TITLE: 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

M. Jourdan[1,2,*], F. Lebourgeois[3], X. Morin[1]

[1] Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, UMR 5175, FORECAST, Montpellier, France

[2] Agence de l'environnement et de la maitrise de l'énergie, ADEME, Angers, France

[3] Université de Lorraine, AgroParisTech, INRA, UMR Silva, 14 rue Girardet, F-54000 Nancy, France

*corresponding author: marion.jourdan@cefe.cnrs.fr

Abstract

As climate change should lead to an increase in the vulnerability and the sensitivity of forests to extreme climatic events, quantifying and predicting their response to more severe droughts remains a key task for foresters. Furthermore, recent works have suggested that tree diversity may affect forest ecosystem functioning, including their response to extreme events. In this study we aimed at testing whether the growth response of forest stands to stressful climatic events varied between mixed and monospecific stands, under various environmental conditions. We focused on beech-fir forests (*Fagus sylvatica* [L.] and *Abies alba* [L.]) and beech-oak forests (*Fagus sylvatica* [L.] and *Quercus pubescent* [L.]) in the French Alps. We used a dendrochronological dataset sampled in forest plots organized by triplets (one mixture and two monospecific stands) distributed in six sites along a latitudinal gradient. We tested (1) whether stand diversity (two-species stands vs monospecific stands) modulates the stands' response to drought events in terms of productivity, (2) whether species identity may drive the diversity effect on resistance and recovery, and (3) whether this can be explained by interspecific interactions. We found that (1) interspecific differences in response to extreme drought events (possibly due to interspecific differences in hydraulic characteristics) can induce a mixture effect on stand growth, although it appeared (2) to be strongly depending on species identity (positive effect only found for beech-fir mixed stands), while (3) there were no significant non-additive effects of diversity on stand resistance and recovery, except for some specific cases. Overall, our study shows that promoting selected mixed stands management may buffer extrem drought effect on stand productivity.

Key words: Diversity, ecosystem functioning, stand growth, resistance, recovery, climate change, forests, Alps

1 INTRODUCTION

In the coming decades, extreme climatic events are predicted to become more frequent than in the past decades (Dale et al., 2001; Pachauri et al., 2015), especially water and/or heat stresses. Such events may affect ecosystems functioning and related services (Kellomaki et al., 2008; Malhi et al., 2008; Olesen et al., 2007) directly by altering organisms' physiology, but also indirectly by affecting community composition (Bertrand et al., 2011; Lenoir et al., 2008) that in turn impacts ecosystem functioning (Loreau, 2001). In particular, increased extreme drought frequency and intensity could be very damaging for European forest ecosystems (Babst et al., 2019; Maracchi et al., 2005). However, quantifying and predicting climate change impacts on ecosystem functioning remains a difficult but important task (Morin et al., 2018). To better understand and forecast these impacts, many studies aimed at quantified changes in ecosystem functioning along environmental gradients (Gitlin et al., 2006; Kirkman et al., 2001; Pugnaire and Luque, 2001), especially climatic gradients (Dunne et al., 2004; Penuelas et al., 2004). Using such space-for-time substitution appeared as a relevant way to assess the impact of future climate change (Blois et al., 2013; Lester et al., 2014).

Meanwhile, numerous theoretical, empirical and experimental studies have shown that species richness may strongly modify ecosystem functioning, especially productivity (Cardinale et al., 2012; Hooper et al., 2005). In fact, species-rich communities may, on average, show an increase in productivity in comparison to species-poor communities - and especially to monocultures, a pattern called "overyielding effect". Such a result has been mainly shown in herbaceous communities, but a few experimental (Jones, McNamara, & Mason, 2005; Pretzsch, 2005), observation-based (Toïgo et al., 2015) and modelling studies (Morin et al., 2018, 2011) have also shown that overyielding effects may be found in tree communities. Furthermore, it has also been suggested that diversity can stabilize the productivity of ecosystems over time

(Ives and Carpenter, 2007). This relationship was also studied in several ecosystems: grasslands (Cardinale et al., 2007), forests (DeClerck et al., 2006; Thompson et al., 2014) and other types (Allison and Martiny, 2008; Girvan et al., 2005). The stability of an ecosystem process may be quantified by several metrics (Donohue et al., 2016). Most studies have focused, so far, on temporal stability (Tilman, 1999). This metric describes temporal variation of an ecosystem process on the mid- or long-term, generally quantified by the inverse of the coefficient of variation of the temporal series of the studied process. Many studies have tested whether temporal stability varies with species diversity (Isbell et al., 2015; Jucker et al., 2014), usually showing a positive relationship at the community scale.

However, it is also very likely that climate change leads to an increase in the vulnerability and the sensitivity of forests to extreme drought events that are predicted to become more frequent and more intense in the coming decades (Pachauri et al., 2015). The functioning of forest ecosystems could be deteriorated, which may in turn strongly impact the services they provide. These other facets of stability lie in the response of the studied process after a stressful climatic event - eg. extreme drought - like resistance or recovery (McCann, 2000; Van Ruijven and Berendse, 2010; Vogel et al., 2012). In fact there are various definitions of resistance or recovery (Newton and Cantarello, 2015). In the present study, resistance is defined as the inverse of growth reduction experienced during a stressful event, i.e. ratio between the productivity during stressful year and before the stressful year (Lloret et al., 2011). Thus, the larger this ratio, the stronger the resistance. Recovery is defined as the capacity of the ecosystem to recover after a stressful event in terms of growth (Lloret et al., 2011), i.e. ratio between the productivity after the stressful year and the productivity during the stressful year. The effects of diversity on resistance and recovery of ecosystems have been much less studied than for temporal stability (Donohue et al. 2016). Yet, theoretical works have suggested that diversity, especially species richness, may have a negative effect on recovery (Loreau and

Behera, 1999). However, only few empirical studies (usually on grassland ecosystems) have been conducted on this question (Pfisterer and Schmid, 2002; Tilman and Downing, 1994), and no consensus emerged from grassland studies on the effect of diversity on resistance or recovery after a stressful event. Regarding forest ecosystems, the very few examples available showed that community composition may have a contrasted influence on resistance and recovery depending on species - i.e. positive or negative effect for Arthur and Dech (2016) or Pretzsch et al. (2013); not significant for DeClerck et al (2006). These results are often explained by physiological complementarity between species or by environmental differences (Grossiord et al., 2014; Merlin et al., 2015).

Regarding the role of physiological complementarity, it is generally assumed that physiological differences (e.g. hydraulic architecture in tree species) are greater at the interspecific level than at the intraspecific level (Cruiziat et al., 2002). This may induce contrasted responses to climatic constraints between species (Desplanque et al., 1998; Lebourgeois et al., 2014, 2010; Cailleret and Davi, 2010). Forest stands response to drought events should thus be different between mixed and monospecific stands. Two others mechanisms focusing on species interactions may also be involved: competition reduction and facilitation. According to many studies (Brooker et al., 2007; Canham et al., 2006; Forrester and Bauhus, 2016), intra-specific competition may be, on average, stronger than interspecific competition. Thus, we can expect a relaxing inter-individual competition for water or light resources in mixed forests, which may directly increase ecosystem resistance and recovery. Facilitation occurs when, a species could facilitate the establishment or maintenance of another species, without impacting the first species (Callaway et al., 2002; Choler et al., 2001). Some studies have shown that interspecific competition may decrease with increasing stress, consistently with the stress gradient hypothesis (*SGH*, Bertness and Callaway, 1994). This hypothesis initially assumes that competitive interactions should shift to facilitative ones when environmental conditions become very stressful. The positive effect of mixing is therefore stronger under stressful conditions. However, this pattern is challenged by more recent studies showing that in very stressful conditions the facilitation between species does not hold and gives way to a strong competition (Holmgren and Scheffer, 2010; Maestre et al., 2009). According to previous cited studies, we expect different pattern of response depending on mixed stand composition, because of physiologic species differences. One may expect a stronger buffering effect on stand growth, if drought species sensitivity is more different between species. These patterns may be modulated by environmental conditions (i.e. drought intensity).

It is thus crucial to study forest response to drought events and underlying effects, especially to develop relevant silvicultural management scenarios buffering the sensitivity of forest stands to drought by mitigating its negative impacts on growth and generally promoting forest adaptation to new climatic conditions. Some studies in France show that mixed stands management could be more resistant to extreme stressful events than monospecific stands (Millar et al., 2007; Seynave et al., 2018). Increasing the diversity in tree community thus seems to be an efficient solution to sustain forest functioning and to better preserve most of the related services that are especially important in mountain forests (e.g. soil erosion control and protection against avalanches). Studying how species composition and interspecific interactions drive stand response to drought is crucial, and knowing these effects could lead to relevant recommendations for forest management.

In this paper, we thus addressed the three following questions:

(1) Is the productivity of forest communities more resistant and/or does it recover faster to extreme drought events in mixed stands than in monospecific ones?

(2) How does species identity affect the diversity effect on resistance and recovery?

(3) Can this effect be explained by interaction between species (i.e. net diversity effect)?

To answer these questions, we used a field design relying on the comparison of two-species stands with monospecific stands according to a triplet design (Pretzsch et al., 2013b), distributed along a latitudinal gradient including elevation gradients to consider the effect of environmental conditions. We focused on two mixed forest types, i.e. common beech (*Fagus sylvatica*) - pubescent oak (*Quercus pubescens*) and beech-silver fir (*Abies alba*) forests. These mixed forests are widespread in the region, distributed along strong climatic gradients, and have a critical economic importance in France. Moreover, these forests have been identified as especially vulnerable regarding climate change (Courbaud et al., 2011; UNEP, 2010). More specifically, beech-fir stands are common communities in northern external Alps while beech-oak stands are common in southern external Alps (Seynave et al., 2008; Tinner et al., 2013). Comparing these three species is also interesting because of their physiological differences, which are likely to show various response to climatic stress and especially to extreme drought events. We hypothesized that stand resistance and recovery depended on species richness depending mostly of composition. We expect different pattern between beech-oak and beech-fir stand. We also hypothesized that mixed effect is mostly explain by additive effect.

2 MATERIAL AND METHODS

2.1 Field sites

The field design was constituted of forest plots dominated by one (monospecific stands) or two tree species (mixed stands). These plots were located in six forested areas in the French Alps, distributed along a latitudinal gradient with contrasted climatic conditions. These sites were from North to South: Bauges, Vercors, Mont Ventoux, Luberon-Lagarde, Grand Luberon and Sainte-Baume (Fig. 1 and Table A). All sites are characterized by limestone bedrock, with an aspect from North to West, as sites have been selected to minimize variability in all environmental conditions but climate, as much as possible. This gradient has been divided into two parts according to species composition of the sampled stands: the northern sites (Bauges, Vercors, Mont Ventoux) with beech-fir forests, and the southern sites (Luberon Lagarde, Grand Luberon, Sainte-Baume) with beech-oak forests. Beech stands have thus been sampled in the six sites. The stand structure of the stands was high forest, except in Grand Luberon where stands were coppice forests.

The plots have been grouped in triplets inside each site, i.e. the combination of a beech pure stand, a fir or oak monospecific stands (i.e. dominated by at least 90% of the total basal area represented by the target species), and a fir-beech or oak-beech mixed stands (i.e. between 40 and 60% and in average with 45% of each species). Within a site, the triplets are distributed along an elevational gradient, except in Sainte Baume and Luberon-Lagarde sites. Focusing on forest mixed stands with two species allowed testing complementary effects in a more precise way (Aussenac et al., 2017; Forrester and Bauhus, 2016) and better identifying explanatory mechanisms at a local scale. A total of 66 plots were sampled between 2013 and 2015, organized in 22 triplets (Table A).

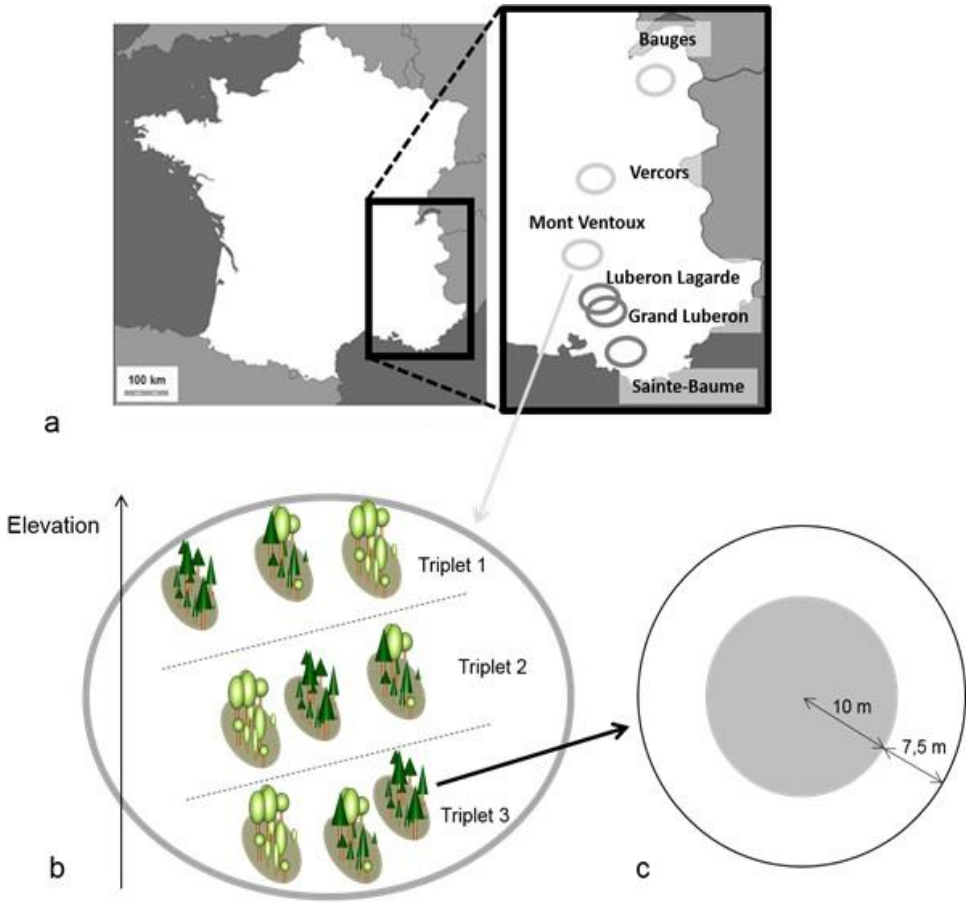

Figure 1: Description of the field design. (a) The study area and sites where the plots have been sampled. North sites (light grey circles) are Mont Ventoux, Vercors and Bauges, with plots sampled in beech-fir forests. South sites (dark gray circles) are in Luberon Lagarde, Grand Luberon and Sainte-Baume, with plots sampled in beech-oak forests. (b) Schematic representation of a site with three triplets of stands (one monospecific stand of species A (beech), one monospecific stand of species B (fir or oak), and one mixed stand with species A and B) distributed along an elevational gradient. (c) Schematic representation of a plot, with an inner circle (grey area) in which all trees with a DBH > 7.5 cm were sampled, and an external 7.5m-crown (buffer zone) in which only the trees with a larger DBH than the median DBH of trees in the inner circle have been sampled (dominant trees).

A plot was constituted of a 17.5 m-radius circle, including a central zone of a 10 m-radius circle (Fig. 1). For each plot, slope, elevation and aspect were measured. In the central zone, tree characteristics were measured (species identity, localization, height, crown depth, diameter at breast height [*DBH*]) and trees with a *DBH* larger than 7.5 cm were cored at breast height using a Pressler borer. In coppice stands, only the largest stem of each coppice was cored. We thus considered all the trees in a plot, regardless their status (dominant or understory).

2.2 Species

In this study, we focused on two kinds of mixed stands: one coniferous-hardwood species, beech-fir (with two late-successional species), and one hardwood-hardwood species, beech-oak (with one late-successional species and one mid-successional species). These three species allowed studying two different cases of mixture effect on stand productivity, because of the physiological differences between species. Common beech is sensitive to dry conditions, but recovers easily after extreme stressful event (Lebourgeois et al., 2005). Silver fir is less sensitive to dry conditions, but grows better in humid conditions (Lebourgeois et al., 2010; Mauri et al., 2016). Moreover, as a coniferous species, its growing season starts earlier than beech, which may affect positively its recovery after a drought year. Pubescent oak is a mid-successional species that is more light-demanding than the two other species and that better tolerates shallow soils and drier atmospheric conditions than the two other species (Pasta et al., 2016). Other species were sampled in some plots when present - maple (*Acer campestre*), spruce (*Picea abies*), and Scots pine (*Pinus sylvestris*) - but they represented less than 10% of total composition for each plot in terms of basal area. As they were equally present in monospecific or mixed stands, we did not consider it for this study.

2.3 Climatic data

We used the Standardized Precipitation Evapotranspiration Index (*SPEI*) to determine the onset, duration and magnitude of drought conditions with respect to normal conditions. *SPEI* is derived of the *SPI* (Standardized Precipitation Index, Guttman, 1999), and represents a climatic water balance (Thornthwaite, 1948) calculated at different time scales, using the monthly (or weekly) difference between precipitation and *PET* (Vicente-Serrano et al., 2013, 2010). These indexes have been already used in several ecological studies analyzing radial growth data (Merlin et al., 2015; Potop et al., 2014; Pretzsch et al., 2016).

We calculated annual *SPEI* using *R* package *SPEI* (Vicente-Serrano et al., 2010), between February and July, hereafter identified as $SPEI_{07}$, i.e. the growth period (Vanoni et al., 2016). It also allowed determining the years with driest growth season of a dataset. Regarding *SPEI* values, the threshold corresponding to a drought event (at the year level) affecting tree growth was likely to vary between species and sites, but for the sake of simplicity we used a unique threshold in our analyses. A sensitivity analysis on threshold level based on AIC comparison (data not shown) showed that the best threshold was -1.17 (exploring value between -0.5 and -1.5 with 0.02 step) for our dataset (Fig. 2). This agreed with a recent experimental study in grasslands that used a threshold of -1.28 (Isbell et al., 2015) and a global study based on remote sensing data that used a threshold of -1 (Schwalm et al., 2017).

Monthly values of precipitation and *PET* were extracted from 1km-resolution GIS layers covering all France for each year from 1995 to 2013. These maps were created using data from 119 and 214 non-interrupted weather stations from the Météo France network, for precipitation and temperature respectively. To build the climatic maps, a monthly model was created for each variable using Geographically Weighted Regression (GWR, Fotheringham et al., 2002) with spatially-distributed variables describing topography, solar radiation, land use and distances to the seas (Piedallu et al., 2016). Cross-validation was used to validate these maps, with a mean

r^2 ranging between 0.80 for precipitation to 0.94 for mean temperature across all pixels in France.

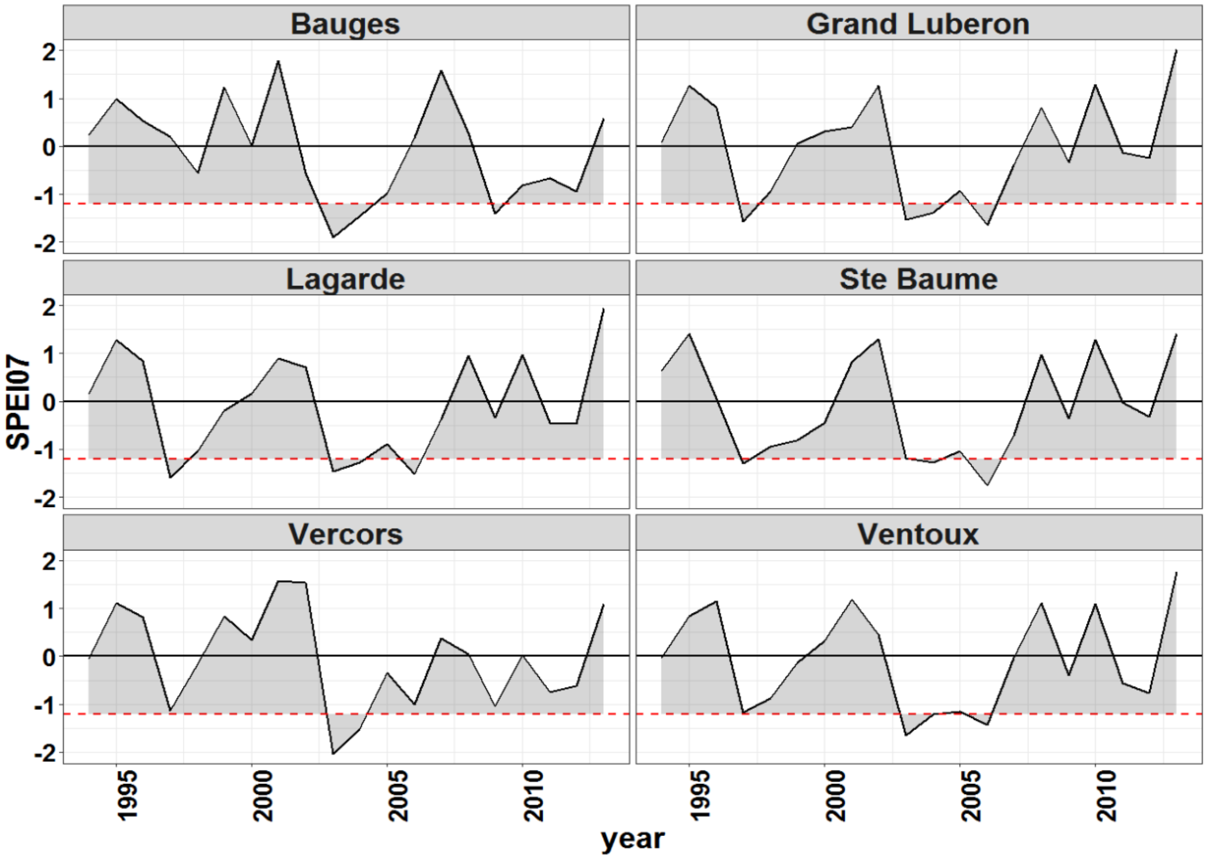

Figure 2: SPEI$_{07}$ trends in the six studied sites. Black line corresponds to the SPEI$_{07}$ calculated between February and July for each year and for each site. Horizontal red lines correspond to the threshold delimiting an extreme dry event (i.e. 10% driest years), with values below the threshold. Horizontal black line represents 0 level.

2.4 Data analyses

<u>Dendrochronological analyses</u>

We studied growth dynamics using tree rings for the last 18 years before sampling, i.e. from 1995 to 2013. Each tree ring was first photographed with a large-resolution camera coupled with binocular lens. Then the width of each ring was assessed with ImageJ software (https://imagej.nih.gov/ij/index.html), with an accuracy of 0.01 mm. All cores, i.e. 2159 trees, were cross-dated for each species using specific species pointer years, as described in Lebourgeois and Merian (2012), but without series standardization. This analysis allowed ensuring that chronologies were synchronized, without corrected interannual variations amplitude. Here, productivity was represented by basal area increment *BAI* instead of diameter increment in Lloret et al. (2011). Diameter increments were transformed into *BAI* using measured DBH, as commonly done (Biondi and Qeadan, 2008). Some cores were too difficult to read with accuracy and were thus not reliable and have been removed for the analyses. Therefore, we finally used growth time-series for 1235 trees, with 596 beeches (mean age: 106±45 year sold), 387 firs (mean age: 75±38 years old) and 240 oaks (mean age: 87±40 years old).

This study aimed at assessing forest productivity by sampling all trees in a plot instead of sampling only some a few trees like classically done (e.g. NFI-based studies). Considering all trees should allow better quantifying the competitive environment between all trees within each plot. However, we did not obtain growth data for all trees due to the difficulty of reading some cores. As these unreadable cores were not equally distributed across the network of plots but also inside each triplet, it was not possible to focus on only the subsample of available trees (i.e. trees with a readable core) to calculate resistance (*Rt*) and recovery (*Rc*) for the whole plot. To assess the productivity of the whole plot, we thus had to reconstruct the temporal series of *BAI* of the missing individuals, i.e. 924 trees – thus *ca.* 40% of total dataset (meaning that the number of sampled trees remains much larger than what is usually done when focusing on only a few dominant trees in a plot). To do so, we fitted a linear model for each stand type and each species in each site for each year, with *BAI* as the variable to explain and tree basal area as explanatory variables. With this approach, we have been able to predict *BAI* time-series for each missing tree (models' estimates shown in Table B), to finally obtain *BAI* time-series for each plot.

Assessing resistance and recovery

To assess resistance and recovery in each plot, we used annual *BAI* at the stand level, for the last 18 years (1995-2013). The annual productivity at year *y* (BAI_y) was calculated by summing the BAI of all trees for each plot:

$$BAI_y = \sum_i^n BAI_{iy} \qquad (1)$$

with *n* being the number of trees in the plot and BAI_{iy} being the basal area increment of tree *i* at year *y*.

Diversity and climate effects on resistance and recovery

Contrary to a lot of studies in forest ecosystems (Lloret et al., 2011; Pretzsch et al., 2013; Trouvé, Bontemps, Collet, Seynave, & Lebourgeois, 2017; Zang, Hartl-Meier, Dittmar, Rothe, & Menzel, 2014) that used a comparison between tree growth before and after a stressful event, we used a distributed lag effect model of $SPEI_{07}$ using the DLNM R package (Gasparrini, 2011). We included these linear lag effects of *SPEI* in a linear model of stand tree growth that controls for additional covariates. More precisely, we modelled stand annual basal area increment (*BAI*) as function of competitive environment (*BA*), and distributed lag effect of *SPEI*.

We modelled the drought lag effect from the current year (lag0) up to four previous year (*i.e.* lag1, lag2, lag3 and lag4) with distributed lag effects based on i) a threshold function below -1.17 *SPEI* and ii) a linear function to represent the temporal lag effect of drought on tree growth. i) The threshold function corresponds to a transformation of *SPEI* into a new variable $SPEI_t$ such as $SPEI_t = 0$ if $SPEI \geq -1.17$ and $SPEI_t = -1.17 - SPEI$, if $SPEI < -1.17$. $SPEI_t$ is a positive and increasing function drought stress intensity (whereas drought stress corresponds to negative values of *SPEI*). ii) The temporal distributed lag effect was modelled using a linear model with an intercept (see Gasparrini, 2011 for model details on distributed lag effect models). This linear trend was supported by a preliminary analysis assuming the unconstrained lag effect. A distributed lag effect allows representing delayed effect of a variable (in our case $SPEI_t$) as the sum of the effect until a given number of lag years is reached (four in our case). The equation 2 shows the lag effect for a given year *y*:

$$\sum_{l=0}^{4} \beta_l SPEIt_{y-l} \qquad (2)$$

A linear lag effect model is fitted by constraining the β coefficients as $\beta_l = a + b * l$, where *l* is the lag year (*l* in 0 to 4). Our distributed lag effect model is closely similar to classical representation of resilience in term of resistance and recovery (see Fig. C and Lloret et al. 2011) with the intercept at lag0 (parameter *a*) representing the immediate growth reduction due to drought and the linear recovery over time (function of the parameter *b*) determining the recovery after stress. The parameters *a* and *b* can be estimated by recasting the equation (2) as:

$$\sum_{l=0}^{4} \beta_l \, SPEIt_{y-l} = a * \sum_{l=0}^{4} SPEIt_{y-l} + b * \sum_{l=0}^{4} l * SPEIt_{y-l}$$

$$= a * lag_{intercept}(SPEI_y) + b * lag_{slope}(SPEI_y), \; (3)$$

with $lag_{intercept}(SPEI_y) = \sum_{l=0}^{4} SPEIt_{y-l}$ and $lag_{slope}(SPEI_y) = \sum_{l=0}^{4} l * SPEIt_{y-l}$.

The full fitted model is given by the following equation:

$$BAI_{s,t,p,y} = c_{0,s} + c_1 * BA_p + a * lag_{intercept}(SPEI_y) + b * lag_{slope}(SPEI_y) + d_t + d_{p,t} + e_{s,t,p,y} \qquad (4)$$

where *t*, *p*, and *y* are respectively the triplet, the plot and the year. $c_{0,s}$ is site dependent intercept (*s* corresponding to one of the different site Bauges, Vercors, Ventoux, Grand Luberon, Luberon Lagarde or Sainte-Baume). BA_p is the total basal area and c_1 is the respective fitted coefficients. d_t and $d_{p,t}$ are respectively the triplet random effects and plot nested in triplet random effects and $e_{s,t,p,y}$ is the residual normal error. *a* and *b* represent respectively the immediate growth reduction due to drought (resistance) and the linear recovery over time (recovery). This model was fitted separately per stand type – i.e. monospecific beech, fir and oak stand, and beech-fir and beech-oak mixed – and region – North (for Bauges, Vercors, Ventoux) and South (for Luberon Lagarde, Grand Luberon and Sainte-Baume) - with *lme* and DLNM with R software (R version 3.3.0).

Resistance and recovery to year with an extreme drought

We tested whether climatic stress may impact forest stands in the short term, i.e. at the year during which the drought stress occurred (hereafter named "current year") and the 3 years just after. Lloret et al. (2011) presented a framework to compute the effects of extreme one-time stress on stand (or tree) productivity during and after. Here, we used resistance (*Rt*) and recovery (*Rc*), defined below in (5) and (6). This metrics were calculated with BAI_y series (Eq. 1), namely BAI_y during climatic stress (*Dr*), BAI_y in the respective pre-stress period (*PreDr),* used as reference period, and BAI_y in the respective post-stress period (*PostDr*) (Zang et al 2014, Lloret et al., 2011) as:

$$Rt = Dr/PreDr \quad (5)$$

$$Rc = PostDr/Dr \quad (6)$$

PreDr and *PostDr* were calculated from an average over three years (Pretzsch et al., 2013). Figure C illustrates graphically the computing method. We focused on years with extreme drought, meaning with $SPEI_{07} < -1.17$ (see above).

To better explore the effect of diversity on forest resistance and recovery, we computed indices inspired by the Net Biodiversity Effect (*NBE,* Loreau, 1998). The *NBE* quantifies non-additive effect of species mixing, i.e. effect of interspecific interaction, on a given ecosystem process (e.g. mean productivity). We compared the productivity of a 2-species stand and the predicted productivity based on the productivity of monospecific stands and the relative abundance of species in the mixed stand - under the null hypothesis that there was no effect of species interactions on ecosystem functioning. We have thus transposed this approach to define two indices for productivity resistance $Rt_{div.eff}$ and productivity recovery $Rc_{div.eff}$. In other words, this method allowed calculating non-additive effect of increasing diversity on Rt (5) or Rc (6).

To compute these new indices, a predicted response of mixed plots is calculated from monospecific stand plots (Rt_{pred} or Rc_{pred}), using a predicted productivity BAI_{pred_y} for each mixed plot and each year y. BAI_{pred_y} was calculated using observed BAI of each species in monospecific stands of the corresponding triplet. Expected resistance (Rt_{pred}) and recovery (Rc_{pred}) were then assessed from BAI_{pred_y} time-series. The productivity of each mixed stand could be partitioned in two parts: productivity of beech trees, productivity of accompanying species (fir or oak). The relative abundance of each species in the mixed stands (p_{Fagus}, $p_{Quercus\ or\ Abies}$) was calculated using the summed initial basal area of each species (i.e. basal area in 1995). Thus, predicted annual productivity BAI_{pred_y} of each mixed stand at year y was calculated as follows:

$$BAI_{pred,y} = BAI_{Fagus_y} * p_{Fagus} + BAI_{Quercus\ or Abies_y} * p_{Quercus\ or\ Abies} \quad (6)$$

where $BAI_{Fagus\ or\ Quercus\ or\ Abies,y}$ were respectively beech/oak/fir monospecific stand basal area increment at year y. Because there was no monospecific stand for the “other species” in this dataset, their predicted productivity was considered as the same than observed productivity BAI_y.

Finally, Rt_{pred} or Rc_{pred} were compared with the observed values (Rt_{obs} or Rc_{obs}). It was noteworthy that these calculations were possible because the plots within a triplet had a similar structure (in terms of basal area). In this analysis, we thus obtained $Rt_{div.eff}$ and $Rc_{div.eff}$ values for each triplet t:

$$Rt_{div.eff_t} = Rt_{obs_t} - Rt_{pred_t} \quad (7)$$

$$Rc_{div.eff_t} = Rc_{obs_t} - Rc_{pred_t} \quad (8)$$

$Rt_{div.eff}$ and $Rc_{div.eff}$ were analyzed separately for each site. To test whether $Rt_{div.eff}$ and $Rc_{div.eff}$ values were significantly different from 0, we used on a Wilcoxon-test. Significant positive or negative values means that diversity had, on average, a positive or negative non-additive effect on resistance and recovery, respectively. If $Rt_{div.eff}$ and $Rc_{div.eff}$ are equal to 0, it means that diversity had no non-additive effect on resistance and recovery.

All analyses were carried-out with R software (R version 3.3.0). The full methodology is summarized in Fig. C.

3 RESULTS

3.1 Diversity and climate effects on resistance and recovery

In fir and beech stands (i.e. in the northern part of the gradient), the response of both metrics to drought events are significant for the three stands. Moreover, resistance and recovery varied between stands (Fig. 3-a, and Table 1). Monospecific beech stands appeared to be more resistant than monospecific fir and mixed stands, as the estimate for monospecific beech (-0.003±0.001) was lower than estimates for monospecific fir (-0.009±0.001) and mixed stands (0.007±0.001).

Dataset		Beech stands	Other pure stands (Fir or Oak)	Mixed stands
	metrics	Estimate (±SE)	Estimate (±SE)	Estimate (±SE)
Beech-Fir	*BA*	0.003 (±0.002)	0.003 (±0.006)	0.006 (±0.005)
	$lag_{intercept}(SPEI_y)$ *(resistance)*	**-0.003** (±0.0008)	**-0.009** (±0.001)	**-0.007** (±0.001)
	$lag_{slope}(SPEI_y)$ *(recovery)*	**0.001** (±0.0003)	**0.003** (±0.0006)	**0.002** (±0.0004)
Beech-Oak	*BA*	-0.004 (±0.002)	0.002 (±0.002)	0.0002 (±0.004)
	$lag_{intercept}(SPEI_y)$ *(resistance)*	-0.001 (±0.001)	-0.0004 (±0.0008)	-0.0003 (±0.001)
	$lag_{slope}(SPEI_y)$ *(recovery)*	0.0003 (±0.0006)	0.0004 (±0.0003)	-0.0001 (±0.0005)

Table 1: Linear models tested to explain BAI for every stands, with the northern (with beech-fir stand, including Mont Ventoux, Vercors and Bauges) and southern (with beech-oak stand including Luberon Lagarde, Grand Luberon and Sainte-Baume) parts of the gradient taken separately. BA is the stand basal area, and resistance and recovery represent stand responses to extreme drought. Significant p-value with t-test at the 0.1 level are represented in bold.

The recovery of all stands (represented by DLSPEI slope, see Table 1) was significantly positive. Mixed stands recovery (estimate: 0.002±0.0004) is higher than beech stands recovery (estimate: 0.001±0.0003) but lower than fir stands recovery (estimate: 0.003±0.0006).

In oak and beech stands (i.e. in the southern part of the gradient) (Fig. 3-b and Table 1), extreme drought events did not significant affect *BAI* at stand level. Monospecific oak and beech stands showed a positive recovery, contrary to mixed stands, although these trends were not significant.

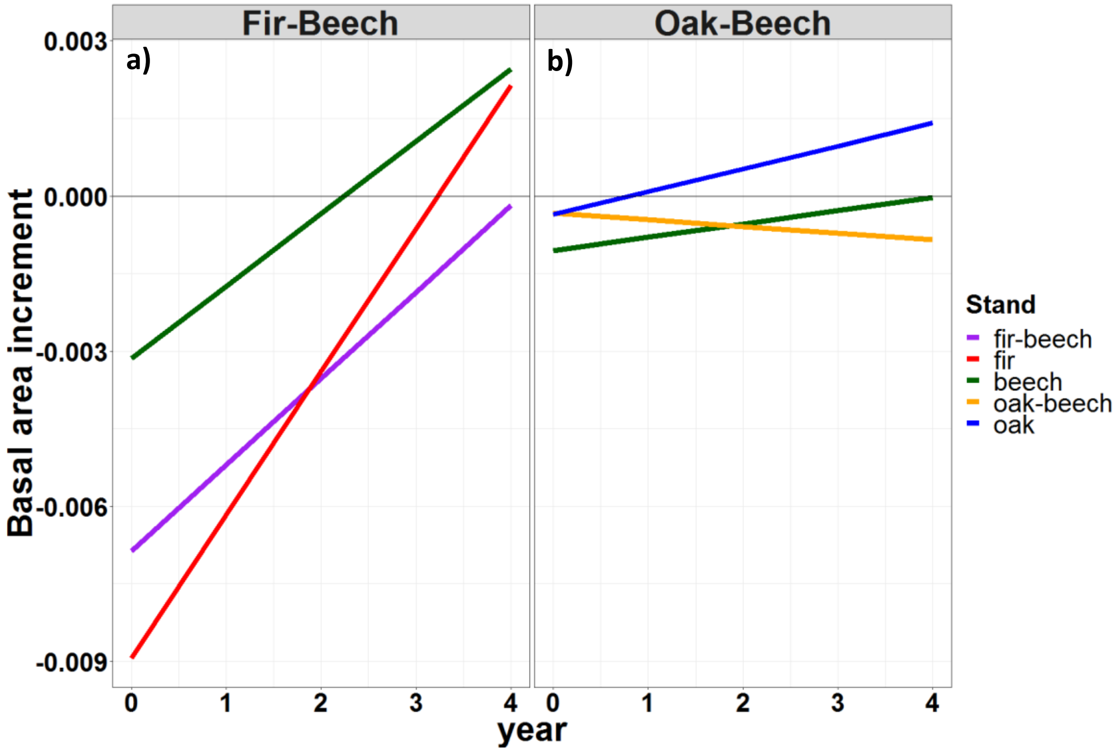

Figure 3: Graphic representation of resistance and recovery. The intercept of each line with y=0 represents the mean response of stand BAI during a year with a significant drought stress, i.e. stand resistance, and the slope of each line represents recovery of stand productivity during four years after the stress. We considered both part of gradient separately (see Table 1): Northern part of the gradient with beech and fir stands (a) and Southern part of the gradient with beech and oak stands (b). Different stands are represented by different colours as shown in the caption on the right.

3.2 Net diversity effect on resistance and recovery

Using the transposition of *NBE* approach to stand resistance during a stressful event ($Rt_{div.eff}$) and stand recovery after a stressful event ($Rc_{div.eff}$), we did not find any strong effect of diversity, either for resistance and recovery (Fig. 4). However, there was a weak negative $Rt_{div.eff}$ for stand in Bauges and Ventoux, only significant for stands in the Ventoux site. Mixed stands did not seem to recover faster or slower than monospecific stands, except in the Bauges site, as $Rc_{div.eff}$ was significantly negative. In the Vercors site, $Rc_{div.eff}$ seemed to be positive, but it was not significant. There was no significant $Rt_{div.eff}$ and recovery in mixed beech-oak stands (i.e. Southern part of the gradient).

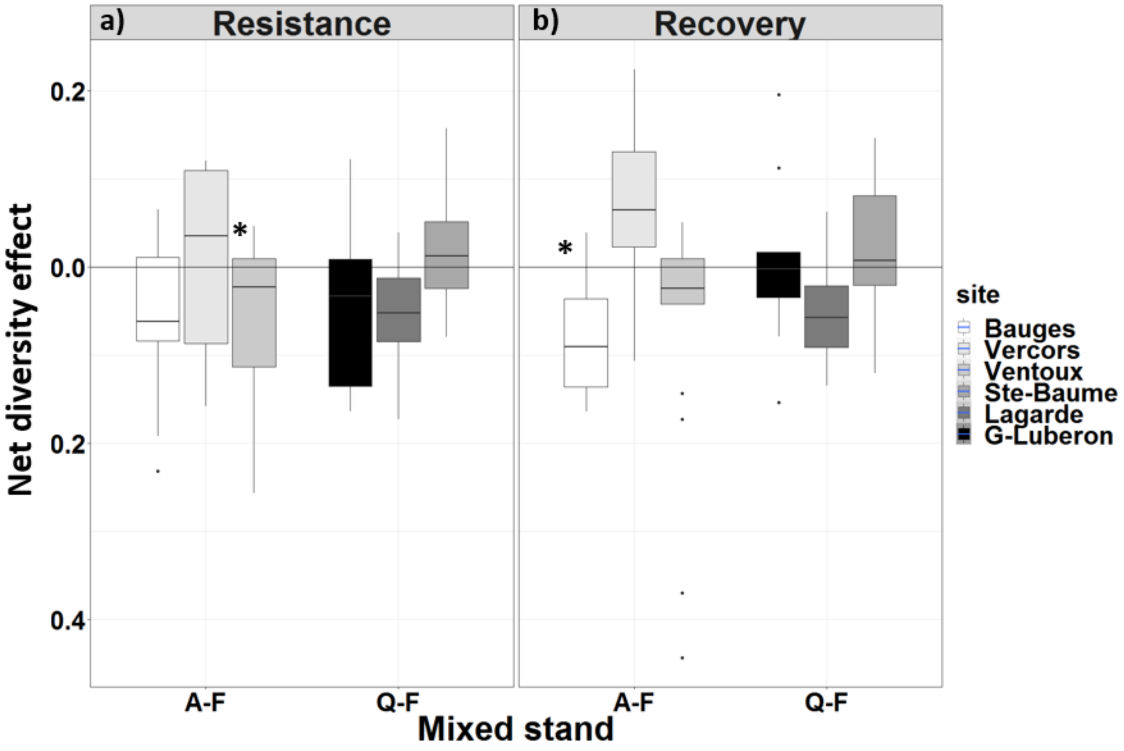

Figure 4: Boxplot of $Rt_{div.eff}$ and $Rc_{div.eff}$, i.e. net diversity effect on stand resistance (a) and on stand recovery (b) respectively, for each site. Averages were computed with all observations for each site. For remembering only driest years were considered for $Rt_{div.eff}$ and $Rc_{div.eff}$ computing, i.e. 2 years by site. Significant differences with 0 are indicated with (*).

4 DISCUSSION

4.1 Resistance and recovery to extreme drought events

We used two complementary approaches in the present study: the *BAI* model allowed quantifying differences between the responses of monospecific and mixed stands, while the

$Rt_{div.eff}$ and $Rc_{div.eff}$ computing dealt with species interactions effect on stand resistance and recovery. The latter approach allowed testing more precisely whether non-additive effects related to species interactions might explain the diversity effect on resistance/recovery, by comparing predicted and observed responses in mixed stands while removing a large part of external variability - such as environmental conditions (climate, soil, topography). The approach relying on the *BAI* model was more focused on the physiological differences between species, by quantifying separately the effect of drought on stand *BAI* during the current year and during the four years following the drought, which contrasts with other studies usually only considering immediate responses (Lloret et al., 2011; Pretzsch et al., 2013).

The analysis of stand *BAI* showed contrasted results. Regardless the metrics used, and the type of mixed stands considered, mixed stands showed an intermediate response compared to monospecific stands. The difference may be significant (beech-fir stands) or not (beech-oak stands). We did not find any strong patterns for $Rt_{div.eff}$ and $Rc_{div.eff}$, regardless the part of gradient considered, which can be explained by the strong dependencies of interspecific interactions to species composition and environmental conditions.

Furthermore, we aimed at testing how environmental conditions may affect the mixed stand effect along the latitudinal gradient (Fig. D and Table D). However, we lacked statistical power to test this effect with the modelling approach represented in equation (4), and the results were not significant for $Rt_{div.eff}$ and $Rc_{div.eff}$.

4.2 How mixed stands can buffer drought impact on stand growth?

According to previous studies, stand resistance and recovery could vary with stand composition (Arthur and Dech, 2016; Pretzsch et al., 2013, as in beech-fir stands in our study), or not (DeClerck et al., 2006, as in beech-oak stands). The discrepancies among studies can be explained by a species-specific effect, related to the various physiological characteristics between species. Delzon (2015) and Klein et al. (2014) recently summarized main hydraulic strategies of trees to respond to an extreme drought. A first strategy is the avoidance of physiological stress, that refers to the mechanisms that allow a tree to avoid drought effects, by relying on water storage (Meinzer et al., 2009) and stomatal regulation (Collatz et al., 1991) or to a deep rooting system (Bréda et al., 2006). Second, the tolerance strategy to physiological stress consists of coping with drought stress, which is possible by investing in xylem resistance to cavitation or in mechanisms allowing to lower the wilting point (Urli et al., 2013). Using their hydraulic characters, it is possible to rank species along an “isohydric-anisohydric” gradient (Martínez-Vilalta and Garcia-Forner, 2017; Tardieu and Simonneau, 1998) that relies on temporal dynamics of gas exchange and drought responses, and thus on various stomatal sensitivity (Martínez-Vilalta and Garcia-Forner 2017). For a same stress intensity, species with more anisohydric hydraulic characters (e.g. oak and beech) should better resist to drought (i.e. stomata remain open longer during drought stress) than species with more isohydric hydraulic characters (e.g. fir) that avoid damage by quickly closing their stomata. Extreme drought events may cause damage on some important organs of trees (roots, leaves or branches) because of cavitation (Delzon and Cochard, 2014; Maherali et al., 2006) for anisohydric species. Previous work focusing on beech, spruce and oak stand resistance (Pretzsch et al., 2013) highlighted the importance of the plurality in hydraulic characters to understand differences in buffering composition effect between mixed stands. Moreover, Cailleret et al. (2017) showed a general difference in drought vulnerability between hardwood and coniferous species (though without considering an “isohydric-anisohydric” gradient). They relied these differences on (i) water use and stomatal conductance (Lin et al., 2015), (ii) wood parenchyma that may increase storage capacity of nonstructural carbohydrates and symplastic water (Morris et al., 2016; Plavcová et al., 2016), (iii) hydraulic safety margins (Choat et al., 2012a), and possibly, (iv) potential capacity to refill embolized xylem conduits (Choat et al., 2015, 2012b; and see Mayr et al., 2014 for passive hydraulic recovery in conifers).

Our study allowed to study mixed stands of two species with very different hydraulic strategies (fir - coniferous and isohydric - and beech - hardwood and anisohydric), and mixed stands of two species with similar hydraulic strategies (oak and beech, hardwood and anisohydric). Our results confirmed that mixed stands composed of two species with similar hydraulic features should show more similar responses to an extreme drought event than the monospecific stands of each species, ie. beech-oak mixed stands. Since we aimed at explaining variation in stand resistance through differences in hydraulic characters between species, we further expected that the effect diversity on resistance may vary with species proportion in mixed stands. When we analyzed mixed stand response to drought events by taking into account the relative abundance (i.e. relative basal area) of beech as an explanatory variable (Eq. 4), we found that beech proportion did not significantly affect stand response to drought events in oak-beech stands, (Fig. E), confirming that species responses to drought should be similar in this case. This result even suggests that mixing species with similar responses to drought may actually increase the negative effect of drought on stand growth.

Contrariwise, mixed stands composed by two species with contrasted hydraulic features are expected to respond differently, as it was the case for fir-beech mixed stands. In this case, one may expect a strong buffering effect on stand growth. First, we found that monospecific beech stands were more resistant than monospecific fir stands, consistently with literature (Anderegg et al., 2015; Niinemets and Valladares, 2006) and with the differences between the hydraulic characters of these two species. Second, mixed beech-fir stands showed an intermediate value between both monospecific stands, but not significantly different from monospecific fir stands. In fact, fir contributed much more than beech to mixed stands *BAI* (73±0.33 % of *BAI* for fir), which may explain why the buffering effect of the mixture seemed limited in comparison with monospecific fir stands in our results. Moreover, when mixed stand response to drought events was analyzed by including beech basal area proportion as an explanatory variable (Eq 4) (see equation E.1), we found that increasing beech proportion induced an increasing stand resistance (Fig. E). In other words, stand resistance decreased with a decreasing proportion of fir. Thus, fir appeared to drive the response of mixed stands in this part of the gradient. Regarding recovery, monospecific fir stands recovered faster than monospecific beech stands probably because damage after extreme drought is weaker for isohydric species like fir, for instance if trees develop reverse embolism strategies (Cochard, 2006; Cochard and Delzon, 2013; Taneda and Sperry, 2008), as it can happen in isohydric species. Mixed stands recovery was also intermediate between monospecific beech and fir stands, but the differences were not significant. To sum up, mixed stands appeared to show intermediate responses in terms of resistance and recovery when compared to monospecific stands. The explanations presented above remained, however, to be further confirmed with more ecophysiological-based approaches on our field gradient (Hochberg et al., 2018).

4.3 Possible consequences for forest management in the Alps

Forests currently provides a multitude of ecosystem services - like wood production, protection in mountain areas or biodiversity conservation - all strongly dependent on species composition. Limiting the impacts of extreme events is thus crucial in forest ecosystems to promote adaptation. In mountain forests, the conservation of stand structure (basal area, density, tree dominant high), without discontinuity, seems more important than species composition (Lebourgeois et al., 2014; Trouvé et al., 2017), to limit erosion, block fall and avalanche, even species are not economically equivalent. Our study showed that mixed beech-fir stands may buffer the effect of extreme drought on stand *BAI*, i.e. showed a stronger resistance, than monospecific fir stands, while recovery was similar between monospecific fir stands and mixed beech-fir stands. Contrariwise, there was no significant buffering effect of mixture on beech-oak stands. Our results yet suggest that mixed stands could be a solution to buffer extreme drought effect in some cases. Therefore, these findings, together with other positive effects of diversity on ecosystem services (Gamfeldt et al., 2013; van der Plas et al., 2018), may argue for the benefits of mixed forest management, instead of monospecific stands. Thus, is especially true for beech-fir stands that can be more resistant to future severe drought events, in comparison with monospecific fir stands, although beech is currently less interesting than fir from an economic point of view. The question is less problematic for the oak-beech mixture, as we found no buffering effect in mixed stands and as these two species share relatively weak economic interest in this region (Southern Alps).

Climate change is likely to induce an economic loss for European forests (including mountain forests) (Hanewinkel et al., 2013). To quantify this loss, it may be important to compare the economic gain or loss of species productivity between mixed and monospecific stands on longer time scale and according to various management scenarios. To do so, we think that forest models considering diversity, climate and management may be key tools, such as gap models (Cordonnier et al., 2018). For instance, this would allow testing whether the increase in fir productivity in mixed stands relatively to monospecific ones across the next decades, due to higher resistance, may counterbalance the mean loss in fir productivity due to decreasing fir proportion. Our results suggest that there may be trade-off in the possible management of these mixed stands: increasing beech proportion may lead to a higher stand resistance but also to a loss in fir productivity, while decreasing beech proportion should induce a lower resistance - possibly leading to higher mortality rate at the stand level - but also the maintenance of fir productivity (Table F). In addition, the other key ecosystem services must also be considered to draw a complete scheme about the interest of mixing for forest management.

5 CONCLUSION

According to our results, managing forest mixed stands may increase the resistance and recovery of forests in future climatic conditions although this may be strongly dependent on species characteristics. More works on other types of mixed stands and their response to drought are required to draw a more comprehensive picture and to better assess when mixture management allows to buffer climate change impacts. Meanwhile, testing silvicultural scenarios under climate change with forest gap-models seems to be an interesting and complementary alternative to improve our knowledge and help our decision-making to maintain key ecosystem services provided by forests (Cordonnier et al., 2018).

AUTHORS' CONTRIBUTIONS

XM conceived the original question and field setup of this study; MJ and XM designed the research, developed the methodology and collected the data; MJ processed and analyzed the data; MJ, FL and XM led the writing of the manuscript. All authors contributed critically to the draft and gave final approval for publication.

DATA ACCESSIBILITY

Data will be deposited in the Dryad Digital Repository

ACKNOWLEDGMENTS

This study strongly benefitted from the help of E. Defossez, for his assistance in collecting the data. We also thank S. Coq and several students for additional help in collecting the data. We are grateful to G. Kunstler for his help in analyzing the data. We greatly thank the French *Office National des Forêts* for allowing access to the sites, and especially J. Ladier, P. Dreyfus and C. Riond for their help in selecting the sites. MJ benefitted from an ADEME grant. This study was mostly funded by the project DISTIMACC (ECOFOR-2014-23, French Ministry of Ecology and Sustainable Development, French Ministry of Agriculture and Forest) and DIPTICC (ANR 16-CE32-0003-01) and benefitted from the ANR project BioProFor (contract no. 11-PDOC-030-01).

REFERENCES

Allison, S.D., Martiny, J.B., 2008. Resistance, resilience, and redundancy in microbial communities. Proc. Natl. Acad. Sci. 105, 11512–11519.

Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Shevliakova, E., Williams, A.P., Wolf, A., Ziaco, E., Pacala, S., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349, 528. https://doi.org/10.1126/science.aab1833

Arthur, C.M., Dech, J.P., 2016. Species composition determines resistance to drought in dry forests of the Great Lakes – St. Lawrence forest region of central Ontario. J. Veg. Sci. 27, 914–925. https://doi.org/10.1111/jvs.12416

Aussenac, R., Bergeron, Y., Ghotsa Mekontchou, C., Gravel, D., Pilch, K., Drobyshev, I., 2017. Intraspecific variability in growth response to environmental fluctuations modulates the stabilizing effect of species diversity on forest growth. J. Ecol. 105, 1010–1020. https://doi.org/10.1111/1365-2745.12728

Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M.P., Frank, D.C., 2019. Twentieth century redistribution in climatic drivers of global tree growth. Sci. Adv. 5, eaat4313. https://doi.org/10.1126/sciadv.aat4313

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends Ecol. Evol. 9, 191–193.

Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C., Gégout, J.-C., 2011. Changes in plant community composition lag behind climate warming in lowland forests. Nature 479, 517–520. https://doi.org/10.1038/nature10548

Biondi, F., Qeadan, F., 2008. A Theory-Driven Approach to Tree-Ring Standardization: Defining the Biological Trend from Expected Basal Area Increment. Tree-Ring Res. 64, 81–96. https://doi.org/10.3959/2008-6.1

Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T., Ferrier, S., 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proc. Natl. Acad. Sci. 110, 9374–9379.

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

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G., Liancourt, P., TielböRger, K., Travis, J.M.J., Anthelme, F., Armas, C., Coll, L., Corcket, E., Delzon, S., Forey, E., Kikvidze, Z., Olofsson, J., Pugnaire, F., Quiroz, C.L., Saccone, P., Schiffers, K., Seifan, M., Touzard, B., Michalet, R., 2007. Facilitation in plant communities: the past, the present, and the future. J. Ecol. 0, 070908024102002–??? https://doi.org/10.1111/j.1365-2745.2007.01295.x

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

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., Cook, B.J., 2002. Positive interactions among alpine plants increase with stress. Nature 417, 844.

Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., Twery, M.J., 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecol. Appl. 16, 540–554.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., Weis, J.J., 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proc. Natl. Acad. Sci. 104, 18123–18128.

Choat, B., Brodersen, C.R., McElrone, A.J., 2015. Synchrotron X-ray microtomography of xylem embolism in Sequoia sempervirens saplings during cycles of drought and recovery. New Phytol. 205, 1095–1105. https://doi.org/10.1111/nph.13110

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012a. Global convergence in the vulnerability of forests to drought. Nature 491, 752–755. https://doi.org/10.1038/nature11688

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012b. Global convergence in the vulnerability of forests to drought. Nature 491, 752–755. https://doi.org/10.1038/nature11688

Choler, P., Michalet, R., Callaway, R.M., 2001. Facilitation and competition on gradients in alpine plant communities. Ecology 82, 3295–3308.

Cochard, H., 2006. Cavitation in trees. Comptes Rendus Phys. 7, 1018–1026. https://doi.org/10.1016/j.crhy.2006.10.012

Cochard, H., Delzon, S., 2013. Hydraulic failure and repair are not routine in trees. Ann. For. Sci. 70, 659–661. https://doi.org/10.1007/s13595-013-0317-5

Collatz, G.J., Ball, J.T., Grivet, C., Berry, J.A., 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. Agric. For. Meteorol. 54, 107–136.

Cordonnier, T., Kunstler, G., Courbaud, B., Morin, X., 2018. Managing tree species diversity and ecosystem functions through coexistence mechanisms. Ann. For. Sci. 75. https://doi.org/10.1007/s13595-018-0750-6

Courbaud, B., Kunstler, G., Morin, X., Cordonnier, T., 2011. What is the future of the ecosystem services of the Alpine forest against a backdrop of climate change? Rev. Géographie Alp. https://doi.org/10.4000/rga.1317

Cruiziat, P., Cochard, H., Améglio, T., 2002. Hydraulic architecture of trees: main concepts and results. Ann. For. Sci. 59, 723–752.

Dale, V.H., Joyce, L.A., Mcnulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Michael Wotton, B., 2001. Climate Change and Forest Disturbances. BioScience 51, 723. https://doi.org/10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2

DeClerck, F.A., Barbour, M.G., Sawyer, J.O., 2006. Species richness and stand stability in conifer forests of the Sierra Nevada. Ecology 87, 2787–2799.

Delzon, S., 2015. New insight into leaf drought tolerance. Funct. Ecol. 29, 1247–1249. https://doi.org/10.1111/1365-2435.12500

Delzon, S., Cochard, H., 2014. Recent advances in tree hydraulics highlight the ecological significance of the hydraulic safety margin. New Phytol. 203, 355–358.

Desplanque, C., Rolland, C., Michalet, R., 1998. Dendroécologie comparée du sapin blanc (Abies alba) et de l'épicéa commun (Picea abies) dans une vallée alpine de France. Can. J. For. Res. 28, 737–748.

Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., Healy, K., Jackson, A.L., Lurgi, M., McClean, D., O'Connor, N.E., O'Gorman, E.J., Yang, Q., 2016. Navigating the complexity of ecological stability. Ecol. Lett. 19, 1172–1185. https://doi.org/10.1111/ele.12648

Dunne, J.A., Saleska, S.R., Fischer, M.L., Harte, J., 2004. Integrating experimental and gradient methods in ecological climate change research. Ecology 85, 904–916.

Forrester, D.I., Bauhus, J., 2016. A Review of Processes Behind Diversity—Productivity Relationships in Forests. Curr. For. Rep. 2, 45–61. https://doi.org/10.1007/s40725-016-0031-2

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., Bengtsson, J., 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

Gasparrini, A., 2011. Distributed lag linear and non-linear models in R: the package dlnm. J. Stat. Softw. 43, 1.

Girvan, M.S., Campbell, C.D., Killham, K., Prosser, J.I., Glover, L.A., 2005. Bacterial diversity promotes community stability and functional resilience after perturbation. Environ. Microbiol. 7. https://doi.org/10.1111/j.1462-2920.2005.00695.x

Gitlin, A.R., Sthultz, C.M., Bowker, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., MuñOz, A., Bailey, J.K., Whitham, T.G., 2006. Mortality Gradients within and among Dominant Plant Populations as Barometers of Ecosystem Change During Extreme Drought. Conserv. Biol. 20, 1477–1486. https://doi.org/10.1111/j.1523-1739.2006.00424.x

Grossiord, C., Granier, A., Ratcliffe, S., Bouriaud, O., Bruelheide, 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

Guttman, N.B., 1999. Accepting the standardized precipitation index: A calculation algorithm1. JAWRA J. Am. Water Resour. Assoc. 35, 311–322.

Hanewinkel, M., Cullmann, D.A., Schelhaas, M.-J., Nabuurs, G.-J., Zimmermann, N.E., 2013. Climate change may cause severe loss in the economic value of European forest land. Nat. Clim. Change 3, 203–207. https://doi.org/10.1038/nclimate1687

Hochberg, U., Rockwell, F.E., Holbrook, N.M., Cochard, H., 2018. Iso/Anisohydry: A Plant–Environment Interaction Rather Than a Simple Hydraulic Trait. Trends Plant Sci. 23, 112–120. https://doi.org/10.1016/j.tplants.2017.11.002

Holmgren, M., Scheffer, M., 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. J. Ecol. 98, 1269–1275. https://doi.org/10.1111/j.1365-2745.2010.01709.x

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., others, 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75, 3–35.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T.M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J.N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S.T., Mori, A.S., Naeem, S., Niklaus, P.A., Polley, H.W., Reich, P.B., Roscher, C., Seabloom, E.W., Smith, M.D., Thakur, M.P., Tilman, D., Tracy, B.F., van der Putten, W.H., van Ruijven, J., Weigelt, A., Weisser, W.W., Wilsey, B., Eisenhauer, N., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526, 574–577. https://doi.org/10.1038/nature15374

Ives, A.R., Carpenter, S.R., 2007. Stability and diversity of ecosystems. science 317, 58–62.

Jones, H.E., McNamara, N., Mason, W.L., 2005. Functioning of mixed-species stands: evidence from a long-term forest experiment. For. Divers. Funct. 111–130.

Jucker, T., Bouriaud, O., Avacaritei, D., Coomes, D.A., 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecol. Lett. 17, 1560–1569. https://doi.org/10.1111/ele.12382

Kellomaki, S., Peltola, H., Nuutinen, T., Korhonen, K.T., Strandman, H., 2008. Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. Philos. Trans. R. Soc. B Biol. Sci. 363, 2339–2349. https://doi.org/10.1098/rstb.2007.2204

Kirkman, L.K., Mitchell, R.J., Helton, R.C., Drew, M.B., 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. Am. J. Bot. 88, 2119–2128.

Klein, T., Yakir, D., Buchmann, N., Grünzweig, J.M., 2014. Towards an advanced assessment of the hydrological vulnerability of forests to climate change-induced drought. New Phytol. 201, 712–716.

Lebourgeois, F., Bréda, N., Ulrich, E., Granier, A., 2005. Climate-tree-growth relationships of European beech (Fagus sylvatica L.) in the French Permanent Plot Network (RENECOFOR). Trees 19, 385–401. https://doi.org/10.1007/s00468-004-0397-9

Lebourgeois, F., Eberlé, P., Mérian, P., Seynave, I., 2014. Social status-mediated tree-ring responses to climate of Abies alba and Fagus sylvatica shift in importance with increasing stand basal area. For. Ecol. Manag. 328, 209–218. https://doi.org/10.1016/j.foreco.2014.05.038

LEBOURGEOIS, F., MERIAN, P., 2012. Principes et méthodes de la dendrochronologie. LERFOB AgroPariTech Cent. Nancy 85p.

Lebourgeois, F., Rathgeber, C.B.K., Ulrich, E., 2010. Sensitivity of French temperate coniferous forests to climate variability and extreme events (Abies alba, Picea abies and Pinus sylvestris). J. Veg. Sci. 21, 364–376. https://doi.org/10.1111/j.1654-1103.2009.01148.x

Lenoir, J., Gégout, J. c., Marquet, P.A., de Ruffray, P., Brisse, E.L., 2008. A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century. Science 320, 1763–1768. https://doi.org/10.1126/science.1157704

Lester, R.E., Close, P.G., Barton, J.L., Pope, A.J., Brown, S.C., 2014. Predicting the likely response of data-poor ecosystems to climate change using space-for-time substitution across domains. Glob. Change Biol. 20, 3471–3481. https://doi.org/10.1111/gcb.12634

Lin, Y.-S., Medlyn, B.E., Duursma, R.A., Prentice, I.C., Wang, H., Baig, S., Eamus, D., de Dios, V.R., Mitchell, P., Ellsworth, D.S., de Beeck, M.O., Wallin, G., Uddling, J., Tarvainen, L., Linderson, M.-L., Cernusak, L.A., Nippert, J.B., Ocheltree, T.W., Tissue, D.T., Martin-StPaul, N.K., Rogers, A., Warren, J.M., De Angelis, P., Hikosaka, K., Han, Q., Onoda, Y., Gimeno, T.E., Barton, C.V.M., Bennie, J., Bonal, D., Bosc, A., Löw, M., Macinins-Ng, C., Rey, A., Rowland, L., Setterfield, S.A., Tausz-Posch, S., Zaragoza-Castells, J., Broadmeadow, M.S.J., Drake, J.E., Freeman, M., Ghannoum, O., Hutley, L.B., Kelly, J.W., Kikuzawa, K., Kolari, P., Koyama, K., Limousin, J.-M., Meir, P., Lola da Costa, A.C., Mikkelsen, T.N., Salinas, N., Sun, W., Wingate, L., 2015. Optimal stomatal behaviour around the world. Nat. Clim. Change 5, 459.

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., 2001. Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. Science 294, 804–808. https://doi.org/10.1126/science.1064088

Loreau, M., 1998. Biodiversity and ecosystem functioning: a mechanistic model. Proc. Natl. Acad. Sci. 95, 5632–5636.

Loreau, M., Behera, N., 1999. Phenotypic diversity and stability of ecosystem processes. Theor. Popul. Biol. 56, 29–47.

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

Maherali, H., Moura, C.F., Caldeira, M.C., Willson, C.J., Jackson, R.B., 2006. Functional coordination between leaf gas exchange and vulnerability to xylem cavitation in temperate forest trees. Plant Cell Environ. 29, 571–583. https://doi.org/10.1111/j.1365-3040.2005.01433.x

Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W., Nobre, C.A., 2008. Climate Change, Deforestation, and the Fate of the Amazon. Science 319, 169–172. https://doi.org/10.1126/science.1146961

Maracchi, G., Sirotenko, O., Bindi, M., 2005. Impacts of present and future climate variability on agriculture and forestry in the temperate regions: Europe. Clim. Change 70, 117–135.

Martínez-Vilalta, J., Garcia-Forner, 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

Mauri, A., De Rigo, D., Caudullo, G., 2016. Abies alba in Europe: distribution, habitat, usage and threats. Eur. Atlas For. Tree Species Publ EU Luxemb. Pp E01493b Httpsw3id OrgmtvFISE-Commv01e01493b Cited Pages 7 9.

Maxime, C., Hendrik, D., 2010. Effects of climate on diameter growth of co-occurring Fagus sylvatica and Abies alba along an altitudinal gradient. Trees 25, 265–276. https://doi.org/10.1007/s00468-010-0503-0

Mayr, S., Schmid, P., Laur, J., Rosner, S., Charra-Vaskou, K., Dämon, B., Hacke, U.G., 2014. Uptake of Water via Branches Helps Timberline Conifers Refill Embolized Xylem in Late Winter. Plant Physiol. 164, 1731–1740. https://doi.org/10.1104/pp.114.236646

McCann, K.S., 2000. The diversity–stability debate. Nature 405, 228.

Meinzer, F.C., Johnson, D.M., Lachenbruch, B., McCulloh, K.A., Woodruff, D.R., 2009. Xylem hydraulic safety margins in woody plants: coordination of stomatal control of xylem tension with hydraulic capacitance. Funct. Ecol. 23, 922–930. https://doi.org/10.1111/j.1365-2435.2009.01577.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. Manag. 339, 22–33. https://doi.org/10.1016/j.foreco.2014.11.032

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. 17, 2145–2151.

Morin, X., Fahse, L., Jactel, H., Scherer-Lorenzen, M., García-Valdés, R., Bugmann, H., 2018. Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. Sci. Rep. 8. https://doi.org/10.1038/s41598-018-23763-y

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

Morris, H., Plavcová, L., Cvecko, P., Fichtler, E., Gillingham, M.A.F., Martínez-Cabrera, H.I., McGlinn, D.J., Wheeler, E., Zheng, J., Ziemińska, K., Jansen, S., 2016. A global analysis of parenchyma tissue fractions in secondary xylem of seed plants. New Phytol. 209, 1553–1565. https://doi.org/10.1111/nph.13737

Newton, A.C., Cantarello, E., 2015. Restoration of forest resilience: An achievable goal? New For. 46, 645–668. https://doi.org/10.1007/s11056-015-9489-1

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547.

Olesen, J.E., Carter, T.R., Díaz-Ambrona, C.H., Fronzek, S., Heidmann, T., Hickler, T., Holt, T., Minguez, M.I., Morales, P., Palutikof, J.P., Quemada, M., Ruiz-Ramos, M., Rubæk, G.H., Sau, F., Smith, B., Sykes, M.T., 2007. Uncertainties in projected impacts of climate change on European agriculture and terrestrial ecosystems based on scenarios from regional climate models. Clim. Change 81, 123–143. https://doi.org/10.1007/s10584-006-9216-1

Pachauri, R.K., Mayer, L., Intergovernmental Panel on Climate Change (Eds.), 2015. Climate change 2014: synthesis report. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

Pasta, S., de Rigo, D., Caudullo, G., n.d. Quercus pubescens in Europe: distribution, habitat, usage and threats. Eur. Atlas For. Tree Species San-Miguel-Ayanz J Rigo Caudullo G Houst. Durrant T Mauri Eds 156–157.

Penuelas, J., Gordon, C., Llorens, L., Nielsen, T., Tietema, A., Beier, C., Bruna, P., Emmett, B., Estiarte, M., Gorissen, A., 2004. Nonintrusive Field Experiments Show Different Plant Responses to

Warming and Drought Among Sites, Seasons, and Species in a North?South European Gradient. Ecosystems 7. https://doi.org/10.1007/s10021-004-0179-7

Pfisterer, A.B., Schmid, B., 2002. Diversity-dependent production can decrease the stability of ecosystem functioning. Nature 416, 84.

Piedallu, C., Gégout, J.-C., Lebourgeois, F., Seynave, I., 2016. Soil aeration, water deficit, nitrogen availability, acidity and temperature all contribute to shaping tree species distribution in temperate forests. J. Veg. Sci. 27, 387–399. https://doi.org/10.1111/jvs.12370

Plavcová, L., Hoch, G., Morris, H., Ghiasi, S., Jansen, S., 2016. The amount of parenchyma and living fibers affects storage of nonstructural carbohydrates in young stems and roots of temperate trees. Am. J. Bot. 103, 603–612. https://doi.org/10.3732/ajb.1500489

Potop, V., Boroneanţ, 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

Pretzsch, H., 2005. Diversity and productivity in forests: evidence from long-term experimental plots. Ecol. Stud. 176, 41–64.

Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.-P., Kohnle, U., Nagel, J., Spellmann, H., Zasada, M., Zingg, A., 2013a. Productivity of mixed versus pure stands of oak (Quercus petraea (Matt.) Liebl. and Quercus robur L.) and European beech (Fagus sylvatica L.) along an ecological gradient. Eur. J. For. Res. 132, 263–280. https://doi.org/10.1007/s10342-012-0673-y

Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.-P., Kohnle, U., Nagel, J., Spellmann, H., Zasada, M., Zingg, A., 2013b. Productivity of mixed versus pure stands of oak (Quercus petraea (Matt.) Liebl. and Quercus robur L.) and European beech (Fagus sylvatica L.) along an ecological gradient. Eur. J. For. Res. 132, 263–280. https://doi.org/10.1007/s10342-012-0673-y

Pretzsch, H., Del Río, M., Schütze, G., Ammer, C., Annighöfer, P., Avdagic, A., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., 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. Manag. 373, 149–166.

Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress in mixed *versus* pure forests: evidence of stress release by inter-specific facilitation: Drought stress release by inter-specific facilitation. Plant Biol. 15, 483–495. https://doi.org/10.1111/j.1438-8677.2012.00670.x

Pugnaire, F.I., Luque, M.T., 2001. Changes in plant interactions along a gradient of environmental stress. Oikos 93, 42–49.

Schwalm, C.R., Anderegg, W.R.L., Michalak, A.M., Fisher, J.B., Biondi, F., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Wolf, A., Huntzinger, D.N., Schaefer, K., Cook, R., Wei, Y., Fang, Y., Hayes, D., Huang, M., Jain, A., Tian, H., 2017. Global patterns of drought recovery. Nature 548, 202–205. https://doi.org/10.1038/nature23021

Seynave, I., Bailly, A., Balandier, P., Bontemps, J.-D., Cailly, P., Cordonnier, T., Deleuze, C., Dhôte, J.-F., Ginisty, C., Lebourgeois, F., Merzeau, D., Paillassa, E., Perret, S., Richter, C., Meredieu, C., 2018. GIS Coop: networks of silvicultural trials for supporting forest management under changing environment. Ann. For. Sci. 75. https://doi.org/10.1007/s13595-018-0692-z

Seynave, I., Gégout, J.-C., Hervé, J.-C., Dhôte, J.-F., 2008. Is the spatial distribution of European beech (Fagus sylvatica L.) limited by its potential height growth? J. Biogeogr. 35, 1851–1862. https://doi.org/10.1111/j.1365-2699.2008.01930.x

Taneda, H., Sperry, J.S., 2008. A case-study of water transport in co-occurring ring-versus diffuse-porous trees: contrasts in water-status, conducting capacity, cavitation and vessel refilling. Tree Physiol. 28, 1641–1651.

Tardieu, F., Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. J. Exp. Bot. 419–432.

Thompson, I., Mackey, B., McNulty, S., Mosseler, A., Secretariat of the convention on the biological diversity, 2014. Forest resilience, biodiversity, and climate change: a synthesis of the biodiversity, resilience, stabiblity relationship in forest ecosystems.

Thornthwaite, C.W., 1948. An Approach toward a Rational Classification of Climate. Geogr. Rev. 38, 55. https://doi.org/10.2307/210739

Tilman, D., 1999. The Ecological Consequences of Changes in Biodiversity: A Search for General Principles101. Ecology 80, 1455–1474. https://doi.org/10.1890/0012-9658(1999)080[1455:TECOCI]2.0.CO;2

Tilman, D., Downing, J.A., 1994. Biodiversity and stability in grasslands. Nature 367, 363.

Tinner, W., Colombaroli, D., Heiri, O., Henne, P.D., Steinacher, M., Untenecker, J., Vescovi, E., Allen, J.R., Carraro, G., Conedera, M., others, 2013. The past ecology of Abies alba provides new perspectives on future responses of silver fir forests to global warming. Ecol. Monogr. 83, 419–439.

Toïgo, M., Vallet, P., Perot, T., Bontemps, J.-D., Piedallu, C., Courbaud, B., 2015. Overyielding in mixed forests decreases with site productivity. J. Ecol. 103, 502–512. https://doi.org/10.1111/1365-2745.12353

Trouvé, R., Bontemps, J.-D., Collet, C., Seynave, I., Lebourgeois, F., 2017. Radial growth resilience of sessile oak after drought is affected by site water status, stand density, and social status. Trees 31, 517–529. https://doi.org/10.1007/s00468-016-1479-1

UNEP (Ed.), 2010. Mainstreaming the economics of nature: a synthesis of the approach, conclusions and recommendations of teeb, The economics of ecosystems & biodiversity. UNEP, Geneva.

Urli, M., Porte, A.J., Cochard, H., Guengant, Y., Burlett, R., Delzon, S., 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. Tree Physiol. 33, 672–683. https://doi.org/10.1093/treephys/tpt030

van der Plas, F., Ratcliffe, S., Ruiz-Benito, P., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M.A., Ampoorter, E., Baeten, L., Barbaro, L., Bastias, C.C., Bauhus, J., Benavides, R., Benneter, A., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Cornelissen, J.H.C., Dahlgren, J., Checko, E., Coppi, A., Dawud, S.M., Deconchat, M., De Smedt, P., De Wandeler, H., Domisch, T., Finér, L., Fotelli, M., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Jucker, T., Kambach, S., Kaendler, G., Kattge, J., Koricheva, J., Kunstler, G., Lehtonen, A., Liebergesell, M., Manning, P., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock, C., Ohse, B., Paquette, A., Peñuelas, J., Pollastrini, M., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Seidl, R., Selvi, F., Stenlid, J., Valladares, F., van Keer, J., Vesterdal, L., Fischer, M., Gamfeldt, L., Allan, E., 2018. Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality. Ecol. Lett. 21, 31–42. https://doi.org/10.1111/ele.12868

Vanoni, M., Bugmann, H., Nötzli, M., Bigler, C., 2016. Drought and frost contribute to abrupt growth decreases before tree mortality in nine temperate tree species. For. Ecol. Manag. 382, 51–63. https://doi.org/10.1016/j.foreco.2016.10.001

Van Ruijven, J., Berendse, F., 2010. Diversity enhances community recovery, but not resistance, after drought. J. Ecol. 98, 81–86. https://doi.org/10.1111/j.1365-2745.2009.01603.x

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

Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Begueria, S., Trigo, R., Lopez-Moreno, J.I., Azorin-Molina, C., Pasho, E., Lorenzo-Lacruz, J., Revuelto, J., Moran-Tejeda, E., Sanchez-Lorenzo, A., 2013. Response of vegetation to drought time-scales across global land biomes. Proc. Natl. Acad. Sci. 110, 52–57. https://doi.org/10.1073/pnas.1207068110

Vogel, A., Scherer-Lorenzen, M., Weigelt, A., 2012. Grassland Resistance and Resilience after Drought Depends on Management Intensity and Species Richness. PLoS ONE 7, e36992. https://doi.org/10.1371/journal.pone.0036992

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. Change Biol. 20, 3767–3779. https://doi.org/10.1111/gcb.12637