water potential gradients compared to other pines (Martínez-Vilalta and Piñol, 2002) High plasticity in water use efficiency (Fornier et al., 2018)	Under dry soil conditions, a high degree of stomatal control maintains needle water potential well above the cavitation threshold of the species (Corcuera et al. 2012)	low hydraulic conductivity, limiting transpiration when soil moisture deficit reaches a threshold (Martín-Gómez et al. 2017) structural plasticity according to environmental conditions (Sabaté et al. 2002)	Dramatic decrease in photosynthesis (Calama et al. 2013)	High evapotranspiration rates (Gazol and Camarero 2016)	Reduced photosynthesis under mild drought condition (Marozas et al. 2019)	stomatal-limited photosynthesis, reduced assimilation (Voltás et al. 2020)

Because of its minimal data requirement but high explanatory strength, this index has been widely used to describe drought conditions or aridity of a region (Bielak et al. 2014). The higher the index, more water supply is available for tree growth.

$$DMI = \frac{P}{T + 10} \quad (2)$$

$$DMI_{summer} = \frac{P_{summer}}{T_{summer} + 10} \quad (3)$$

In our study, DMI ranged between 19.9 and 66.1 mm °C⁻¹ (mean = 45.9 mm °C⁻¹), and DMI_{summer} from 1.5 to 16.2 mm °C⁻¹ (mean = 8.4 mm °C⁻¹). According to the De Martonne index climatic classification (Baltas 2007), the case studies ranged from semi-dry (in central Spain) to very humid categories (in south-eastern Germany) (Table A1).

2.4. Selection of site specific drought events

To study the effect of drought events on tree growth, we selected for each case study those years with drought conditions that have negatively affected tree growth (namely, site-specific drought events). These site specific drought events had to meet two conditions (see Steckel et al. (2020) for more details): (1) they must be considered as drought years, based on climatic conditions; and (2) they must have significantly reduced tree growth (namely, pointer years).

For this purpose, we first selected drought years using the climate data. Drought years were identified by means of the Standardized Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010) that was calculated using the SPEI R package. This procedure ensures that the observed meteorological anomaly is reflected by drought stress suffered by the individual trees (Steckel et al., 2020). The SPEI is a multi-scalar drought index based on a monthly balance of precipitation and potential evapotranspiration (PET) that estimates the drought intensity, according to its strength and duration. In our study, PET was calculated for a time span of six months using the Thornthwaite equation (Thornthwaite, 1948). An SPEI value below (-1) corresponded to a dry period and SPEI values above (+1) corresponded to wet periods. Following Steckel et al. (2020), we considered drought years those that displayed at least one month with an SPEI ≤ -1 during the growing season. The growing season corresponded to those months with mean minimum temperature above 10 °C.

Secondly, we identified negative pointer years, that is, years that showed a remarkable reduction in tree growth at the individual level. We used the pointerRES R package (Van der Maaten-Theunissen et al., 2015) that uses the normalization in a moving window, relating tree growth in a year to the average growth of a fixed number of preceding years. In our study, we used a window width of four years. Years were considered as pointer when at least 60% of the de-trended BAI series of at least one of the two species in the monospecific plots of each study site showed an episode that indicated a growth decrease of 75% compared to the mean value.

Lastly, in order to confirm that these periods of growth reduction corresponded to drought conditions rather than to other biotic (e.g. pests and diseases) or abiotic (e.g. frosts) factors, we chose years that were both drought years and pointer years. Site specific drought events were then used to evaluate the relationship between the reduction in tree growth and drought in monospecific and mixed stands.

The effect of drought events on tree growth was assessed for the period 1975–2015. As mentioned before, drought events were specific to each case study. The final number of drought events for each case study ranged from one to five (Table A1).

2.5. Growth responses to specific drought events

For each specific drought event and sampled tree, we calculated the tree drought response indices proposed by Lloret et al. (2011): resistance

(Rt) (Eq. (4)), recovery (Rc) (Eq. (5)) and resilience (Rs) (Eq. (6)). The resistance index Rt quantifies the ratio between tree growth during the drought event (G_D) and the mean growth during some previous years (G_{PreDr}). Thus, it quantifies the capacity of trees to cope with drought stress, being able to continue to grow during drought. A value of $R_t = 100$ indicates complete resistance. The recovery index Rc quantifies the ratio in growth between the period after (G_{PostDr}) and during the drought event (G_D). It describes the ability of trees to resume growth after the drought event. A value of $R_c = 100$ indicates the persistence of the growth level during the drought event, $R_c < 100$ indicates further decline and $R_c > 100$ indicates a recovery from the growth level during the drought event. The resilience index Rs quantifies the ratio in tree growth after (G_{PostDr}) and before (G_{PreDr}) the drought event. Thus, it measures the capacity of trees to recover the growth rates observed before the drought event. Values of $R_s = 100$ indicate a full recovery, $R_s > 100$ an increased growth after the drought event, while $R_s < 100$ indicates growth decline.

$$R_t = \frac{G_{Dr}}{G_{PreDr}} * 100 \quad (4)$$

$$R_c = \frac{G_{PostDr}}{G_{Dr}} * 100 \quad (5)$$

$$R_s = \frac{G_{PostDr}}{G_{PreDr}} * 100 \quad (6)$$

The Lloret indices have been used for a large variety of research topics, across a large number of species, which cover different growth characteristics, forest types and climatic regions. Although widely used, there has been some critique regarding the interpretation of the results using these indices due to the hypothesized trade-off between recovery and resistance, not being clear which of these two indices is more important to overall resilience (Schwarz et al. 2020). Complementing these three indices with the relative resilience index (RRs) (Eq. (7)) could mitigate these effects, as this index accounts for the damage experienced during disturbance (Lloret et al. 2011). The rationale of RRs is that the ability to achieve the levels of pre-disturbance performance depends on the impact (i.e., tree growth reduction) during disturbance. Values of RRs < 100 indicates that the effect of the event persists after disturbance, with lower values indicating decreasing resilience. High resistance to the disturbance reduces to relative resilience, while low resistance increases RRs.

$$RR_s = \frac{G_{PostDr} - G_{Dr}}{G_{PreDr}} * 100 \quad (7)$$

All four indices were obtained from de-trended BAI series for all individual trees. Tree growth for the periods before (G_{PreDr}) and after (G_{PostDr}) the drought event were calculated as the average growth during the four years before or after the drought event. We used a period of four years because it was assumed to be more robust than results obtained for 2 or 3 years.

2.6. Data analysis

To test our hypotheses we studied how the four components of the growth response to drought varied as a function of stand composition. Models were fitted separately using R_t , R_c , R_s and RR_s response variables. We constructed linear mixed-effect models including case study and drought event as random effects, in order to cope with the lack of independence associated with observations at that level. All fitted models were visually checked for homoscedasticity and normal distribution of the residuals (Zuur et al. 2009, 2010). All statistical analysis were performed using SAS® PROC MIXED.

The different hypotheses were tested by including and checking the level of significance of different continuous or categorical explanatory covariates (see Table A3).

Hypothesis I: Tree growth response to specific drought events differs between mixed and monospecific stands

To test whether there was a general effect of stand composition (mixed vs monospecific) on the response components of tree growth to specific drought events we fitted Eq. (8) to the whole database.

$$Y_{ijkl} = \mu + SCM_{jk} + CS_k + D_{kl} + \epsilon_{ijkl} \quad (8)$$

where Y refers to the response variable (R_c , R_t , R_s or RR_s); SCM represents the fixed effect for stand composition (Mixed or Monospecific); CS and D are random effects of case study and drought event, respectively, D being nested into the case study. Finally, μ is the intercept of the model and ϵ_{ijkl} represents the independent and identically distributed residual error. Subscripts i , j , k and l refers to the i^{th} tree within the j^{th} plot of the k^{th} case study, for the l^{th} drought event.

Hypotheses II: The benefits of mixture to cope with drought events cannot be generalized to the three types of admixtures found (conifer-conifer, conifer-broadleaved and broadleaved-broadleaved)

To check whether the effect of stand composition (mixed vs monospecific) on tree growth response to drought events were dependent on the three types of admixtures found (TM, Table A3), we fitted Eq. (9).

$$Y_{ijkl} = \mu + TM_k + SCM_{jk} + [TM \times SCM]_{jk} + CS_k + D_{kl} + \epsilon_{ijkl} \quad (9)$$

Hypotheses III: Tree growth response to drought events in monospecific and mixed stands is mediated by the identity of tree species

To test this hypothesis we first fitted Eq. (10).

$$Y_{ijkl} = \mu + Species_i + SCM_{jk} + [Species \times SCM]_{jk} + CS_k + D_{kl} + \epsilon_{ijkl} \quad (10)$$

If a significant effect of the species was detected, we refitted Eq. (8) separately for each species in order to analyze their response in monospecific and mixed stands

In addition, in order to check the differences in growth response for a given tree species between monospecific and mixed stands, we fitted Eq. (9) separately, for those species that were present in more than one case study (*Pinus pinaster*, *P. sylvestris*, *Fagus sylvatica*, *Picea abies*, *Abies alba*, *Quercus petraea*).

Hypothesis IV: Tree growth response to drought events in monospecific and mixed stands varied along an aridity gradient.

To test this hypothesis we expanded Eq. (8) by adding as explanatory covariate the general De Martonne aridity index during the studied period (1975–2015) at each case study (Eq. (11)):

$$Y_{ijkl} = \mu + SCM_{jk} + DMI_{jkl} + [SCM \times DMI]_{jkl} + CS_k + D_{kl} + \epsilon_{ijkl} \quad (11)$$

Hypothesis V: Tree growth response to drought events in monospecific and mixed stands depends on stand characteristics (basal area and age)

To analyze the influence of stand characteristics (basal area and age) at plot level on tree growth response to drought events in mixed vs monospecific stands, we expanded Eq. (8) by adding as explanatory covariates the basal area (BA) and the age (Age) of the plot at the time of the drought event (Eq. (12) and Eq. (13)):

$$Y_{ijkl} = \mu + SCM_{jk} + BA_{jkl} + [SCM \times BA]_{jkl} + CS_k + D_{kl} + \epsilon_{ijkl} \quad (12)$$

$$Y_{ijkl} = \mu + SCM_{jk} + Age_{jkl} + [SCM \times Age]_{jkl} + CS_k + D_{kl} + \epsilon_{ijkl} \quad (13)$$

The full methodology is summarized in Figure A2.

3. Results

3.1. Influence of stand composition (monospecific vs mixed stands) on tree growth response to specific drought events

When considering the whole database with 30 case studies (Hypothesis I) we observed that overall mixed stands showed greater resistance (P-value = 0.0564), resilience (P-value < 0.0001) and relative resilience (P-value = 0.0283) compared to monospecific stands, while

no significant differences were detected for recovery (Fig. 2). Interestingly, monospecific stands showed a slight growth decline after the drought event ($R_s = 99\%$), while growth slightly increased in mixed stands after the drought event ($R_s = 102\%$). Despite these general trends, we detected a large variability among case studies, even for those case studies that share the same species composition and have similar climates (Figure A3).

3.2. Influence of the type of admixture (conifer-conifer, conifer-broadleaved and broadleaved-broadleaved) on tree drought response in monospecific and mixed stands

The effect of species mixing on drought responses varied with the type of admixture (Hypothesis II), as stated by the significant interaction effect of stand composition \times type of admixture for R_c (P-value = 0.0250), R_t (P-value = 0.0458) and R_s (P-value = 0.0499) (Table A4, Fig. 3). Mixed stands in broadleaved-broadleaved (P-value = 0.0458) and conifer-broadleaved (P-value = 0.0045) admixtures were more resistant to drought than monospecific stands. Resilience in mixed stands was also greater than in monospecific stands for these two types of admixtures (P-value = 0.0696 in broadleaved-broadleaved and P-value < 0.0001 in conifer-broadleaved admixtures). Trees in the three types of admixtures resumed growth after the drought event, but only in the conifer-conifer admixtures did mixed stands show higher recovery (P-value = 0.0289). Mixed stands in the conifer-conifer admixtures showed greater relative resilience compared to monospecific stands (P-value = 0.0510).

3.3. Influence of tree species identity on tree drought response in monospecific and mixed stands

The effect of drought on tree growth (Hypothesis III) differed between tree species (Table A5). As we detected a large significant effect of the species on the indices, and on the interaction between stand composition and tree species in recovery, resistance and relative resilience, we analyzed the response of each species separately in monospecific and mixed stands (Fig. 4). While recovery, resistance and relative resistance differed between species, both in monospecific (P-

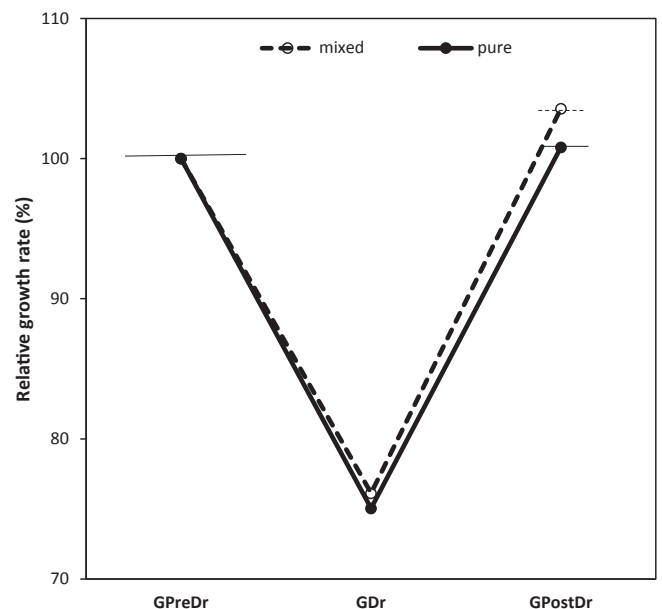


Fig. 2. Estimated growth responses to drought (GDr), and growth levels before (GPreDr) and after (GPostDr) drought for pure (black line) and mixed stands (dashed lines) according to Eq.(7). Due to the relation to growth before drought, GDr represents Resistance (R_t) and GPostDr represents Resilience (R_s).

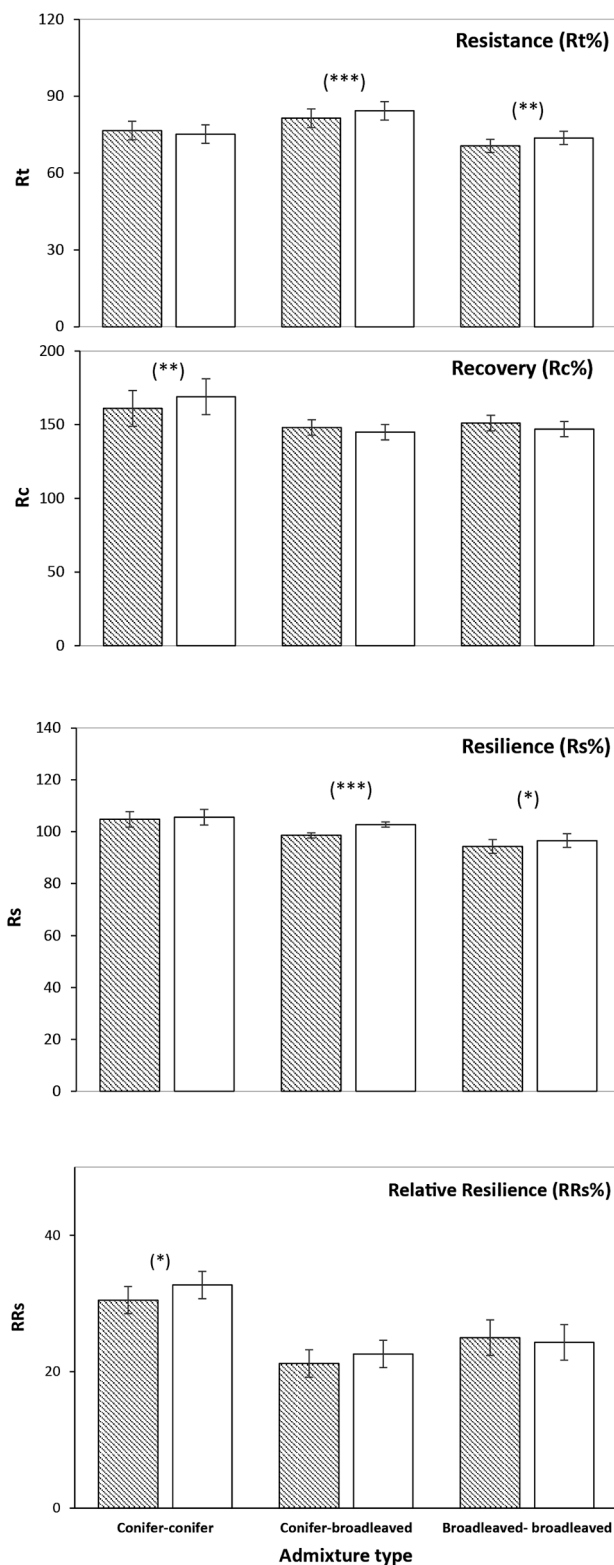


Fig. 3. Resistance (Rt), Recovery (Rc), Resilience (Rs) and Relative resilience (RRs) to drought events in pure (dashed) vs mixed (white) stands according to the type of admixture (Hypothesis II, Eq. (9)). Bars show standard errors. Asterisks indicate significant differences between pure and mixed stands within an admixture type (* $P < 0.1$; ** $P < 0.05$; *** $P < 0.001$; **** $P < 0.0001$).

value < 0.0001) and mixed stands (P -value < 0.0001), resilience differed between species only in monospecific stands (P -value = 0.0053). The greatest recovery was shown in *Pinus pinea* for monospecific and mixed stands, while the lowest values were observed in *Abies alba* for monospecific stands and for *Quercus pubescens* in mixed stands. The greatest resistance was shown for *Pinus nigra* in monospecific stands and for *Quercus pyrenaica* in mixed stands, while the lowest values were shown for *Quercus pyrenaica* for monospecific and mixed stands. Greatest relative resilience was shown in *Pinus pinea*, both in monospecific and mixed stands, while the lowest values were shown for *Pinus nigra* in monospecific stands and for *Abies alba* in mixed stands.

When focusing on the tree species that were present in different admixtures, we found that the species differed in their response patterns to drought (Table A5). *Pinus pinaster* (P -value < 0.0001), *Fagus sylvatica* (P -value = 0.0020) and *Abies alba* (P -value = 0.0579) showed a greater resistance in mixed stands compared to monospecific stands, although *Pinus pinaster* and *Fagus sylvatica* in mixed stands showed lower recovery (P -value = 0.0003 for *Pinus pinaster*, P -value < 0.0001 for *Fagus sylvatica*) and relative resilience (P -value = 0.0262 for *Pinus pinaster*, P -value = 0.0035 for *Fagus sylvatica*). *Pinus sylvestris* (P -value = 0.0357) showed higher resistance in monospecific stands, but lower recovery (P -value = 0.0011). *Pinus pinaster* (P -value = 0.0662), *Picea abies* (P -value = 0.0389), *Pinus sylvestris* (P -value = 0.0148), *Quercus petraea* (P -value = 0.0004) and *Larix decidua* (P -value = 0.0407) showed a significantly higher resilience in mixed stands compared to monospecific stands. *Larix decidua* (P -value = 0.0465), *Picea abies* (P -value = 0.0269) and *Pinus sylvestris* (P -value < 0.0001) showed a significantly higher relative resilience in mixed stands compared to monospecific stands.

If we analyzed in more detail the response to drought of the species according to whether it is accompanied by a conifer or a broadleaved species (Table 2), we found that *Fagus sylvatica* was more resistant in mixed stands, both when mixed with a conifer (P -value = 0.0173) and a broadleaved species (P -value = 0.0261), while the recovery was greater in monospecific stands (P -value = 0.0004 when mixed with a conifer, P -value = 0.0798 when mixed with a broadleaved species). Relative resilience in *Fagus sylvatica* was greater in monospecific stands when mixed with a conifer (P -value = 0.0086). *Pinus sylvestris* resilience (P -value < 0.0001), relative resilience (P -value < 0.0001) and recovery from drought (P -value = 0.0027) only increased when mixed with a broadleaved species, but not with a conifer. *Abies alba* and *Pinus pinaster* resistance to drought increased when mixed with a broadleaved species (P -value = 0.0068, P -value < 0.0001 , respectively), but not with a conifer, and the recovery was greater in monospecific stands (P -value = 0.058, P -value < 0.0001 , respectively). Relative Resilience of *Pinus pinaster* was greater in pure stands when mixed with a broadleaved species (P -value = 0.0275). Resilience of *Quercus petraea* was greater both when mixed with a conifer (P -value = 0.0075) and a broadleaved species (P -value = 0.0161).

3.4. Influence of the site aridity gradient (De Martonne index) and stand characteristics (basal area and age) on tree growth response to specific drought events in monospecific and mixed stands

Resilience to specific drought events was not constant along the site aridity gradient (Hypothesis IV). Thus, resilience increased under drier site conditions (P -value = 0.0311) (Table A6, Fig. 5). The increase in resilience in drier sites was not significantly different in monospecific compared to mixed stands (non-significant interaction between stand composition and DMI), although a trend to higher resilience was observed in mixed stands in the drier sites (Fig. 5). This effect was found for relative resilience, i.e., higher relative resilience in mixed stands in the drier sites (P -value interaction = 0.0854).

Stand basal area and stand age (Hypothesis V) had also a significant effect on the growth response to drought, both in monospecific and mixed stands (Table A6, Fig. 6). Stands with older trees were more

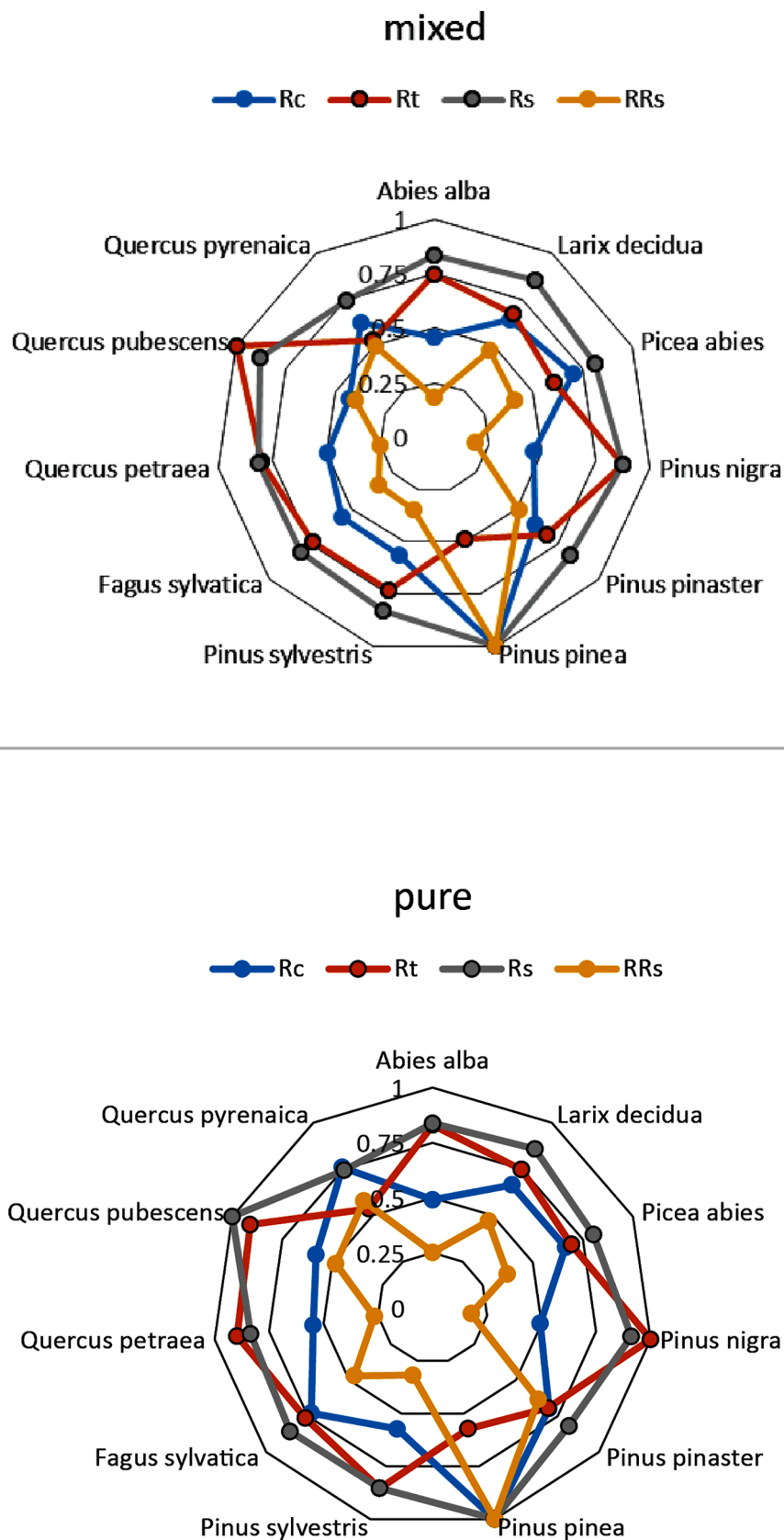


Fig. 4. Amoeba diagrams for pure and mixed stands representing Resistance (Rt), Recovery (Rc), Resilience (Rs) and Relative Resilience (RRs) for the eleven species studied. The value 1 represents the maximum value observed for Rt, Rc or Rs in pure or mixed stands.

Table 2

Results of the linear mixed models for hypothesis III (Eq. (9)), for those species that are found both mixed with conifers and broadleaves (ns: non-significant at $P > 0.1$). Highest value of each mixed/pure pair is in bold when differences are significant.

Species	Type of companion species	Stand composition (SCM)	Resistance	Recovery	Resilience	Relative resilience RRs (%)
			Rt (%)	Rc (%)	Rs (%)	
<i>Fagus sylvatica</i>	conifer	Mixed	88.65	130.52	100.58	12.8
		Pure	82.19	156.34	101.43	20.1
		P-value	0.0137	0.0004	ns	0.0086
	broadleaved	Mixed	72.23	153.17	95.04	27.3
		Pure	68.03	165.62	93.78	30.2
		P-value	0.0345	0.0668	ns	0.2083
<i>Pinus sylvestris</i>	conifer	Mixed	85.35	134.64	105.42	21.0
		Pure	89.00	130.20	107.24	19.6
		P-value	0.0245	ns	ns	0.4669
	broadleaved	Mixed	76.91	152.54	103.58	26.2
		Pure	78.44	141.77	98.63	19.9
		P-value	ns	0.0027	<0.0001	<0.0001
<i>Abies alba</i>	conifer	Mixed	67.50	201.85	101.31	33.8
		Pure	60.76	167.64	89.92	29.2
		P-value	ns	ns	ns	0.5623
	broadleaved	Mixed	97.06	118.04	101.10	15.7
		Pure	83.81	150.7	101.92	18.1
		P-value	0.0068	0.0158	ns	0.1478
<i>Pinus pinaster</i>	conifer	Mixed	72.89	160.39	107.52	34.6
		Pure	74.26	161.35	107.59	33.3
		P-value	ns	ns	ns	0.4403
	broadleaved	Mixed	58.40	165.11	92.63	34.3
		Pure	49.09	197.29	89.18	40.1
		P-value	<0.0001	<0.0001	ns	0.0275
<i>Quercus petraea</i>	conifer	Mixed	80.36	151.77	101.50	21.0
		Pure	77.61	153.92	97.76	20.0
		P-value	ns	ns	0.0075	0.6769
	broadleaved	Mixed	78.85	127.92	96.44	17.6
		Pure	76.66	125.97	92.60	16.0
		P-value	ns	ns	0.0161	0.3697

resistant (P -value < 0.0001) to drought, as well as more resilient (P -value = 0.0658) and with greater relative resilience (P -value = 0.0014). Stands with higher stand basal area were also more resistant (P -value < 0.0001) and resilient (P -value < 0.0001) to drought events. The significant interaction between stand age and stand composition for resistance (Rt) (P -value = 0.0545) indicated a greater effect of stand age in mixed stands than in monospecific stands. Regarding recovery (P -value = 0.0135) and relative resilience (P -value = 0.0024), mixed stand showed lower recovery and lower relative resilience with increasing age, while monospecific stands recovery and relative resilience remained relatively constant with age. The significant interaction between stand basal area and stand composition for resilience Rs (P -value = 0.0045) indicated that mixed stands with greater basal area recovered better from drought than monospecific stands.

4. Discussion

In line with a number of recent studies (e.g. Pretzsch et al. 2013; Metz et al. 2016; Jucker et al. 2016; Steckel et al., 2020), our results using a large database from thirty case studies covering a wide climatic gradient and including eleven common tree species in Europe indicated, on average, a positive effect of mixing on tree growth response to drought, especially on resilience and relative resilience and to a lesser extent on resistance. However, we found a large species-specific variability in growth response to drought in monospecific and mixed stands, being mediated by the type of admixture and more particularly the association of conifers and broadleaves. Moreover, the general positive effect of mixing on resilience to drought was influenced by stand age and basal area, while relative resilience was influenced by stand age. Meanwhile, the resilience along an aridity gradient decreased both in monospecific and mixed stands, although higher resilience to drought was observed in the Mediterranean case study (SP1) characterized by

the driest and hottest environment. Additionally, this case study showed higher relative resilience. These findings confirm the general trend towards improved resilience of mixed forests. It is important to note that while these correlative studies are important, they have not proven to be adequate for predicting which mixtures and on which sites certain species will be appropriate (Grossiord 2019). Meanwhile, process-based approaches, including models and carefully designed experiments, can be of great help to predict the growth limitations to climate and species interactions, and therefore these could be used as well (e.g. Pretzsch et al., 2015).

The indices studied displayed different patterns across the case studies. The negative correlation observed between resistance to drought and recovery from drought has been previously reported (Galiano et al., 2010; Thurm et al. 2016; Gazol et al. 2017). According to Steckel et al. (2020) the negative relationship suggests a trade-off between both indices, and could be attributed to more nutrients available following low growth episodes in monospecific stands than in mixed stands. Thus, under the improving belowground resources that follow a drought event, the relationship between species may change from positive to negative, which is in line with the stress gradient hypothesis (Maestre et al. 2009) and Forrester's framework (Forrester, 2014).

4.1. Monospecific and mixed stands respond differently to drought events

Our results show that tree species mixing can have a significantly positive effect on forest response to drought, which means that trees have greater resistance, resilience and relative resilience when growing with heterospecific neighbours than when growing with conspecifics (Fig. 2). Favourable interactions between heterospecific neighbours in mixed stands generally increase forest resistance to natural disturbances and environmental fluctuations (Pretzsch et al. 2013; Jactel et al. 2017), which suggests that trees might be able to sustain growth even under

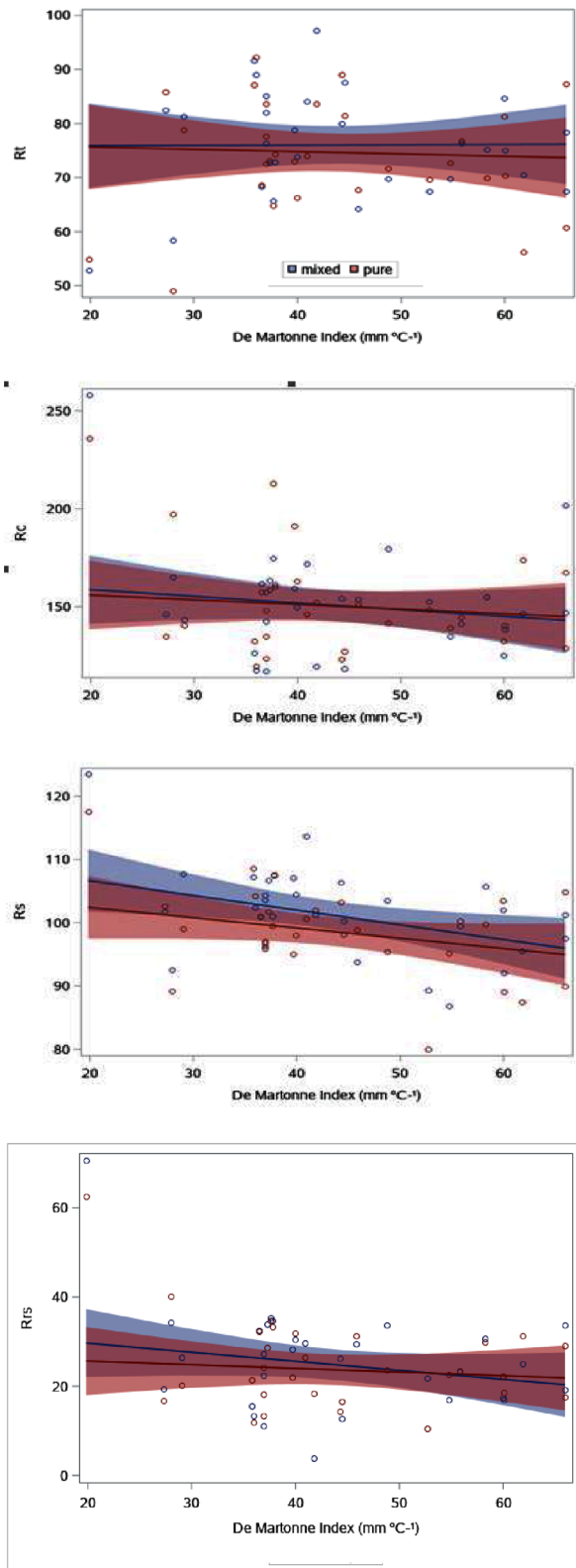


Fig. 5. Relationships between the De Martonne aridity index and Resistance (Rt), Recovery (Rc), Resilience (Rs) and Relative Resilience (Rrs) to drought events in mixed (blue line) and pure stands (red line) Hypothesis IV, Eq. (10). Confidence intervals are shown. Points represent mean values per case study for mixed (blue points) and pure stands (red points). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

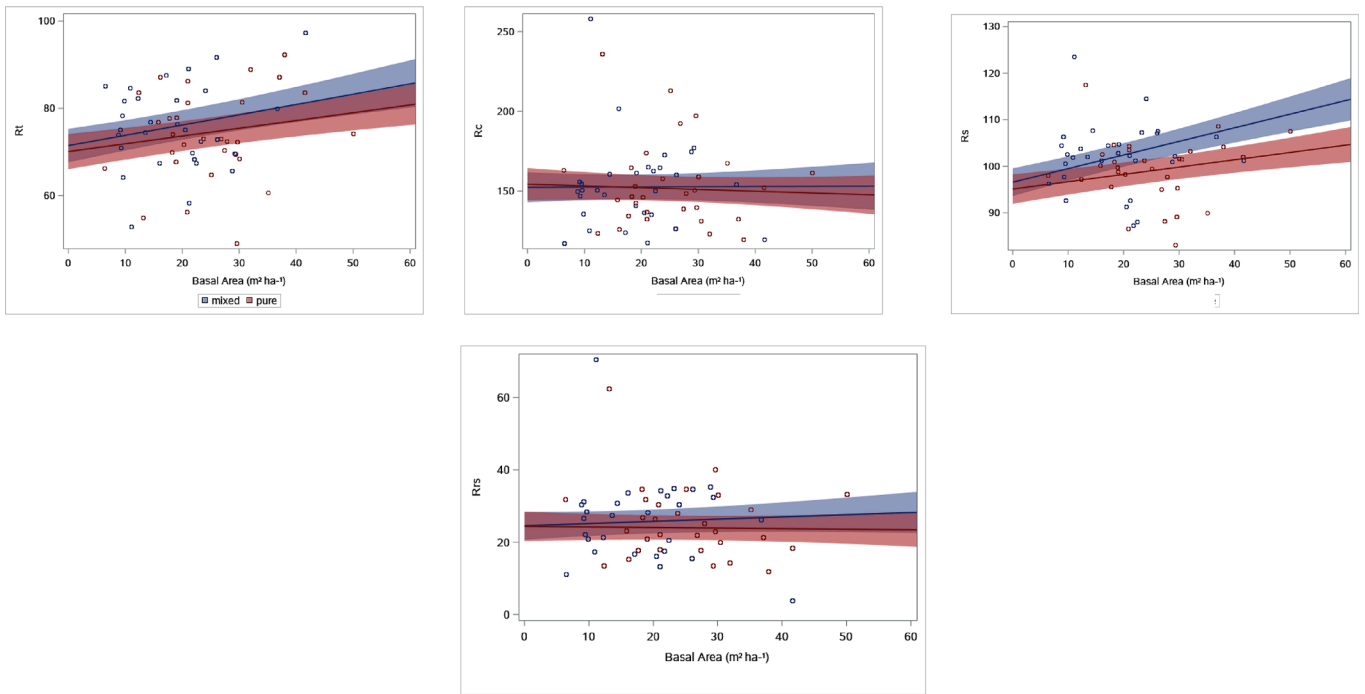
suboptimal growing conditions (e.g. del Río et al. 2014; Pretzsch et al. 2013; Forrester 2014). Greater resistance and resilience in mixed stands are mainly explained by two interconnected processes, which are reduced competition through niche partitioning (Jucker et al. 2014) and facilitation (Vandermeer, 1989; Steckel et al., 2020). In terms of niche partitioning, the development of multi-layered canopies in mixed stands, with different crown architecture and phenology, where shade tolerant species can establish below taller, light demanding species, may enable an efficient complementary light use (Binkley et al., 2003; Sapjanskas et al., 2014 and Forrester et al., 2018). This can allow mixed forests to exploit canopy space more efficiently (Morin et al. 2011, Pretzsch 2014; Toigo et al. 2018), thereby maximizing light interception (Ammer 2019), even under drought conditions. Similar belowground complementarity may occur when there is a partitioning in the use of water resources in the soil. Thus, some species that extend their root systems towards deeper soil layers can coexist with others that occupy superficial layers. Underlying facilitation processes such as hydraulic lift and higher functional diversity of the fungal community can also improve water access and use in mixed stands (Grossiord et al. 2014). Higher relative resilience can be interpreted in two ways, as it can reflect either higher buffer capacity to recover or compensating positive effects of the impact via increased neighbour mortality and resource availability to surviving trees (Lloret et al. 2011).

4.2. The benefits of tree mixing to cope with drought events depend on the type of admixture (conifer-conifer, conifer-broadleaved and broadleaved-broadleaved)

The strength of the positive effect of mixed stands on drought response varied considerably with the type of admixture, being mainly observed in conifer-broadleaved admixtures, and to a lesser extent in broadleaved-broadleaved admixtures (Table A4, Fig. 3). Mixed stands formed only by conifers likely exhibit higher competition and niche overlapping due to more similar species traits, whereas in conifer-broadleaved admixtures, belowground partitioning and spatiotemporal niche separation between species may drive complementary or asynchronous response to drought (de Dios García et al. 2018). The trait complementarity between conifer and broadleaved species can result in improved exploitation of underground water resources, as their root morphology and architecture differs considerably (Ammer 2019). Conifers and broadleaves in mixed stands are known to utilize deep water resources more efficiently than in monospecific stands and even exhibit complementarity for limited water resources (Bello et al. 2019). In this type of admixtures, broadleaves (mainly *Quercus* species) play an important facilitating role. They drive a hydraulic lift under drought conditions, thereby increasing the water available in the upper soil layers (Steckel et al. 2020) that could be more easily used by the shallow root system of the conifers, thus, increasing resistance to drought. Furthermore, different growth dynamics such as the date of budburst, radial growth onset and contrasting patterns of carbon allocation (e.g. Michelot et al. 2012; Zweifel et al. 2006), together with differences in optimum temperature for photosynthesis in broadleaves compared to conifers, may also favour complementarity effects (de Dios García et al. 2018). Conifer-conifer mixtures did not differ in terms of resistance and resilience with monospecific conifer stands, which could be linked to their more similar traits and mainly isohydric behaviour (Table 1). However, these mixtures showed a better recovery than the respective monospecific stands. We can hypothesize that as conifers show in general a drought avoidance strategy (see Table 1 for references), niche complementarity between them may help during the recovery phase.

In our study, we found that the type of mixture matters not only at the functional or phylogenetic level (i.e. conifer vs broadleaved) but also at the tree species composition level (Table A5, Fig. 4), pointing out to a species identity effect (Forrester et al. 2016). According to Anderreg et al. (2018) and Fichtner et al. (2020), positive effects of mixing increase with increasing taxonomic diversity of neighbours, mainly, with

(A)



(B)

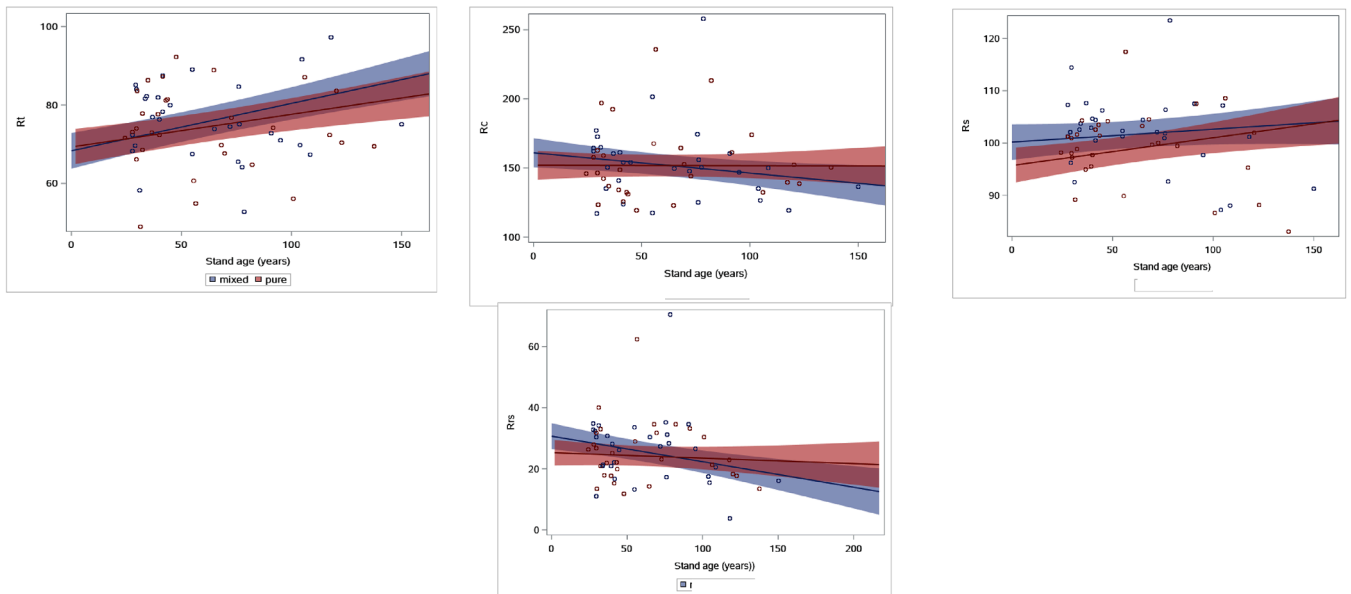


Fig. 6. Relationships of stand basal area (A) and stand age (B) with Resistance (Rt), Recovery (Rc), Resilience (Rs) and Relative Resilience (RRs) to drought events in mixed (blue line) and pure stands (red line) (Hypothesis V, Eqs. (11) and (12)). Confidence intervals are shown. Points represent mean values per case study for mixed (blue points) and pure stands (red points). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species hydraulic traits. Let us focus on the two species (*Pinus sylvestris* and *Fagus sylvatica*) that are most commonly found in the different case studies (Table 2). The positive effect of mixing could be explained by a complementarity effect that arises from facilitation (one species improves the environmental conditions for another species) or reduced competition (niche differentiation), although both types can be present at the same time (Forrester and Bauhus 2016). Thus, the isohydric, drought sensitive *Pinus sylvestris* would benefit from species mixture when growing with anisohydric broadleaved species such as *Fagus*

sylvatica or *Quercus petraea*. Furthermore, the differences in the demands for light between the species (e.g. shade tolerance, crown architecture and leaf phenology) could favour their complementarity (e.g. pioneer, shade intolerant *Pinus sylvestris* vs late-successional, shade tolerant *Fagus sylvatica*) (Pretzsch et al. 2015; Pretzsch et al. 2019), although this was not clearly observed in our study. *Fagus sylvatica* was found to exhibit higher resistance to drought when mixed with both conifers (*Picea abies*, *Abies alba*, *Pinus sylvestris* or *Pinus nigra*) and broadleaves (*Quercus petraea* or *Quercus pubescens*), while the recovery and relative resilience was

greater in monospecific stands compared to mixed stands. Thus, it seems that *Fagus sylvatica* can benefit from the mixture in terms of resistance to drought, irrespective of the type of admixture. It has been shown that *Fagus sylvatica* strongly determines the microclimate when mixed with other species (Heinrichs et al. 2019), usually benefiting more from the mixture than its neighbours.

4.3. Drought responses in monospecific and mixed stands along the site aridity gradient

Resilience and relative resilience to specific drought events were not constant along the site aridity gradient (Table A6, Fig. 5). Thus, we observed how both indices increased in those sites with drier conditions, ie, with lower De Martonne index. Several studies have reported drier forests to be more adaptable to the future drought events than the wetter forests (Zang et al. 2014). However, there is not a general consensus, when comparing monospecific vs mixed stands located along an aridity gradient, if the facilitative processes among coexisting species in a mixture will be more beneficial in drought-prone environments (Ruhk et al. 2020). In our study, the increase in resilience to drought events along the site aridity gradient was not significantly different in monospecific compared to mixed stands, although a trend towards higher resilience was observed in mixed stands in the drier sites along the gradient. In particular, higher resilience and relative resilience to drought was observed in mixed stands in the most drought-prone case study, which corresponded to the Mediterranean continental case study SP1 (Table A1), characterized by a high acclimation to high drought stress intensity (de-Dios-García et al., 2015). However, based on our results, the overall pattern we found along the studied site aridity gradient was not consistent with the stress-gradient hypothesis, which suggests that facilitation occur more frequently and are more important under drier sites (Grossiord et al. 2014).

4.4. Stand basal area and age affect growth response to drought in mixed and monospecific stands

Based on our observations, both basal area and stand age significantly affected the growth response to drought in the studied stands (Table A6, Fig. 6). Stands with greater basal area were more resistant and resilient to drought than stands with lower basal area. This result may suggest that trees in denser plots tend to grow more than expected in drier years, a result that has been previously found in drought-prone sites, resulting in an attenuated effect of competition (Calama et al. 2019).

Older stands were more resistant and resilient to drought, this effect being greater in mixed stands than in monospecific stands. The lower sensitivity to drought with age has been observed in other tree species (Thurm et al. 2016; Carrer and Urbinati 2006). Drought stress may decrease with increasing age as trees get better access to water in deeper soil layers by their extended root systems (Pretzsch et al. 2018). However, it has been also hypothesized that hydraulic constraints increase with tree age, which would lead to an increase in drought stress sensitivity in some tree species (Carrer and Urbinati 2004). The lack of uniformity in trees responses of different ages to drought reflects the complexity of climate-growth relationships.

5. Conclusions

Overall, tree species mixing seems to provide forests with greater resistance and resilience to drought events, but these average effects cannot be generalized to all types of admixtures. The more resilient mixed-species forests combines conifer and broadleaved species, and to a lesser extent broadleaved and broadleaved species, suggesting the importance of functional traits diversity and complementarity and the general observation that diversity – ecosystem functioning relationships are context dependent (Ratcliffe et al. 2017). In addition, we found that

the benefit of mixing species was similar to monospecific stands along the studied site aridity gradient, although a greater resilience and relative resilience to drought was observed in the driest environmental conditions. Last, the observed response patterns to drought largely varied among the eleven studied species. Such complex interactions between species composition and site conditions makes it difficult to predict how tree mixing may improve the resistance and resilience of mixed-species forests to drought. As mentioned before, process-based approaches could be useful for such predictions. Long-term studies are now needed to understand how monospecific and mixed forests can adapt to the more frequent and intense droughts they will experience under climate change.

6. Authors' contribution

M. Pardos arranged the common database, carried out the analysis and wrote the main body of the manuscript. R. Calama helped with the statistical analysis. R. Calama, M. del Río, H. Jactel and H. Pretzsch reviewed the manuscript. All authors provided data at stand level (field data) and tree level (increment core measurements) for each case study and helped with their comments to improve the manuscript.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118687>.

References

- Ammer, C., 2019. Diversity and forest productivity in a changing climate. *New Phytol.* 221, 50–66. <https://doi.org/10.1111/nph.15263>.
- Anderegg, L.D.L., HilleRisLambers, J., 2015. Drought stress limits the geographic ranges of two tree species via different physiological mechanisms. *Global Ch. Biol.* 22, 1029–1045. <https://doi.org/10.1111/gcb.13148>.
- Anderegg, W.R., Konings, A.G., Trugman, A.T., Yu, K., Bowling, D.R., Gabbitas, R., Zenes, N., 2018. Hydraulic diversity of forests regulates ecosystem resilience during drought. *Nature* 561 (7724), 538–541.
- Aranda, I., Cadahía, E., Fernández de Simón, B., 2020. Leaf ecophysiological and metabolic response in *Quercus pyrenaica* Willd seedlings to moderate drought under enriched CO₂ atmosphere. *J. Pl. Physiol.* 244, 153083. <https://doi.org/10.1016/j.jplph.2019.153083>.
- Aubin, I., Munson, A.D., Cardou, F., Burton, P.J., Isabel, N., Pedlar, J.H., et al., 2016. Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change. *Environ. Rev.* 24, 164–186. <https://doi.org/10.1139/er-2015-0072>.
- Baeten, L., Verheyen, K., Wirth, C., Bruehlheide, H., Bussotti, F., Finér, L., et al., 2013. A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspect Pl Ecol Evol Syst* 15, 281–291. <https://doi.org/10.1016/j.ppees.2013.07.002>.
- Baltas, E., 2007. Spatial distribution on climatic indices in north Greece. *Met. Apps.* 14, 69–78. <https://doi.org/10.1002/met.7>.

- Bello, J., Vallet, P., Perot, T., Balandier, P., Seigner, V., Perret, S., et al., 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>.
- Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–193. [https://doi.org/10.1016/0169-5347\(94\)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4).
- Bielak, K., Dudzinska, M., Pretzsch, H., 2014. Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) Karst] can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments. *Forest Syst.* 23 (3), 573–589. <https://doi.org/10.5424/fs/2014233-06195>.
- Binkley, D., Senock, R., Bird, S., Cole, T.G., 2003. Twenty years of stand development in pure and mixed stands of *Eucalyptus saligna* and N-fixing *Facaltaria moluccana*. *For. Ecol. Manage.* 182, 93–102. [https://doi.org/10.1016/S0378-1127\(03\)00028-8](https://doi.org/10.1016/S0378-1127(03)00028-8).
- Bonal, D., Pau, M., Toigo, M., Granier, A., Perot, T., 2017. Mixing oak and pine trees does not improve the functional response to severe drought in central French forests. *Ann. For. Sci.* 74, 72. <https://doi.org/10.1007/s13595-017-0671-9>.
- Bottero, A., D'Amato, A.W., Palik, B.J., Bradford, J.B., Fraver, S., Battaglia, M.A., Asherin, L.A., 2017. Density-dependent vulnerability of forest ecosystems to drought. *J. Appl. Ecol.* 4 (6), 1605–1614. <https://doi.org/10.1111/1365-2664.12847>.
- Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. *Dendrochronologia* 28, 251–258. <https://doi.org/10.1016/J.DENDRO.2009.12.001>.
- Calama, R., Conde, M., de-Dios-García, J., Madrigal, G., Vázquez-Piqué, J., Gordo, F.J., Pardos, M., 2019. Linking climate, annual growth and competition in a Mediterranean forest: *Pinus pinea* in the Spanish Northern Plateau. *Agric. For. Meteorol.* 264, 309–321.
- Calama, R., Puértolas, J., Madrigal, G., Pardos, M., 2013. Modeling the environmental response of leaf net photosynthesis in *Pinus pinea* L. natural regeneration. *Ecol. Model.* 251, 9–21. <https://doi.org/10.1016/j.ecolmodel.2012.11.029>.
- Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78, 1958–1965. [https://doi.org/10.1890/0012-9658\(1997\)078\[1958:CAFASA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2).
- Canadell, J., Jackson, R.B., Ehleringer, J.B., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108, 583–595. <https://doi.org/10.1007/BF00329030>.
- Carré, M., Urbinati, C., 2004. Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology* 85, 730–740. <https://doi.org/10.1890/02-0478>.
- Carré, M., Urbinati, C., 2006. Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix decidua*. *New Phytol.* 170, 861–872. <https://doi.org/10.1111/j.1469-8137.2006.01703.x>.
- Ceballos, L., Ruiz de la Torre, J., 1979. Arboles y arbustos. ETSI Montes, 511 p.
- Corcuera, L., Gil-Pelegrín, E., Notivol, E., 2012. Differences in hydraulic architecture between mesic and xeric *Pinus pinaster* populations at the seedling stage. *Tree Physiol.* 32 (12), 1442–1457. <https://doi.org/10.1093/treephys/tps103>.
- de-Dios-García, J., Manso, R., Calama, R., Fortin, M., Pardos, M., 2018. A new multifactorial approach for studying intra-annual secondary growth dynamics in Mediterranean mixed forests: integrating biotic and abiotic interactions. *Can. J. For. Res.* 48(4), 1–12. <https://doi.org/10.1139/cjfr-2017-0139>.
- de-Dios-García, J., Pardos, M., Calama, R., 2015. Interannual variability in competitive effects in mixed and monospecific forests of Mediterranean stone pine. *For. Ecol. Manage.* 358, 230–239. <https://doi.org/10.1016/j.foreco.2015.09.014>.
- del Río, M., Condes, S., Sterba, H., 2013. Productividad en masas mixtas vs. masas puras: influencia de la espesura en la interacción entre especies. In: *Actas del 6º Congreso Forestal Español 6CPE01-121:13*. Sociedad Española de Ciencias Forestales, Pontevedra.
- del Río, M., Schütze, G., Pretzsch, H., 2014. Temporal variation of competition and facilitation in mixed species forests in Central Europe. *Plant Biology* 16, 166–176.
- del Río, M., Pretzsch, H., Ruiz-Peinado, R., Ampoorter, E., Annighofer, P., Barbeito, I., et al., 2017. Species interactions increase the temporal stability of community productivity in *Pinus sylvestris*-*Fagus sylvatica* mixtures across Europe. *J. Ecol.* 105, 1032–1043. <https://doi.org/10.1111/1365-2745.12727>.
- Epron, D., Nouvellon, Y., Mareschal, L., Moreira, R., Koutika, L.-S., Geneste, B., Delgado-Rojas, J.S., Laclau, J.-P., Sola, G., Gonçalves, J.L.d.M., Bouillet, J.-P., 2013. Partitioning of net primary production in *Eucalyptus* and *Acacia* stands and in mixed-species plantations: Two case-studies in contrasting tropical environments. *Forest Ecology and Management* 301, 102–111.
- FAO, 2016. *State of the World's forests 2016. Forests and agriculture: land-use challenges and opportunities*. FAO, Rome, Italy.
- Fichtner, A., Schnabel, F., Bruehlheide, H., Kunz, M., Mausolf, K., et al., 2020. Neighbourhood diversity mitigates drought impacts on tree growth. *J. Ecol.* 00, 1–11. <https://doi.org/10.1111/1365-2745.13353>.
- Filipiak, M., 1992. *Modrzew japoński pospolite drzewo naszych lasów. Przegląd Leśniczy* 2, 12–13.
- Forner, A., Valladares, F., Bonal, D., Granier, A., Grossiord, Ch., et al., 2018. Extreme droughts affecting Mediterranean tree species' growth and water-use efficiency: the importance of timing. *Tree Physiol.* 38 (8), 1127–1137. <https://doi.org/10.1093/treephys/tpy022>.
- Forest Europe, 2015. *State of Europe's forests 2015*. Ministerial Conference on the Protection of Forests in Europe, 312 p.
- Forrester, D.I., 2014. The spatial and temporal dynamics of species interactions in mixed species forests: from pattern to process. *For. Ecol. Manage.* 312, 282–292. <https://doi.org/10.1016/j.foreco.2013.10.003>.
- Forrester, D.I., Bauhus, J., Cowie, A.L., 2006. Carbon allocation in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. *For. Ecol. Manage.* 233, 275–284.
- Forrester, D., Ammer, D.I., Annighöfer, P.J., et al., 2018. Effects of crown architecture and stand structure on light absorption in mixed and monospecific *Fagus sylvatica* and *Pinus sylvestris* forests along a productivity and climate gradient through Europe. *J. Ecol.* 106, 746–760. <https://doi.org/10.1111/1365-2745.12803>.
- Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity—productivity relationships in forests. *Curr. Forestry Rep* 2, 45–61. <https://doi.org/10.1007/s40725-016-0031-2>.
- Forrester, D.I., Bonal, D., Dawud, S., Gessler, A., Granier, A., Pollastrini, M., Grossiord, C., 2016. Drought responses by individual tree species are not often correlated with tree species diversity in European forests. *J. Appl. Ecol.* 53, 1725–1734. <https://doi.org/10.1111/1365-2664.12745>.
- Friedman, J.H., 1984. *A Variable Span Scatterplot Smoother*. Stanford University, Stanford.
- Fritts, H.C., Guioit, J., Gordon, G.A., Schweingruber, F., 1990. *Methods of Calibration, Verification, and Reconstruction*. In: *Methods of Dendrochronology*. Springer, Netherlands, Dordrecht, pp. 163–217.
- Fu, X., Meinzer, F.C., 2019. Metrics and proxies for stringency of regulation of plant water status (iso/anisohydry): a global data set reveals coordination and trade-offs among water transport traits. *Tree Physiol.* 39 (1), 122–134. <https://doi.org/10.1093/treephys/tpy087>.
- Galiano, L., Martínez-Vilalta, J., Lloret, F., 2010. Drought-induced multifactor decline of Scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. *Ecosystems* 13, 978–991. <https://doi.org/10.1007/s10021-010-9368-8>.
- Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., et al., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nat. Commun.* 4, 1340. <https://doi.org/10.1038/ncomms2328>.
- Gazol, A., Camarero, J.J., 2016. Functional diversity enhances silver fir growth resilience to an extreme drought. *J. Ecol.* 104, 1063–1075. <https://doi.org/10.1111/1365-2745.12575>.
- 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/geb.12526>.
- Grassi, G., Bagnaresi, U., 2001. Foliar morphological and physiological plasticity in *Picea abies* and *Abies alba* saplings along a natural light gradient. *Tree Physiol.* 21 (12–13), 959–967. <https://doi.org/10.1093/treephys/21.12-13.959>.
- 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., et al., 2014. Tree diversity does not always improve resistance of forest ecosystems to drought. *PNAS* 111, 14812–14815. <https://doi.org/10.1073/pnas.1411970111>.
- Heinrichs, S., Ammer, C., Mund, M., Boch, S., Budde, S., et al., 2019. Landscape-scale mixtures of tree species are more effective than stand-scale mixtures for biodiversity of vascular plants, bryophytes and lichens. *Forests* 10, 73. <https://doi.org/10.3390/f10010073>.
- Herguido, E., Granda, E., Benavides, R., García-Cervigón, A.I., Camarero, J.J., Valladares, F., 2016. Contrasting growth and mortality responses to climate warming of two pine species in a continental Mediterranean ecosystem. *For. Ecol. Manage.* 363, 149–158. <https://doi.org/10.1016/j.foreco.2015.12.038>.
- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., et al., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105–108. <https://doi.org/10.1038/nature11118>.
- Jactel, H., Bauhus, J., Boberg, J., et al., 2017. Tree Diversity Drives Forest Stand Resistance to Natural Disturbances. *Curr. For. Rep.* 3, 223–243. <https://doi.org/10.1007/s40725-017-0064-1>.
- Jactel, H., Gritti, E. S., Drössler, L., Forrester, D. I., Mason, W. L., Morin, X., et al., 2018. Positive biodiversity–productivity relationships in forests: climate matters. *Biology Letters* 14(4), 20170747.
- Jourdan, M., Lebourgeois, F., Morin, X., 2019. The effect of tree diversity on the resistance and recovery of forest stands in the French Alps may depend on species differences in hydraulic features. *For. Ecol. Manage.* 450, 117486. <https://doi.org/10.1016/j.foreco.2019.117486>.
- 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>.
- Jucker, T., Avăcăriței, D., Bărnoaiea, I., Duduman, G., Bouriaud, O., Coomes, D.A., 2016. Climate modulates the effects of tree diversity on forest productivity. *J. Ecol.* 104, 388–398. <https://doi.org/10.1111/1365-2745.12522>.
- Jucker, T., Bouriaud, O., Avacaritei, D., Danila, I., Duduman, G., Valladares, F., Coomes, D.A., 2014. Competition for light and water play contrasting roles in driving diversity–productivity relationships in Iberian forests. *J. Ecol.* 102, 1202–1213.
- Köstler, J.N., Brückner, E., Bibelriether, H. 1968. *Die Wurzeln der Waldbaume. Untersuchungen zur Morphologie der Waldbaume in Mitteleuropa*. Verlag Paul Parey, Hamburg and Berlin 1968, pp. 284.
- Kunert, N., Schwendenmann, L., Potvin, C., Hölscher, D., 2012. Tree diversity enhances tree transpiration in a Panamanian forest plantation. *J. Appl. Ecol.* 49, 135–144. <https://doi.org/10.1111/j.1365-2664.2011.02065.x>.
- Lebourgeois, F., Gomez, N., Pinto, P., Merian, P., 2013. Mixed stands reduce *Abies alba* tree-ring sensitivity to summer drought in the Vosges mountains, western Europe. *For. Ecol. Manage.* 303, 61–71. <https://doi.org/10.1016/j.foreco.2013.04.003>.

- Lindholm, M., Eronen, M., Timonen, M., Jouko Meriläinen, J., 1999. A ring-width chronology of Scots pine from northern Lapland covering the last two millennia. *Annales Botanici Fennici* 36 (2), 119–126. <https://www.jstor.org/stable/23726620>.
- 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>.
- López-Tirado, J., Hidalgo, P.J., 2014. A high resolution predictive model for relict trees in the Mediterranean-mountain forests (*Pinus sylvestris* L., *P. nigra* Arnold and *Abies pinsapo* Boiss.) from the south of Spain: A reliable management tool for reforestation. *For. Ecol. Mana.* 330, 105–114.
- Maestre, F.T., Callaway, R.M., Valladares, F., Lortie, C.J., 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.* 97, 199–205. <https://doi.org/10.1111/j.1365-2745.2008.01476.x>.
- Marozas, V., Augustaitis, A., Pivoras, A., Baumgarten, M., Mozgeris, G., et al., 2019. Comparative analyses of gas exchange characteristics and chlorophyll fluorescence of three dominant tree species during the vegetation season in hemi-boreal zone. *Lithuania. J. Agric. Meteor.* 75 (1), 3–12. <https://doi.org/10.2480/agrmet.D-18-00004>.
- Martín-Gómez, P., Aguilera, M., Pemán, J., Gil-Pelegrín, E., Ferrio, J.P., 2017. Contrasting ecophysiological strategies related to drought: the case of a mixed stand of Scots pine (*Pinus sylvestris*) and a submediterranean oak (*Quercus subpyrenaica*). *Tree Physiol.* 37, 1478–1492.
- Martínez-Vilalta, J., García-Fórner, N., 2017. Water potential regulation, stomatal behaviour and hydraulic transport under drought: deconstructing the iso/anisohydric concept. *Plant. Cell Environ.* 40, 962–976. <https://doi.org/10.1111/pce.12846>.
- Martínez-Vilalta, J., Piñol, J., 2002. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *For. Ecol. Managem.* 161 (1–3), 247–256. [https://doi.org/10.1016/S0378-1127\(01\)00495-9](https://doi.org/10.1016/S0378-1127(01)00495-9).
- Mayoral, C., Pardos, M., Sánchez-González, M., Brendel, O., Pita, P., 2016. Ecological implications of different water use strategies in three coexisting Mediterranean tree species. *For. Ecol. Managem.* 382, 76–87. <https://doi.org/10.1016/j.foreco.2016.10.002>.
- Mayoral, C., Calama, R., Sánchez-González, M., Pardos, M., 2015. Modelling the influence of light, water and temperature on photosynthesis in young trees of mixed Mediterranean forests. *New For.* 46, 485–506. <https://doi.org/10.1007/s11056-015-9471-y>.
- McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., et al., 2020. Pervasive shifts in forest dynamics in a changing world. *Science* 368 (6494).
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., et al., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178, 719–739. <https://doi.org/10.1111/j.1469-8137.2008.02436.x>.
- 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. Managem.* 339, 22–33. <https://doi.org/10.1016/j.foreco.2014.11.032>.
- Metz, J., Annighöfer, P., Schall, P., Zimmermann, J., Kahl, T., Schulze, E.D., Ammer, C., 2016. Site adapted admixed tree species reduce drought susceptibility of mature European beech. *Glob. Change Biol.* 22, 903–920. <https://doi.org/10.1111/gcb.13113>.
- Mitchell, P.J., Veneklaas, E.J., Lambers, H., Burgess, S.S.O., 2008. Leaf water relations during summer water deficit: differential responses in turgor maintenance and variation in leaf structure among different plant communities in south-western Australia. *Plant. Cell Environ.* 31, 1791–1802. <https://doi.org/10.1111/j.1365-3040.2008.01882.x>.
- Michélot, A., Simard, S., Rathgeber, C., Dufrene, E., Damesin, C., 2012. Comparing the intra-annual wood formation of three European species (*Fagus sylvatica*, *Quercus petraea* and *Pinus sylvestris*) as related to leaf phenology and non-structural carbohydrate dynamics. *Tree Physiol.* 32 (8), 1033–1045. <https://doi.org/10.1093/treephys/tps052>.
- Morin, X., Fahse, L., Scherer-Lorenzen, M., Bugmann, H., 2011. Tree species richness promotes productivity in temperate forests through strong complementarity between species: species richness promotes forest productivity. *Ecol. Lett.* 14, 1211–1219. <https://doi.org/10.1111/j.1461-0248.2011.01691.x>.
- Mutke S., Calama R., González-Martínez S.C., Montero G., Gordo J., Bono D., Gil L., 2012. Mediterranean Stone Pine: Botany and Horticulture. *Horticultural Reviews* 39, John Wiley & Sons, Inc., Hoboken, New Jersey: 153-201. <https://doi.org/10.1002/9781118100592.ch4>.
- Nothdurft, A., Engel, M., 2020. Climate sensitivity and resistance under monospecific and mixed stands scenario in Lower Austria evaluated with distributed lag models and penalized regression splines for tree-ring time series. *Eur. J. For. Res.* 139, 189–211. <https://doi.org/10.1007/s10342-019-01234-x>.
- Pardos, M., Calama, R., Maroschek, M., Rammer, W., Lexer, M.J., 2015. A model-based analysis of climate change vulnerability of *Pinus pinea* stands under multiobjective management in the Northern Plateau of Spain. *Ann. For. Sci.* 72, 1009–1021. <https://doi.org/10.1007/s13595-015-0520-7>.
- Pardos, M., Puértolas, J., Madrigal, G., Garriga, E., de Blas, S., Calama, R., 2010. Seasonal changes in the physiological activity of regeneration under a natural light gradient in a *Pinus pinea* regular stand. *For. Syst.*, 19(3). <https://doi.org/10.5424/fs/2010193-9102>.
- Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. *For. Ecol. Managem.* 327, 251–264. <https://doi.org/10.1016/j.foreco.2014.04.027>.
- Pretzsch, H., 2017. Individual tree structure and growth in mixed compared with monospecific stands. In: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), *Mixed-Species Forests: Ecology and Management*. Springer, Berlin Heidelberg, Berlin, Heidelberg, pp. 271–336.
- Pretzsch, H., del Río, M., Ammer, C., Avdagic, A., Barbeito, I., et al., 2015. Growth and yield of mixed versus monospecific stands of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) analysed along a productivity gradient through Europe. *Eur. J. For. Res.* 134, 927–947. <https://doi.org/10.1007/s10342-015-0900-4>.
- Pretzsch, H., del Río, M., Schütze, G., Ammer, Ch., Annighöfer, P., et al., 2016. Mixing of Scots pine (*Pinus sylvestris* L.) and European beech (*Fagus sylvatica* L.) enhances structural heterogeneity, and the effect increases with water availability. *For. Ecol. Managem.* 373, 149–166. <https://doi.org/10.1016/j.foreco.2016.04.043>.
- Pretzsch, H., Schütze, G., Biber, P., 2018. Drought can favour the growth of small in relation to tall trees in mature stands of Norway spruce and European beech. *For. Ecosyst.* 5 (20) <https://doi.org/10.1186/s40663-018-0139-x>.
- Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress in mixed versus monospecific forests: evidence of stress release by inter-specific facilitation. *Plant Biol.* 15, 483–495. <https://doi.org/10.1111/j.1438-8677.2012.00670.x>.
- Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, M., Ehbrecht, M., et al., 2019. Stand growth and structure of mixed-species and monospecific stands of Scots pine (*Pinus sylvestris* L.) and oak (*Q. robur* L., *Quercus petraea* (Matt.) Liebl.) analysed along a productivity gradient through Europe. *Eur. J. For. Res.* 162, 141. <https://doi.org/10.1007/s10342-019-01233-y>.
- Prieto-Recio, C., Martín-García, J., Bravo, F., Diez, J.J., 2015. Unravelling the associations between climate, soil properties and forest management in *Pinus pinaster* decline in the Iberian Peninsula. *For. Ecol. Managem.* 356, 74–83. <https://doi.org/10.1016/j.foreco.2015.07.033>.
- Puhe, J., 2003. Growth and development of the root system of Norway spruce (*Picea abies*) in forest stands—a review. *For. Ecol. Manag.* 175, 253–273. [https://doi.org/10.1016/S0378-1127\(02\)00134-2](https://doi.org/10.1016/S0378-1127(02)00134-2).
- Ramírez-Valiente, J.A., López, R., Hipp, A.L., Aranda, I., 2020. Correlated evolution of morphology, gas exchange, growth rates and hydraulics as a response to precipitation and temperature regimes in oaks (*Quercus*). *New Phytol.* <https://doi.org/10.1111/nph.16320>.
- Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., et al., 2017. Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecol. Lett.* 20 (11), 1414–1426.
- Sabaté, S., Gracia, C.A., Sánchez, A., 2002. Likely effects of climate change on growth of *Quercus ilex*, *Pinus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica* forests in the Mediterranean region. *For. Ecol. Managem.* 162, 23–37.
- Sapijanskas, J., Paquette, A., Potvin, C., Kunert, N., Loreau, M., 2014. Tropical tree diversity enhances light capture through crown plasticity and spatial and temporal niche differences. *Ecology* 95, 2479–2492. <https://doi.org/10.1890/1313-1366.1>.
- Schwarz, J., Skiadaresis, G., Kohler, M., Kunz, J., Schnabel, F., Vitali, V., Bauhus, J., 2020. Quantifying growth responses of trees to drought—A critique of commonly used resilience indices and recommendations for future studies. *Current Forestry Reports* 6, 185–200. <https://doi.org/10.1007/s40725-020-00119-2>.
- Sohn, J.A., Saha, S., Bauhus, J., 2016. Potential of forest thinning to mitigate drought stress: A meta-analysis. *For. Ecol. Manag.* 380, 261–273. <https://doi.org/10.1016/j.foreco.2016.07.046>.
- Speer, J.H., 2010. *Fundamentals of tree-ring research*. University of Arizona Press.
- Sperlich, D., Chang, C.T., Peñuelas, J., Sabaté, S., 2019. Responses of photosynthesis and component processes to drought and temperature stress: are Mediterranean trees fit for climate change? *Tree Physiol.* 39 (11), 1783–1805. <https://doi.org/10.1093/treephys/tpz089>.
- Steckel, M., del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., et al., 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. Managem.* 461, 117908 <https://doi.org/10.1016/j.foreco.2020.117908>.
- Toigo, M., Perot, T., Courbaud, B., Castagneyrol, B., Gégout, J.C., Longuetaud, F., et al., 2018. Difference in shade tolerance drives the mixture effect on oak productivity. *J. Ecol.* 106 (3), 1073–1082.
- Trasobares, A., Pukkala, T., Miina, J., 2004. Growth and yield model for uneven-aged mixtures of *Pinus sylvestris* L. and *Pinus nigra* Arn. in Catalonia, north-east Spain. *Ann. For. Sci.* 61 (1), 9–24.
- Thornthwaite, C.W., 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38 (1), 55–94. <https://doi.org/10.2307/210739>.
- Thurm, E.A., Uhl, E., Pretzsch, H., 2016. Mixture reduces climate sensitivity of Douglas-fir stem growth. *For. Ecol. Managem.* 376, 205–220. <https://doi.org/10.1016/j.foreco.2016.06.020>.
- Van der Maaten-Theunissen, M., van der Maaten, E., Bouriaud, O., 2015. PointRes: An R package to analyze pointer years and components of resilience. *Dendrochronologia* 35, 34–38. <https://doi.org/10.1016/j.dendro.2015.05.006>.
- Vandermeer, J., 1989. *The Ecology of Intercropping*. Cambridge University Press, Cambridge.
- Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A multiscale drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J. Climate* 23, 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>.
- Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the Average Value of Correlated Time Series, with Applications in Dendroclimatology and Hydrometeorology. *J. Clim. Appl. Meteorol.* 23, 201–213. [https://doi.org/10.1175/1520-0450\(1984\)023<0201:OTAVOC>2.0.CO;2](https://doi.org/10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2).

- Zhang, Y., Chen, H.Y.H., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J. Ecol.* 100, 742–749. <https://doi.org/10.1111/j.1365-2745.2011.01944.x>.
- Zang, C., Hartl-Meier, C., Dittmar, C., Rothe, A., Menzel, A., 2014. Patterns of drought tolerance in major european temperate forest trees: climatic drivers and levels of variability. *Glob. Chang. Biol.* 20, 3767–3779. <https://doi.org/10.1111/gcb.12637>.
- Zuur, A.F., Ieno, E.N., Waler, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer Link.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1 (3–14) <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.
- Zweifel, R., Zimmermann, L., Zeugin, F., Newbery, D.M., 2006. Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *J. Exp. Bot.* 57 (6), 1445–1459. <https://doi.org/10.1093/jxb/erj125>.