

## Research article

# Tree diversity and identity modulate the growth response of thermophilous deciduous forests to climate warming

Giovanni Iacopetti<sup>1</sup>✉, Federico Selvi<sup>1</sup>, Filippo Bussotti<sup>1</sup>, Martina Pollastrini<sup>1</sup>, Tommaso Jucker<sup>2</sup> and Olivier Bouriaud<sup>3,4</sup>

<sup>1</sup>Dept of Agriculture, Food, Environment and Forestry (DAGRI), Univ. of Florence, Florence, Italy

<sup>2</sup>School of Biological Sciences, Univ. of Bristol, Bristol, UK

<sup>3</sup>Laboratoire de l'Inventaire Forestier, Inst. National de l'Information Géographique et Forestière, Nancy, France

<sup>4</sup>Univ. Stefan cel Mare of Suceava, Suceava, Romania

Correspondence: Giovanni Iacopetti ([giovanni.iacopetti@gmail.com](mailto:giovanni.iacopetti@gmail.com))

Oikos

2022: e08875

doi: [10.1111/oik.08875](https://doi.org/10.1111/oik.08875)

Subject Editor:

Oscar J. Valverde-Barrantes

Editor-in-Chief: Dries Bonte

Accepted 30 October 2022

Tree diversity and species identity are known to play an important role in modulating forest productivity and its capacity to buffer the effects of climatic events. The FunDivEurope exploratory platform allowed us to analyse this modulating effect in a medium-term time span, after an abrupt rise to a new stable level of the average summer temperature of ca 2°C, in Mediterranean forests in central Italy.

This paper aims to answer the following questions: 1) did increasing temperature and drought events affect the growth of thermophilous deciduous forests? 2) Was this effect buffered in mixed stands compared to monocultures? 3) Did co-occurring tree species with different ecological characteristics, from more mesophilous to more xerophilous, have different responses?

In 2012 and 2017, wood cores were collected from 659 trees in 36 plots representative of thermophilous deciduous forests. The selected tree species were *Castanea sativa*, *Ostrya carpinifolia*, *Quercus cerris*, *Quercus ilex* and *Quercus petraea*. In the sampling plots, they were present in pure stands and mixtures from two to four species. After measuring annual rings on cores, chronologies of basal area increment were built, and inventory data were used to estimate tree growth. Results showed a strong reduction of growth, lasting at least 18 years, after the temperature rise. Tree diversity significantly reduced the growth drop after the sudden and stable rise in summer average temperature. Tree mixture effect on growth stability appeared to be dependent on the tree species present in the mixture.

Temperature rise and associated drought events, even without changes in rainfall, are one of the main challenges that European forests will face in the current scenarios of climate change. Tree diversity can buffer the effects of climate change over periods of at least 15 years and should be considered in forest management plans.

Keywords: drought, FunDivEurope, species richness, stress, temperature, tree growth, tree rings



[www.oikosjournal.org](http://www.oikosjournal.org)

© 2022 Nordic Society Oikos. Published by John Wiley & Sons Ltd

## Introduction

The role of higher temperatures in tree growth is complex: while generally positive in temperate biomes (Way and Oren 2010) where the temperature is often a limiting factor, it can also have complex impacts on forest dynamics under Mediterranean climates, where rise in mean temperature is accompanied by other disturbances as the increased fire frequency and intensity (Mouillot et al. 2002, Moriondo et al. 2006, Pausas and Paula 2012). Moreover, higher temperatures are often associated with increasing drought conditions, with severe consequences for tree growth (Sperlich et al. 2019, DeSoto et al. 2020). Recurrent dry spells and heat waves can provoke widespread tree health decline and mortality in the forests of the Mediterranean basin (Lloret et al. 2004, Carnicer et al. 2011, Camarero et al. 2015a, b, Colangelo et al. 2017, Gentilesca et al. 2017), but species diversity has been repeatedly shown to improve resistance, resilience and recovery of forest communities to several biotic and abiotic stress factors (Jactel et al. 2017), and to enhance productivity and carbon storage (Zhang et al. 2012, Gamfeldt et al. 2013, Liang et al. 2016).

The relationship between tree diversity and the forest's response to drought is complex, with several mechanisms involved, such as niche complementarity, sampling effect and ecological insurance (summarized in Scherer-Lorenzen et al. (2005) and Scherer-Lorenzen (2014)). The role and effectiveness of diversity are not always positive, as some species can be subjected to asymmetric competition by others (Grossiord et al. 2014), but is expected to be higher in stressful conditions as stated by the stress gradient hypothesis (He et al. 2013) and by more forest-oriented frameworks (Forrester and Buhus 2016, Ammer 2018). Indeed, Jucker et al. (2014) and Ratcliffe et al. (2017) found a tendency for stronger biodiversity–ecosystem function relations in drier climates as well as in areas with longer growing seasons and more functionally diverse tree species.

Tree resistance, resilience and recovery are often evaluated in terms of productivity (Gazol et al. 2017). It is important to assess the ability of the system to keep growing at the same rate under a stress (resistance), to recover the previous growth rate after the stress is removed (resilience), to increase the growth rate from the disturbed level (recovery) (Lloret et al. 2011). Based on worldwide datasets, Liang et al. (2016), proposed a global and general positive correlation between tree diversity and forest growth, although local conditions or environmental stresses may cause this correlation to have a different sign. Diversity has been found to improve wood production in Mediterranean ecosystems (Vilà et al. 2007, 2013).

The temperature stressor considered in this study, with its expected effects on plants' water balance, should be considered in the context of drought stress. Even if growth under drought stress was influenced by species identity and site characteristics, determining whether mixed forests can mitigate the effect of drought episodes in the long run is of great interest. Tree resistance, resilience and recovery under drought

stress, and the mixture effect, are usually evaluated in mono-specific and bi-specific stands (Pretzsch et al. 2013, Merlin 2015, Steckel 2020), or artificial formations (Palandrani 2020). While these experiments bring essential information and help test hypotheses on the diversity–productivity relationship, there are little experimental data on mixtures with more species where species interactions and identity effects could come into play. Another important aspect is the temporary (single event) versus long-lasting stressors: usually, studies compare the stand performances during drought events against previous (or later) growth rates while there is almost no literature about forest dynamics under durable temperature increase. Our study is the first to our knowledge to investigate the buffering effect of higher tree diversity levels in natural stands, under a lasting increase in temperature.

The tree species involved in our study have major economical and silvicultural relevance in Italy and southern Europe and the ecology of mixed forests under climate change is of great interest in the perspective of sustainable management (Bravo-Oviedo et al. 2018), therefore some relationships and relative performances under stress are already present in literature. Concerning the tree species of our study (*Castanea sativa*, *Ostrya carpinifolia*, *Quercus cerris*, *Quercus petraea*, *Quercus pubescens*), *Q. petraea* in central European forests subjected to increasing temperatures showed to be more competitive than *Fagus sylvatica* (Zimmermann et al. 2015), because of their higher radial growth under drought stress. Competitive interactions (due to differences in water use efficiency, mostly via the *Q. petraea* ability to access water from deeper soil layers, and *Q. cerris* acclimations to stronger water deficit conditions) between *Q. cerris* and *Q. petraea* under drought stress have been observed by Grossiord et al. (2014) and a negative impact on *Q. petraea* has been found. Fonti et al. (2006) observed a competitive advantage (larger tree ring width) of *Q. cerris* growing with *C. sativa* even in cold areas. Tognetti et al. (2007) found, in a mixed oak stand, *Q. pubescens* at advantage on xeric ridges because, arguably thanks to its greater ability to access soil water and use it more conservatively compared with *Q. cerris*. Moreover, Iacopetti et al. (2019) found that crown conditions and vitality of *Q. ilex* were better in mixed stands than in monocultures, but it remains to be determined whether the tree species mixture can buffer its response to climate.

The FunDivEurope exploratory platform has proved to be a solid framework for analysing the separate effects of tree species diversity and identity on a broad range of forest functions and processes (Baeten et al. 2013). In particular, the Italian sites located in Tuscany represent a unique opportunity to study the response of thermophilous deciduous forests formed by both evergreen and deciduous tree species, such as *Q. ilex*, *Q. cerris*, *Q. petraea*, *C. sativa* and *O. carpinifolia*, in the same environmental conditions and with different mixture levels (Bussotti et al. 2012).

This paper aims to answer the following questions: 1) did increasing temperature and drought events affect the growth of thermophilous deciduous forests? 2) Was this effect buffered in mixed stands compared to monocultures? 3) Did

co-occurring tree species with different ecological characteristics, from more mesophilous to more xerophilous, have different responses?

## Material and methods

### Study area

The Italian sites of the FunDivEurope platform are located on the hills of central Tuscany (plots are comprised between 43°04' and 43°27' N, and between 10°55' and 11°26' E) at 350–450 m a.s.l., and belong to the thermophilous deciduous forest category (Barbati and Marchetti 2004). They are grouped in two main clusters, one more to the north in the river Cecina valley (Tatti forest) and one more to the south in the Farma-Merse valley (Belagiao forest). The mean annual precipitation at the plots is  $825 \pm 22$  mm and the mean annual temperature is  $14.15 \pm 0.10^\circ\text{C}$ , broadly calculated over the 1975–2016 period. The bedrock is predominantly siliceous (sandstones and various conglomerates) and the soil is Cambisol (FAO classification), with a mean soil depth of 68 cm. Almost all plots are on north-facing slopes with mean inclination  $< 50\%$ . Thirty-six plots ( $30 \times 30$  m) with five focal tree species (*Quercus ilex*, *Quercus cerris*, *Quercus petraea*, *Ostrya carpinifolia* and *Castanea sativa*) were established.

Forest structure is typical for Italian nearly mature stands, about 50–70 years old, originated from the abandonment of coppice practices after World War II, and are representative of

the category of 'thermophilous deciduous forests' as defined in the European Environment Agency classification (EEA). The height of the dominant plane is about 20 m, while the totality of the measured trees has an average height of 14.8 m and a standard error of 4.6 m; the tree diameters are more diverse, as expected by this forest type where natural dynamics show, with average DBH of 16 and 8.8 cm of standard error. The average basal area of the plot is  $25.4 \text{ m}^2 \text{ ha}^{-1}$ , with a 6.0 standard error. *Castanea sativa* trees are ca 60-year-old suckers originated from the stumps of old trees cultivated in former times for fruit production and then abandoned. The status and history of the stands were measured during the fieldwork by the authors and/or discussed with the site managers and local authorities.

At present, the forests considered in this study are public and managed as natural reserves.

The plots were selected to minimize the influence of any other variables than tree diversity, therefore all plots share, as much as possible, similar soil, climate, elevation, structure, canopy cover, age and management (Baeten et al. 2013). In order to be able to disentangle species identity and diversity almost all the species combinations were realized, monospecific plots with replications. The full list of species combinations and the number of plots for each species richness level is given in Table 1, translated from Bussotti et al. (2012). In this work, we will not include the analysis of the five-species plot that, while acting accordingly to our thesis, does not have any replications in this analysis limited in scope to the Italian sites.

Table 1. Tree species composition and replicas of the Italian FunDivEurope plots.

Type	Species	No. of plots
Monospecific	<i>Castanea sativa</i>	2
	<i>Ostrya carpinifolia</i>	2
	<i>Quercus cerris</i>	2
	<i>Quercus ilex</i>	2
	<i>Quercus petraea</i>	2
Two species mixture	<i>C. sativa</i> + <i>O. carpinifolia</i>	1
	<i>C. sativa</i> + <i>Q. cerris</i>	1
	<i>C. sativa</i> + <i>Q. ilex</i>	1
	<i>C. sativa</i> + <i>Q. petraea</i>	1
	<i>O. carpinifolia</i> + <i>Q. cerris</i>	1
	<i>O. carpinifolia</i> + <i>Q. ilex</i>	1
	<i>Q. cerris</i> + <i>Q. ilex</i>	1
	<i>Q. cerris</i> + <i>Q. petraea</i>	1
	<i>Q. ilex</i> + <i>Q. petraea</i>	1
	Three species mixture	<i>Q. cerris</i> + <i>Q. ilex</i> + <i>C. sativa</i>
<i>Q. cerris</i> + <i>Q. ilex</i> + <i>Q. petraea</i>		1
<i>Q. cerris</i> + <i>C. sativa</i> + <i>Q. petraea</i>		2
<i>Q. ilex</i> + <i>C. sativa</i> + <i>Q. petraea</i>		1
<i>Q. cerris</i> + <i>Q. ilex</i> + <i>O. carpinifolia</i>		1
<i>Q. cerris</i> + <i>Q. petraea</i> + <i>O. carpinifolia</i>		1
<i>Q. ilex</i> + <i>C. sativa</i> + <i>O. carpinifolia</i>		1
<i>Q. ilex</i> + <i>Q. petraea</i> + <i>O. carpinifolia</i>		1
Four species mixture	<i>Q. cerris</i> + <i>Q. ilex</i> + <i>C. sativa</i> + <i>Q. petraea</i>	2
	<i>Q. cerris</i> + <i>Q. ilex</i> + <i>C. sativa</i> + <i>O. carpinifolia</i>	2
	<i>Q. cerris</i> + <i>Q. ilex</i> + <i>Q. petraea</i> + <i>O. carpinifolia</i>	2
	<i>Q. ilex</i> + <i>Q. petraea</i> + <i>C. sativa</i> + <i>O. carpinifolia</i>	1
Five species mixture	<i>Q. cerris</i> + <i>Q. ilex</i> + <i>C. sativa</i> + <i>Q. petraea</i> + <i>O. carpinifolia</i>	1

## Climatic data

We derived temperature and precipitation data from the Agri4Cast dataset (Tilman et al. 1997, Cardinale et al. 2007, Zhang et al. 2012). The dataset is built on a  $25 \times 25$  km grid, therefore the 36 plots were linked to the closest point on the grid forming two groups (site\_group\_1 and site\_group\_2). The Supporting information shows how different plots were linked to different reference points of the climatic dataset. Site\_group\_1 (Belagaio Forest) is linked to  $43.2^{\circ}\text{N}$ ,  $11.1^{\circ}\text{E}$  (Grid No. 67113), while Site\_group\_2 (Tatti Forest) is linked to  $43.4^{\circ}\text{N}$ ,  $10.8^{\circ}\text{E}$  (grid no. 68112). The database provides the daily data from 1975 used in this study. All the subsequent analysis refers to this climatic summarized data, where temperature used is the average, over the vegetative period (April to August), of the daily average temperature given in the dataset, and precipitations are the cumulative mm of rain during the same period. We also tested the choice of different vegetative periods, and the results are not presented here because substantially identical to the main findings here illustrated, while full-year averages lose most of the detected signal.

## Collection of wood cores

In July 2017, a wood core sampling was carried out to update the sampling carried out in 2012 within the FunDivEurope project (Jucker et al. 2014). The sampling was stratified by species and tree size (i.e. stem diameter, stratified in 6 diameter classes with the same basal area), so that one tree per species and diameter class is sampled one time on each plot (Table 2), two times in monospecific plots. With a 5.15 mm diameter increment borer, a new core 7–8 cm long was taken within a small distance from the trace of the previous core, in order to minimize the distance without being affected by eventual ring deformations caused by the tree reaction to the previous coring. In case of death of the previously cored tree, a new core was taken from another tree of the same species and the same DBH inside the plot perimeter. In total, 659 cores were collected from the 36 plots.

## Wood cores analysis

### Climate series

Intervention detection is a statistical tool used to determine significant changes in the mean of a time series (Killick and Eckley 2014), while the choice of this model over a simple

Table 2. Number of trees and DBH summary for each taxon.

Species	No. of trees	Diameter breast height (DBH)				
		Average (cm)	SD (cm)	Median (cm)	Min (cm)	Max (cm)
<i>Castanea sativa</i>	129	21	8.3	19	8	62
<i>Ostrya carpinifolia</i>	110	17	5.8	16	10	36
<i>Quercus cerris</i>	142	26	10.4	25	10	55
<i>Quercus ilex</i>	150	26	12.7	23	10	75
<i>Quercus petraea</i>	128	26	11.3	24	10	67

linear regression offers just a slight increase of goodness of fit, the issue here is about how we think of our climatic systems: we expect annual fluctuations of temperatures to move around a normal value in such a short interval like the one here examined (climatological normals are calculated over periods of at least 30 years) (Climate Change Service, online) and intervention detection tools are able to detect statistically significant deviations of a part of a time series from the previous distribution around a given average, when part of a time series is not consistent with the previous average and the previous distribution around said average. However, while it is possible to consider a model of rising temperatures, with an unusually higher temperature from 1998 ending with the 2003 peak, as data will show, this interpretation seems less likely to reflect the response of the trees in the present context. While this situation is still under study, the general knowledge and some new insights about the link between global warming and the onset of this higher temperature in Europe can be found in Rousi et al. (2022).

The analysis showed that, while the precipitation regime was statistically stable despite strong year-to-year variations (Fig. 1a), in 1998 there was a significant  $2^{\circ}\text{C}$  increase in mean annual temperature, which remained constant until the last assessment in 2016 (Fig. 1b). To put the temperature rise in an eco-geographical context we looked for the Italian sites with pre-1998 conditions similar to our plots' post-1998 temperatures. Those sites were, on average, 180 km south and 260 m lower than the study site.

### Wood cores measurements

In order to maximize the compatibility with the FunDivEurope dataset, we followed the FunDivEurope protocol: the cores were air dried, mounted on wooden boards and sanded with progressively finer grits. The boards were then scanned with a high-resolution flatbed scanner at 2400 dpi and the resulting images were used to measure the annual growth increment. The individual cores were cross-dated with the previous core from the same tree or, in the case of cores taken from a new tree, with the core of the corresponding dead tree. The new (2012–2016) tree ring width series were rescaled to consistently extend the previous series that started from 20 to almost 200 years before, depending on tree age and core readability. For this purpose, a quadratic model was fitted on the common years of each core: in order to build a no-intercept model – no negative tree ring width should be possible – that would not be distorted by the quite common high-leverage outliers, those outliers could not be eliminated being the data on strong growth years, therefore outliers for the model, but essential data point for the tree rings rescaling. Those models were used to rescale the new measures, to account for any eventual discrepancy of magnitude and standard deviation between the new and the old core.

### Basal area increment

We then used the tree ring width series and distance to pith to calculate the basal area increment of each tree. Missing distance to pith data were imputed considering species,

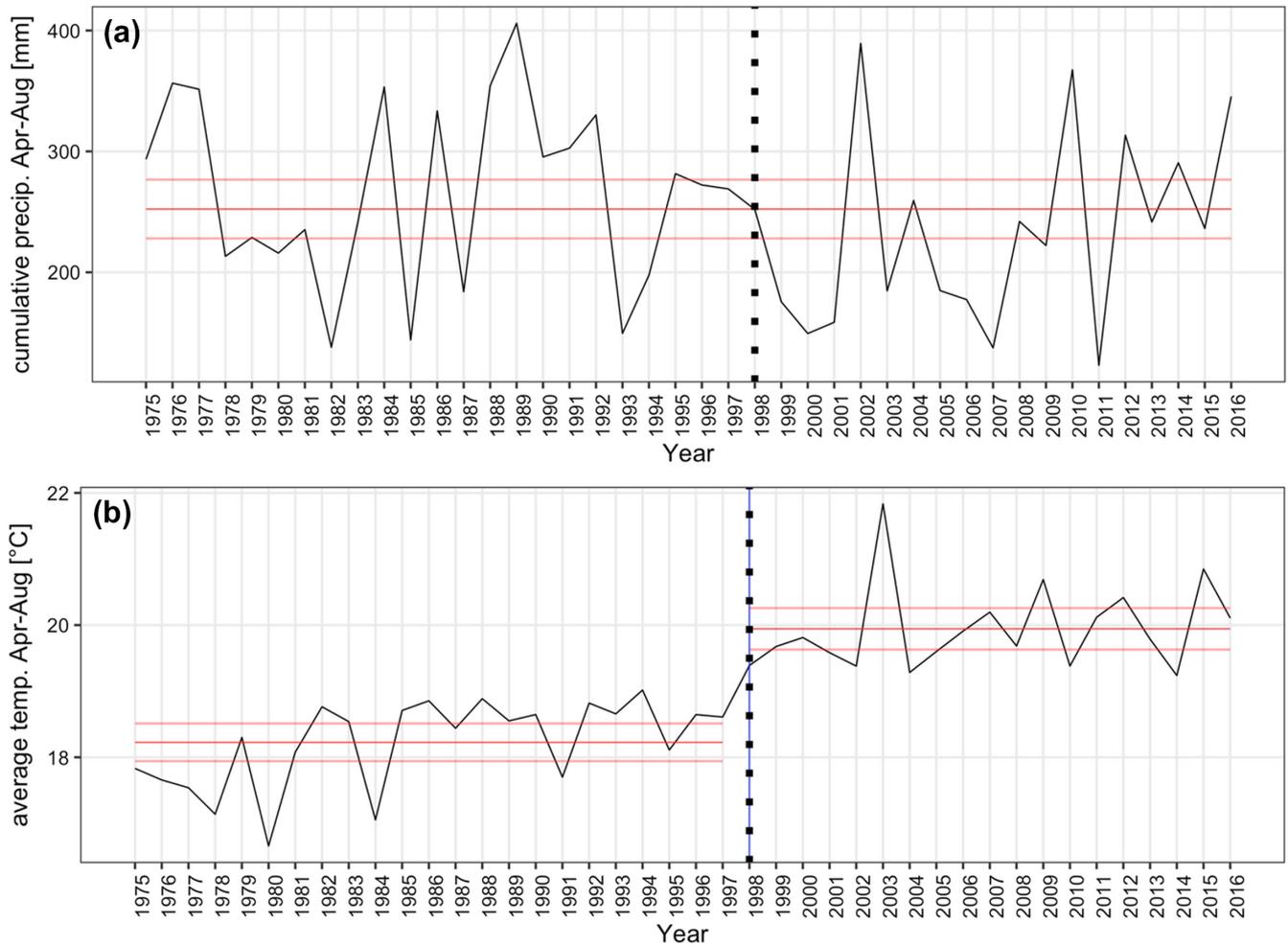


Figure 1. Intervention detection on the April–August period: (a) average daily precipitation, (b) average temperature. Vertical line: statistically identifiable structural break point of the time series. Horizontal lines: averages for the structurally homogenous periods with 95% confidence intervals. Vertical dotted lines: year 1998.

diameter at breast height and tree height using the ‘mice’ R package (Buuren and Groothuis-Oudshoorn 2011). In order to account for the bark thickness and the hygroscopic contraction of the cores, a reduction coefficient ( $c_r$ ) was calculated using the diameter at breast height (DBH) (mm), the distance to pith (DTP) (mm) and the sum of tree ring width (TRW) (mm) using the formula:

$$c_r = \frac{\text{DBH}}{2 \times (\text{DTP} + \sum \text{TRW})}$$

Then each tree ring width series and distance to pith was multiplied by its own  $c_r$  and converted to basal area increment (BAI) ( $\text{mm}^2$ ) by the ‘dplR’ R package (Bunn 2008).

#### Basal area increment (BAI) series de-trending, testing and sliding window correlation

The study aims to understand the influence of the forest diversity level on tree growth under a specific stressor, therefore the study unit we considered is the single tree, with its

basal area increment as a proxy of the overall tree growth. The single tree data have been pooled together in chronologies for testing the shifting correlation with climate variables.

BAI individual series were detrended via the detrend function of the ‘dplR’ package, using a spline with a 50% cut-off over 50 years, stiff enough to exclude the biological trend of the trees without losing the short period climatic effect (usually of decadal wavelength) (Cook 1985), in order to remove age- and size-related trends while preserving higher frequency variations. BAI series were truncated at 1965, in order to build the chronologies on enough complete series (at least 15 series per chronology). Then we reduced the individual BAI series into chronologies, to be linked and correlated with the climatic time series, all the analyses reported in this work will refer to the detrended BAI series. Structural change in chronologies was tested with the Chow test (Chow 1960), a statistical test that allows to confront two regression lines with different slope or intercept, and also to identify the presence of two different processes underlying time series’ generation (Stock and Watson 2015).

In order to detect changes in correlation between BAI chronologies and climatic time series, a sliding window correlation was calculated using an 11-years moving window and the Pearson correlation coefficient. Sliding (or rolling, or moving) window correlation is a technique that computes a succession of correlations between subsequent subsets of two time series.

### Growth quantification before and during the hot period

In order to answer the three main questions of this paper we needed to estimate a growth rate before the hot period (that started in 1998) from the previous growth data. To this end we used two models: 1) the most conservative approach, which considers the BAI of the last five years before 1998 as data from a stable forest system and averaged the BAI of that five years as the 'potential growth rate'; 2) a more data-driven approach, that considered the best performing category of plots (4 species stands) as reference, where the trend of the last twenty years before 1998 remained steady. In order to assess the statistical significance of the growth trend change before and after 1998 we used the Chow test (Chow 1960) with 1998 as the structural break point. Statistical significances are presented for p-values < 0.05 (\*); < 0.01 (\*\*) and < 0.001 (\*\*\*)

## Results

### Climate-growth correlation

The moving window correlation between global BAI and mean temperature varies largely over time (Fig. 2), becoming strongly negative after the 1998 temperature increase, and needing several years to recover from a strong negative correlation toward a neutral value. The positive correlation never reaches statistical significance. Figure 2 shows how monospecific sites take three years longer to recover, while for the 4 species mixture the adverse effects are delayed by two years: the correlation is significantly negative for seven years (over an eight years span) in monospecific sites, and three years for the most diverse formations.

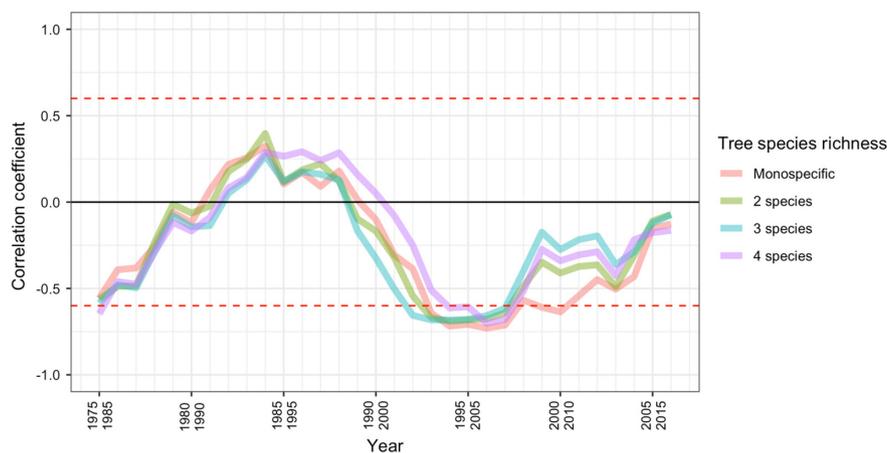


Figure 2. Mean temperature – global BAI correlation on 11 years moving window, red dashed lines for significance critical values ( $\pm 0.602$ ). On the x-axis the starting and ending years of the window.

Figure 2 also represents a good example of the non-linearity of the diversity effect: while the monospecific sites have a markedly longer negative effect and the 4 species sites have the last onset and shortest significantly negative period, the effects are not clearly ranked by diversity for the greater part of the analysed period, with a fast and complex evolution making the interpretation delicate.

### Basal area index chronologies

The BAI chronology of the whole dataset (all trees of all species, in all plots) showed a highly significant ( $p < 0.001$ ) drop in basal area increment following the temperature rise of 1998 (Fig. 3). Evaluating the growth loss, the most conservative approach (Fig. 3a) estimated a loss of 16% of the growth over 10 years. When considering the optimum as a continuation of the linear trend (like Fig. 3b) the estimated loss is 22.5%. It is worth noting that these estimations are relative to the detrended BAI series, not on the original scale values.

The species-level chronologies (Fig. 4) highlighted significantly different responses in the five focal tree species (significance is indicated as \* for  $p \leq 0.05$ ; \*\* for  $p \leq 0.01$ ; \*\*\* for  $p \leq 0.001$ ). While *Q. ilex*\*\*\* and *O. carpifolia*\*, after a slight decline recovered a positive growing trend, *Q. cerris*\* was subject to a marked decrease of its positive trend before 1998 and *Q. petraea*\*\*\* and *C. sativa*\*\*\* initiated a sudden growth decline that showed some recovery only in 2016 (statistical significance refers to the Chow test for a trend change in 1998, cf. Material and methods section, pre-post linear model slope values and errors in Table 3).

While Fig. 4 shows the trend line flexing a few years before 1998 that is mostly an artifact of statistical smoothing: the dashed lines show a peak growth or at least a growth in line with the previous years still in 1997.

The chronologies obtained by grouping together the trees in the species richness levels (Fig. 5) brought to the light an additional difference: the 1-, 2- and 3-species plots showed a similar drop in growth, while the 4-species mixtures

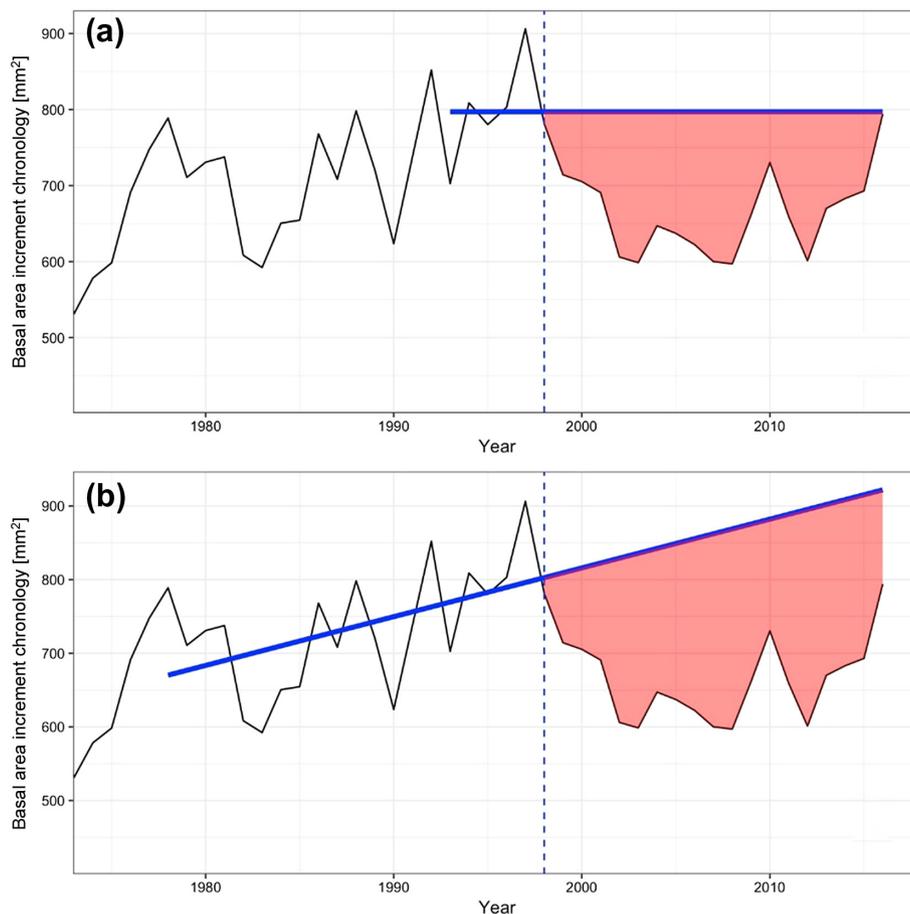


Figure 3. BAI loss (filled area) of the pooled data after the 1998 ‘crisis’ (vertical dashed line). (a) Thick line for the average value of the period 1993–1998. (b) Thick line for the linear regression of the 1978–1998 values.

underwent only a slight slowdown with a fast recovery in less than 10 years. The growth rate change for all the mixtures is highly significant ( $p$ -value < 0.001) except for the 4-species mixture that has no detectable change (no-change hypothesis,  $p$ -value = 0.708).

Single-taxa chronologies were calculated and graphed for each species richness level in order to gain insights into possible identity effects (Fig. 6). *O. carpinifolia* showed a unique growth pattern in the 2-species plots, with the difference in growth lost after 1998. *Q. cerris* showed stable growth,

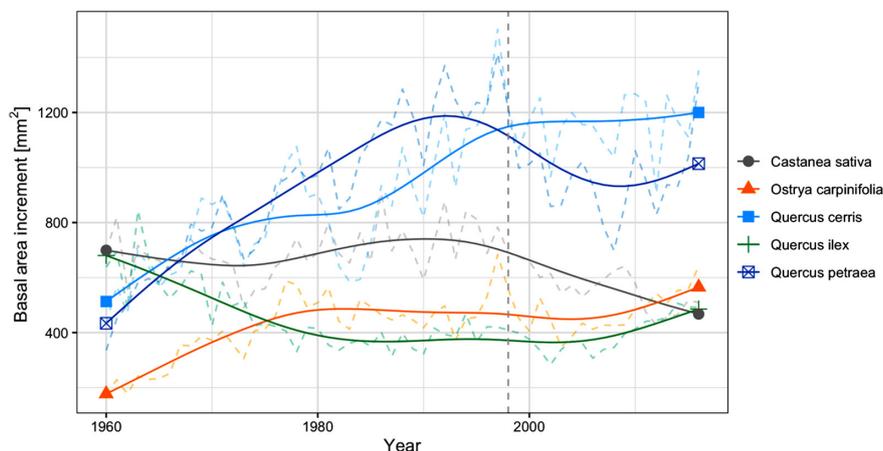


Figure 4. BAI chronologies for the five focal species, pooled together from different species mixtures and balanced by the study design. Dashed lines for the values, continuous lines for the statistical smoothing, vertical dashed line on 1998.

Table 3. BAI chronologies for the five focal species, slope coefficient and standard errors of separated linear regressions (BAI ~ year) pre and post 1998.

Species	Coeff. pre 1998	SE pre 1998	Coeff. post 1998	SE post 1998
<i>Castanea sativa</i>	3.2	3.2	-10.6	2.1
<i>Ostrya carpinifolia</i>	-0.2	2.7	6.8	2.7
<i>Quercus cerris</i>	25.6	6.9	3.4	4.7
<i>Quercus ilex</i>	2.5	1.5	8.0	2.0
<i>Quercus petraea</i>	20.7	3.7	-0.4	6.1

except for the 4-species plot that continued its positive trend after the temperature rise. *Q. ilex* showed consistently higher growth in the 3-species mixtures and a stronger gain from the temperature rise in the 4-species mixtures. *Q. petraea* was characterized by a consistent trend through the years, with growth increasing along the species richness gradient. *C. sativa* trend will not be discussed here, because the cooccurrence of damages from *Dryocosmus kuriphilus* makes impossible to disentangle the effect of abiotic and biotic stressors.

## Discussion

The most relevant climatic event during the considered period (1975–2016) was an abrupt increase in the mean temperatures (+2°C) starting from the year 1998. We started this work with three questions about the impact of this temperature shift, hereby we discuss our findings in the context of these questions and the currently available knowledge.

### Did increasing temperature and drought events affect the growth of thermophilous deciduous forests?

Our findings showed that the 1998 increase in mean temperatures, with no detectable change in rainfall, was associated with the start of an 18-year-period of slow growth of the total basal area in the forest study plots in Tuscany (central Italy) (-16% over 18 years). This temperature

rise seems even more significant and meaningful after the Paris Agreement (2018) set as target a 1.5°C rise in average annual temperature: we can be looking here at a model for the consequences of a similar temperature increase on forest ecosystems, moreover at the importance of tree diversity in preserving the functionality of Mediterranean forests in the eventuality of this future scenario.

The response of tree growth to temperature has been the object of several studies (Way and Oren 2010) but the resulting evidence was variable depending on tree species growth strategy and functional group (Way and Oren 2010). Elevated temperatures enhanced growth (measured as shoot height, stem diameter and biomass) because trees in temperate regions are generally temperature-limited. Growth, however, increased in deciduous species more than in evergreen trees, and in Nordic cold regions more than in the warm Mediterranean ones (Way and Oren 2010). In the Mediterranean areas, moreover, increasing temperatures are associated with drought stress, which is ultimately the cause of growth reduction (Sperlich et al. 2019). Silva et al. (2010) observed that tree growth is declining also in boreal forests despite the favourable conditions (increasing temperature and CO<sub>2</sub> concentrations), because of a heat-induced drought and other disturbances related to climate change.

### Was this effect buffered in mixed stands compared to monocultures?

Our results indicate that the growth drop after the recent summer temperature increase was attenuated by species mixture: the sites with the highest species richness (four species) showed no growth loss, even if not enough to compensate for the loss of the less species-rich sites. The mean tree growth over all plots and species, however, showed some recovery at the end of the 18-years-period (Fig. 3), although this trend should be confirmed by analysing future radial growth. The recovery observed here seems to occur especially in the 4-species mixtures (Fig. 5) and in the oak species *Q. cerris* (Fig. 4), which was apparently strongly favoured by tree diversity in

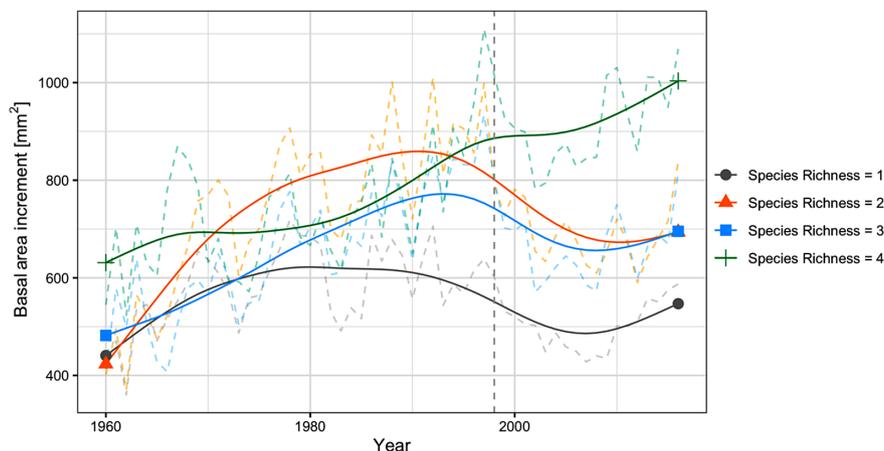


Figure 5. BAI chronologies for the four different species richness levels, coloured dashed lines for the values, continuous lines for the statistical smoothing, grey dashed line on 1998.

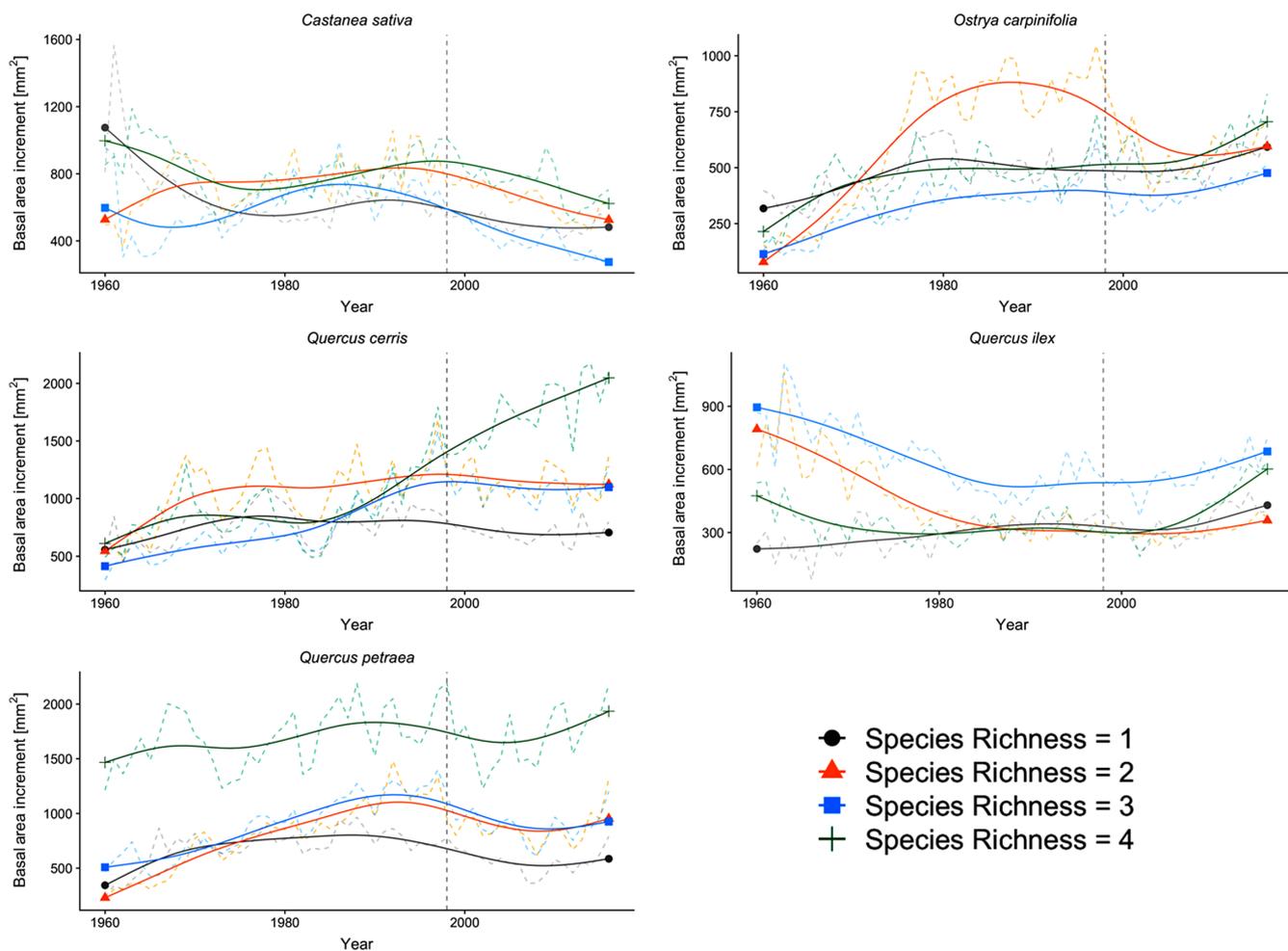


Figure 6. BAI chronologies for each focal species, separately for the four species richness level in which they occur.

such conditions. This behaviour suggests that tree diversity can act as a stabilizing factor, although under climate change the stabilization of tree growth is reached mostly by changing the competitive relationships between species (McCann 2000, Jucker et al. 2014, Hutchison et al. 2018). The 4-species plots kept stable growth trajectories for all the species, where *Q. ilex* and *O. carpinifolia* slight increase in productivity counterbalanced the slow decline of *C. sativa*.

Tree species richness proved itself able to buffer the stressors' effect on the growth rate, providing some degree of resistance and resilience to the forest ecosystem. Its role seems to have a non-linear relationship with the number of species (Vilà et al. 2013). The diversity effect on resilience cannot be quantified yet because the less diverse forests have not returned to the initial growth rate. For this purpose, long-term observations and measurements in permanent study areas can be especially useful (Bussotti and Pollastrini 2017). The increased resistance of tree growth to stressors in mixed stand seems to underline ecological mechanisms, like temporal and spatial niche differentiation, that will require further study and are in line with the most recent studies that identify the key role of species identity in the mixture (Baeten et al. 2019).

### Did co-occurring tree species with different ecological characteristics, from more mesophilous to more xerophilous, have different responses?

It is widely acknowledged that different species have divergent responses to drought, in relation to their adaptation to this ecological factor. Niinemets and Valladares (2006) classified the resistance to drought of several forest species, according to their scale, the focal species in this study are ordered, from less drought adapted to most, as *Q. petraea*, *O. carpinifolia*, *C. sativa*, *Q. cerris*, *Q. ilex*.

The strongest negative reaction was observed in the drought-sensitive species (*Q. petraea*, *C. sativa*), whereas no growth drop in the Mediterranean evergreen *Q. ilex* was observed. In *C. sativa* the decline of the growth may be a consequence of the co-occurrence of climatic and non-climatic factors including insect and pathogen attacks in the study area (Pollastrini et al. 2016), the last of which, since 2008, was represented by the Asian wasp *Dryocosmus kuriphilous* (Guyot et al. 2015, Fernandez-Conradi et al. 2018).

*Quercus petraea* is a widely distributed species in central Europe, with several scattered populations in the

Mediterranean region (Bruschi et al. 2003), where it behaves as a mesophilous tree (Coppi et al. 2019). The radial growth of this species proved to be affected by climate, with special reference to the spring air temperature and precipitation (Lebourgeois et al. 2004). Analysing the growth of this species in sub-Mediterranean stands in Slovenia, Saražin et al. (2018) found the tree ring width was negatively affected by high temperatures in June. According to Bartsch et al. (2016), the early spring meteorological conditions (especially temperature and precipitations) strongly affect the accumulation of biomass (GPP, gross primary production) in Mediterranean forest ecosystems.

According to some authors (Jump et al. 2006, Pretzsch et al. 2013, Hackett-Pain et al. 2016) tree species with a large distribution in Europe, such as *F. sylvatica*, are more sensitive to heat and drought stress at the southern limits of their range and at the more unfavourable sites, in full accord with *Q. petraea*'s decline found in our study. These findings suggest problems for the conservation of residual populations in refuge sites, where even widely distributed species still conserve an important pool of genetic diversity, with a potentially substantial subsequent loss of biodiversity (Di Paola et al. 2012).

### About other factors

The variation in medium-term climatic conditions on the sites appears to be temperature-driven; precipitation data show no significant deviation from the norm for the specific area and period studied in this work. This doesn't exclude the effect of precipitation dynamics preceding the focus period of this work, for which we have no data available, and could have impacted the forest in a dynamic stage too close to the stop of forest utilization and therefore with too many unknowns for the scopes of this work. The strongly negative correlation of temperature and tree growth in the five years after the temperature rise, and the negative effect lasting roughly other ten years after the initial shock, highlight a growth reduction in warmer years.

The data of this study showed no identifiable correlation or link between tree growth and precipitations which, according to our tests, remained stationary during the studied period (Fig. 1). On this basis we did not try to disentangle the water availability from the temperature effect: being outside of the study design we did not have the necessary data to tackle such interesting research question that should not go overlooked in future studies. Hence, we consider that water effects are indirect consequences of the temperature increase. The physiology of this kind of stressor, and its complex dependency on precipitation regimes and seasonal patterns, make it impossible to impute the forest growth dynamics to simple thermal stress. Therefore this work will assume an unspecified temperature-induced drought as the main stressor and cause of increment reduction and inverted temperature-increment relation. Ongoing studies will try to address this question.

Among the effects of a temperature increase, several mechanisms should be considered that can influence tree

growth: direct physiological effects like thermal limitation and heat damages, and indirect effects that involve water dynamics, like increased respiration loss, water potential reduction, growth reduction, leaf senescence and stomatal control. Direct physiological effects of temperature, while impossible to eliminate from the contributing causes, should be investigated separately, being linked to short-term heat waves more than mean growing season temperature increase.

Increased respiration loss and water potential reduction have complex dynamics and impact on trees' respiration and carbon uptake (Rodríguez-Calcerrada et al. 2011) together with decrease in nutrient levels under water-related stress (Díaz and Roldán 2000), and a cascade effect increasing the tree vulnerability (Choat et al. 2018). A lower shoot elongation observed in Mediterranean trees (Lobo-do-Vale et al. 2019) would both refer to limited growth mechanisms and a reduced LAI, which also has negative effects on photosynthesis. Leaf senescence is a typical response to drought (Lobo-do-Vale et al. 2019). Trees respond to drought by shedding leaves, which enables them to mitigate water losses (Lloret et al. 2004) as part of an avoidance mechanism. Defoliations and canopy senescence were indeed observed on the site and can be taken as indices of a damaged photosynthetic apparatus along with preventive senescence, but asynchronicity of crown damages could also play a role in interspecific competition (Camarero et al. 2015a). Stomatal control and regulation (for water-saving strategies, Manzanera et al. 2017) play also a part in the cavitation avoidance strategy of trees. We can conjecture that there was no particular cavitation or any long-term damage to the trees, allowing them to recuperate quickly, hence the very dynamic BAI series and response to temperatures. But interaction with other factors like masting, which is linked to drought stress and has effects on both growth and defoliation (Camarero et al. 2015a) should be investigated, together with short-term stressors linked with tree phenology, that could be hidden by the use of annual averages.

Medium term-effects on long cycles like litter cycling, nutrient reabsorption and general shifts in soil properties can also be affected by a long drought, but medium-term effects should have prevented the relatively quick recovery of forest growth we detected.

Other important factors are expected to play a role in the climate-productivity dynamics. Factors such as soil, elevation, canopy structure and density, stand age and so on should be considered. The present study design was specifically made to minimise the role of these factors in this study, allowing to isolate the effect of diversity on stands representative of one of the country's main forest types. The results of this study could be safely extended to other Mediterranean forests only after other studies will be able to account for these other factors, while the temperature drive seems to be limited to Italy, therefore reducing the opportunity to extend results on Italian high elevation stands to similar lowland continental forests.

## Conclusions

The summer temperature shift observed in central Tuscany was equivalent to a general latitudinal shift of 180 km and an elevational shift of 260 m. We can try to answer the three questions we posed.

- 1) How has the growth of deciduous tree species been affected by this temperature shift? The overall growth of the examined stands has swiftly declined but slowly returned to the original rates after about 20 years, displaying some acclimation processes.
- 2) Was this effect buffered in mixed stands compared to monocultures? Yes, the negative effect on monocultures was stronger and more lasting than in mixed stands, even if the diversity effect appears to be non-linear, dynamic and largely impacted by the species identity.
- 3) Did co-occurring tree species with different ecological characteristics, from more mesophilous to more xerophilous, have different responses? Yes: the five different species we examined reacted differently, foreshadowing a shift in species composition in the long term. The more drought-sensitive tree species are expected to decline more and faster than the drought-resistant ones. The contribution of less adapted species such as the *C. sativa* and *Q. petraea* to the stand growth was significantly reduced, hence the competitive ability and persistence of these species in the long term are at risk.

Long-term observational studies in networks of plots established 'ad hoc' should aim at understanding the impact of climate change on stand dynamics. Our results suggest that the more resilient tree species (*Q. cerris* in our case) is favoured with respect to the other species, but further studies could shed some light on the complex mechanics involved. Temperature rise, however, could trigger species-specific changes in growth patterns in co-occurring species close to their optimum climate (Castagneri et al. 2014), and an increase of 1.5°C poses a serious threat even to drought-adapted forests.

**Acknowledgements** – A special acknowledgement to Michael Scherer-Lorenzen and Kris Verheyen for their role in the coordination of FunDivEurope and SoilForEurope projects. We are grateful to the Regional Government of Tuscany, the National Forest Service (Corpo Forestale dello Stato) – UTB Follonica, the Comunità Montana Colline Metallifere, the Municipality of Volterra for having supported the logistic aspects of the research.

**Funding** – The research leading to these results received funding from the European Union Seventh Framework Programme (FP7/2007-2013) under grant 265171. The work was supported by a grant of the Research Doctorate in Agricultural and Environmental Science, XXXII course, Univ. of Firenze. OB acknowledges fundings from a grant of the Romania National Council for Higher Education Funding, CNFIS, project number CNFIS-FDI-2019-0600 and CNFIS-FDI-2022-0259. TJ was supported by a UK NERC Independent Research Fellowship (grant no. NE/S01537X/1).

## Author contributions

**Giovanni Iacopetti**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (lead); Software (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Olivier Bouriaud**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (lead); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Federico Selvi**: Formal analysis (equal); Supervision (equal); Writing – review and editing (equal). **Filippo Bussotti**: Conceptualization (equal); Writing – review and editing (equal). **Martina Pollastrini**: Conceptualization (equal); Writing – review and editing (equal). **Tommaso Jucker**: Data curation (equal); Writing – review and editing (equal).

## Data availability statement

Data are available from the Official FunDivEUROPE site: <http://www.fundiveurope.eu> (FunDivEUROPE).

## Supporting information

The Supporting information associated with this article is available with the online version.

## References

- Ammer, C. 2018. Diversity and forest productivity in a changing climate. – *New Phytol.* 221: 50–66.
- Baeten, L., Bruelheide, H., Plas, F., Kambach, S., Ratcliffe, S., Jucker, T., Allan, E., Ampoorter, E., Barbaro, L., Bastias, C. C., Bauhus, J., Benavides, R., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Čečko, E., Coomes, D. A., Dahlgren, J., Dawud, S. M., De Wandeler, H., Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A., Grossiord, C., Guyot, V., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F., Koricheva, J., Lehtonen, A., Müller, S., Muys, B., Nguyen, D., Pollastrini, M., Radoglou, K., Raulund-Rasmussen, K., Ruiz-Benito, P., Selvi, F., Stenlid, J., Valladares, F., Vesterdal, L., Verheyen, K., Wirth, C., Zavala, M. A. and Scherer-Lorenzen, M. 2019. Identifying the tree species compositions that maximize ecosystem functioning in European forests. – *J. Appl. Ecol.* 56: 733–744.
- Baeten, L., Verheyen, K., Wirth, C., Bruelheide, H., Bussotti, F., Finér, L., Jaroszewicz, B., Selvi, F., Valladares, F., Allan, E., Ampoorter, E., Auge, H., Avăcăriei, D., Barbaro, L., Bărnoaiea, I., Bastias, C. C., Bauhus, J., Beinhoff, C., Benavides, R., Beneter, A., Berger, S., Berthold, F., Boberg, J., Bonal, D., Brüggemann, W., Carnol, M., Castagneyrol, B., Charbonnier, Y., Čečko, E., Coomes, D., Coppi, A., Dalmaris, E., Dănilă, G., Dawud, S. M., de Vries, W., De Wandeler, H., Deconchat, M., Domisch, T., Duduman, G., Fischer, M., Fotelli, M., Gessler, A., Gimeno, T. E., Granier, A., Grossiord, C., Guyot, V., Hantsch, L., Hättenschwiler, S., Hector, A., Hermy, M., Holland, V., Jactel, H., Joly, F.-X., Jucker, T., Kolb, S., Koricheva, J., Lexer, M. J., Liebergesell, M., Milligan, H., Müller, S., Muys,

- B., Nguyen, D., Nichiforel, L., Pollastrini, M., Proulx, R., Rabasa, S., Radoglou, K., Ratcliffe, S., Raulund-Rasmussen, K., Seiferling, I., Stenlid, J., Vesterdal, L., von Wilpert, K., Zavala, M. A., Zielinski, D. and Scherer-Lorenzen, M. 2013. A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. – *Perspect. Plant Ecol. Evol. Syst.* 15: 281–291.
- Barbati, A. and Marchetti, M. 2004. Forest Types for Biodiversity Assessment (FTBAs) in Europe: the revised classification scheme. – In: Marchetti, M. (ed.), *Monitoring and indicators of forest biodiversity in Europe – from ideas to operationality*. EFI Proceedings No. 51, pp. 105–126.
- Bartsch, S., Guenet, B., Boissard, C., Lathièrre, J., Peterschmitt, J.-Y., Stegehuis, A., Reiter, I.-M., Gauquelin, T., Baldy, V. and Fernandez, C. 2016. Impact of annual and seasonal precipitation and air temperature on gross primary production in Mediterranean ecosystems in Europe. – *Biogeosci. Discuss.* doi: [10.5194/bg-2016-491](https://doi.org/10.5194/bg-2016-491)
- Bravo-Oviedo, A., Pretzsch, H. and del Río, M. (eds) 2018. *Dynamics, silviculture and management of mixed forests*. – Springer.
- Bruschi, P., Grossoni, P. and Bussotti, F. 2003. Within- and among-tree variation in leaf morphology of *Quercus petraea* (Matt.) Liebl. natural populations. – *Trees* 17: 164–172.
- Bunn, A. G. 2008. A dendrochronology program library in R (dplR). – *Dendrochronologia* 26: 115–124.
- Bussotti, F. and Pollastrini, M. 2017. Observing climate change impacts on European forests: what works and what does not in ongoing long-term monitoring networks. – *Front. Plant Sci.* 8: 629.
- Bussotti, F., Coppi, A., Pollastrini, M., Feducci, M., Baeten, L., Scherer-Lorenzen, M., Verheyen, K. and Selvi, F. 2012. The Italian forest sites of FunDivEUROPE: a new FP7 project on the functional significance of forest biodiversity in Europe. – *For. Riv. Selvic. Ed. Ecol. For.* 9: 251–259.
- Buuren, S. van and Groothuis-Oudshoorn, K. 2011. mice: multi-variate imputation by chained equations in R. – *J. Stat. Softw.* 45: 1–67.
- Camarero, J., Franquesa, M. and Sangüesa-Barreda, G. 2015a. Timing of drought triggers distinct growth responses in Holm oak: implications to predict warming-induced forest defoliation and growth decline. – *Forests* 6: 1576–1597.
- Camarero, J. J., Gazol, A., Sangüesa-Barreda, G., Oliva, J. and Vicente-Serrano, S. M. 2015b. To die or not to die: early warnings of tree dieback in response to a severe drought. – *J. Ecol.* 103: 44–57.
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G. and Penuelas, J. 2011. Widespread crown condition decline, food web disruption and amplified tree mortality with increased climate change-type drought. – *Proc. Natl Acad. Sci. USA* 108: 1474–1478.
- Castagneri, D., Nola, P., Motta, R. and Carrer, M. 2014. Summer climate variability over the last 250 years differently affected tree species radial growth in a mesic *Fagus-Abies-Picea* old-growth forest. – *For. Ecol. Manage.* 320: 21–29.
- Choat, B., Brodribb, T. J., Brodersen, C. R., Duursma, R. A., López, R. and Medlyn, B. E. 2018. Triggers of tree mortality under drought. – *Nature* 558: 531–539.
- Chow, G. C. 1960. Tests of equality between sets of coefficients in two linear regressions. – *Econometrica* 28: 591.
- Colangelo, M., Camarero, J. J., Battipaglia, G., Borghetti, M., De Micco, V., Gentilesca, T. and Ripullone, F. 2017. A multi-proxy assessment of dieback causes in a Mediterranean oak species. – *Tree Physiol.* 37: 617–631.
- Cook, E. R. 1985. A time series analysis approach to tree ring standardization. – PhD thesis, Univ. of Arizona.
- Coppi, A., Lazzaro, L., Ampoorter, E., Baeten, L., Verheyen, K. and Selvi, F. 2019. Understorey phylogenetic diversity in thermophilous deciduous forests: overstorey species identity can matter more than species richness. – *For. Ecosyst.* 6: 37.
- DeSoto, L., Cailleret, M., Sterck, F., Jansen, S., Kramer, K., Robert, E. M. R., Aakala, T., Amoroso, M. M., Bigler, C., Camarero, J. J., Čufar, K., Gea-Izquierdo, G., Gillner, S., Haavik, L. J., Hereş, A.-M., Kane, J. M., Kharuk, V. I., Kitzberger, T., Klein, T., Levanič, T., Linares, J. C., Mäkinen, H., Oberhuber, W., Papadopoulos, A., Rohner, B., Sangüesa-Barreda, G., Stojanovic, D. B., Suárez, M. L., Villalba, R. and Martínez-Vilalta, J. 2020. Low growth resilience to drought is related to future mortality risk in trees. – *Nat. Commun.* 11: 545.
- Di Paola, A., Valentini, R. and Paparella, F. 2012. Climate change threatens coexistence within communities of Mediterranean forested wetlands. – *PLoS One* 7: e44727.
- Díaz, E. and Roldán, A. 2000. Effects of reforestation techniques on the nutrient content, photosynthetic rate and stomatal conductance of *Pinus halapensis* seedlings under semiarid conditions. – *Land Degrad. Dev.* 11: 475–486.
- Fernandez-Conradi, P., Borowiec, N., Capdevielle, X., Castagneyrol, B., Maltoni, A., Robin, C., Selvi, F., Van Halder, L., Vétillard, F. and Jactel, H. 2018. Plant neighbour identity and invasive pathogen infection affect associational resistance to an invasive gall wasp. – *Biol. Invas.* 20: 1459–1473.
- Fonti, P., Cherubini, P., Rigling, A., Weber, P. and Biging, G. 2006. Tree rings show competition dynamics in abandoned *Castanea sativa* coppices after land-use changes. – *J. Veg. Sci.* 17: 103–112.
- Forrester, D. I. and Bauhus, J. 2016. A review of processes behind diversity-productivity relationships in forests. – *Curr. Forestry Rep.* 2: 45–61.
- 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. and Bengtsson, J. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. – *Nat. Commun.* 4: 1340.
- Gazol, A., Camarero, J. J., Anderegg, W. R. L. and Vicente-Serrano, S. M. 2017. Impacts of droughts on the growth resilience of Northern Hemisphere forests: forest growth resilience to drought. – *Global Ecol. Biogeogr.* 26: 166–176.
- Gentilesca, T., Camarero, J., Colangelo, M., Nolè, A. and Ripullone, F. 2017. Drought-induced oak decline in the western Mediterranean region: an overview on current evidences, mechanisms and management options to improve forest resilience. – *IForest Biogeosci. For.* 10: 796–806.
- Grossiord, C., Gessler, A., Granier, A., Pollastrini, M., Bussotti, F. and Bonal, D. 2014. Interspecific competition influences the response of oak transpiration to increasing drought stress in a mixed Mediterranean forest. – *For. Ecol. Manage.* 318: 54–61.
- Guyot, V., Castagneyrol, B., Vialatte, A., Deconchat, M., Selvi, F., Bussotti, F. and Jactel, H. 2015. Tree diversity limits the impact of an invasive forest pest. – *PLoS One* 10: e0136469.
- Hacket-Pain, A. J., Cavin, L., Friend, A. D. and Jump, A. S. 2016. Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European beech indicates widespread vulnerability to changing climate. – *Eur. J. For. Res.* 135: 897–909.

- He, Q., Bertness, M. D. and Altieri, A. H. 2013. Global shifts towards positive species interactions with increasing environmental stress. – *Ecol. Lett.* 16: 695–706.
- Hutchison, C., Gravel, D., Guichard, F. and Potvin, C. 2018. Effect of diversity on growth, mortality and loss of resilience to extreme climate events in a tropical planted forest experiment. – *Sci. Rep.* 8: 15443.
- Iacopetti, G., Bussotti, F., Selvi, F., Maggino, F. and Pollastrini, M. 2019. Forest ecological heterogeneity determines contrasting relationships between crown defoliation and tree diversity. – *For. Ecol. Manage.* 448: 321–329.
- Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagneyrol, B., Gardiner, B., Gonzalez-Olabarria, J. R., Koricheva, J., Meurisse, N. and Brockerhoff, E. G. 2017. Tree diversity drives forest stand resistance to natural disturbances. – *Curr. For. Rep.* 3: 223–243.
- Jucker, T., Bouriaud, O., Avacaritei, D. and Coomes, D. A. 2014. Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. – *Ecol. Lett.* 17: 1560–1569.
- Jump, A. S., Hunt, J. M. and Peñuelas, J. 2006. Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. – *Global Change Biol.* 12: 2163–2174.
- Killick, R. and Eckley, I. A. 2014. changepoint: an R package for changepoint analysis. – *J. Stat. Softw.* 58: 1–19.
- Lebourgeois, F., Cousseau, G. and Ducos, Y. 2004. Climate-tree-growth relationships of *Quercus petraea* Mill. stand in the Forest of Bercé ('Futaie des Clos', Sarthe, France). – *Ann. For. Sci.* 61: 361–372.
- Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A. D., Bozzato, F., Pretzsch, H., de-Miguel, S., Paquette, A., Herault, B., Scherer-Lorenzen, M., Barrett, C. B., Glick, H. B., Hengeveld, G. M., Nabuurs, G.-J., Pfautsch, S., Viana, H., Vibrans, A. C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J. V., Chen, H. Y. H., Lei, X., Schelhaas, M.-J., Lu, H., Gianelle, D., Parfenova, E. I., Salas, C., Lee, E., Lee, B., Kim, H. S., Bruelheide, H., Coomes, D. A., Piotta, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonke, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E. B., Neldner, V. J., Ngugi, M. R., Baraloto, C., Frizzera, L., Baazy, R., Oleksyn, J., Zawia-Niedwiecki, T., Bouriaud, O., Bussotti, F., Finer, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A. M., Peri, P. L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E. H., Marshall, A. R., Rovero, F., Bitarho, R., Niklaus, P. A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N. L., Ferreira, L. V., Odeke, D. E., Vasquez, R. M., Lewis, S. L. and Reich, P. B. 2016. Positive biodiversity–productivity relationship predominant in global forests. – *Science* 354: aaf8957.
- Lloret, F., Keeling, E. G. and Sala, A. 2011. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. – *Oikos* 120: 1909–1920.
- Lloret, F., Siscart, D. and Dalmases, C. 2004. Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). – *Global Change Biol.* 10: 2092–2099.
- Lobo-do-Vale, R., Kurz Besson, C., Caldeira, M. C., Chaves, M. M. and Pereira, J. S. 2019. Drought reduces tree growing season length but increases nitrogen resorption efficiency in a Mediterranean ecosystem. – *Biogeosciences* 16: 1265–1279.
- Manzanera, J., Gómez-Garay, A., Pintos, B., Rodríguez-Rastrero, M., Moreda, E., Zazo, J., Martínez-Falero, E. and García-Abril, A. 2017. Sap flow, leaf-level gas exchange and spectral responses to drought in *Pinus sylvestris*, *Pinus pinea* and *Pinus halepensis*. – *IForest Biogeosci. For.* 10: 204–214.
- McCann, K. S. 2000. The diversity–stability debate. – *Nature* 405: 228–233.
- Merlin, M. 2015. Effects of stand composition and tree size on resistance and resilience to drought in sessile oak and Scots pine. – *For. Ecol. Manage.* 339: 22–33.
- Moriondo, M., Good, P., Durao, R., Bindi, M., Giannakopoulos, C. and Corte-Real, J. 2006. Potential impact of climate change on fire risk in the Mediterranean area. – *Clim. Res.* 31: 85–95.
- Mouillot, F., Rambal, S. and Joffre, R. 2002. Simulating climate change impacts on fire frequency and vegetation dynamics in a Mediterranean-type ecosystem. – *Global Change Biol.* 8: 423–437.
- Niinemets, Ü. and Valladares, F. 2006. Tolerance to shade, drought and waterlogging of temperate Northern Hemisphere trees and shrubs. – *Ecol. Monogr.* 76: 521–547.
- Palandrani, C. 2020. Influence of tree species richness on tree growth and intrinsic water-use efficiency after drought in tree plantations in north-eastern Italy. – *Eur. J. For. Res.* 139: 869–877.
- Pausas, J. G. and Paula, S. 2012. Fuel shapes the fire–climate relationship: evidence from Mediterranean ecosystems: fuel shapes the fire–climate relationship. – *Global Ecol. Biogeogr.* 21: 1074–1082.
- Pollastrini, M., Feducci, M., Bonal, D., Fotelli, M., Gessler, A., Grossiord, C., Guyot, V., Jactel, H., Nguyen, D., Radoglou, K. and Bussotti, F. 2016. Physiological significance of forest tree defoliation: results from a survey in a mixed forest in Tuscany (central Italy). – *For. Ecol. Manage.* 361: 170–178.
- Pretzsch, H., Schütze, G. and 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.
- Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C. C., Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., Češko, E., Dawud, S. M., Wandeler, H. D., Domisch, T., Finér, L., Fischer, M., Fotelli, M., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Haase, J., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Kambach, S., Kolb, S., Koricheva, J., Liebersgesell, M., Milligan, H., Müller, S., Muys, B., Nguyen, D., Nock, C., Pollastrini, M., Purschke, O., Radoglou, K., Raulund-Rasmussen, K., Roger, F., Ruiz-Benito, P., Seidl, R., Selvi, F., Seiferling, I., Stenlid, J., Valladares, F., Vesterdal, L. and Baeten, L. 2017. Biodiversity and ecosystem functioning relations in European forests depend on environmental context. – *Ecol. Lett.* 20: 1414–1426.
- Rodríguez-Calcerrada, J., Shahin, O., del Carmen del Rey, M. and Rambal, S. 2011. Opposite changes in leaf dark respiration and soluble sugars with drought in two Mediterranean oaks. – *Funct. Plant. Biol.* 38: 1004.
- Rousi, E., Kornhuber, K., Beobide-Arsuaga, G., Luo, F. and Coumou, D. 2022. Accelerated western European heatwave trends linked to more-persistent double jets over Eurasia. – *Nat. Commun.* 13: 3851.
- Saražin, J., Resente, G. A., Balzano, A., de Luis, M., Merela, M. and Čufar, K. 2018. Dendrochronology of sessile oak *Quercus petraea* on the transition between the sub-Mediterranean and

- temperate Continental climatic zones in Slovenia. – *Les/Wood* 67: 5–20.
- Scherer-Lorenzen, M. 2014. The functional role of biodiversity in the context of global change. – In: Coomes, D. A., Burslem, D. F. R. P. and Simonson, W. D. (eds), *Forests and global change*. Cambridge Univ. Press, pp. 195–238.
- Scherer-Lorenzen, M., Körner, C. and Schulze, E.-D. 2005. Forest diversity and function temperate and boreal systems. – Springer.
- Silva, L. C. R., Anand, M. and Leithead, M. D. 2010. Recent widespread tree growth decline despite increasing atmospheric CO<sub>2</sub>. – *PLoS One* 5: e11543.
- Sperlich, D., Chang, C. T., Peñuelas, J. and Sabaté, S. 2019. Responses of photosynthesis and component processes to drought and temperature stress: are Mediterranean trees fit for climate change? – *Tree Physiol.* 39: 1783–1805.
- Steckel, M. 2020. Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – site water supply and fertility modify the mixing effect. – *For. Ecol. Manage.* 416: 1–18.
- Stock, J. H. and Watson, M. W. 2015. *Introduction to econometrics* 3rd ed, Pearson Education, Inc. Publishing as Addison Wesley.
- Tognetti, R., Cherubini, P., Marchi, S. and Raschi, A. 2007. Leaf traits and tree rings suggest different water-use and carbon assimilation strategies by two co-occurring *Quercus* species in a Mediterranean mixed-forest stand in Tuscany, Italy. – *Tree Physiol.* 27: 1741–1751.
- Vilà, M., Carrillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., Haase, J., Kunstler, G., Schelhaas, M. and Trasobares, A. 2013. Disentangling biodiversity and climatic determinants of wood production. – *PLoS One* 8: e53530.
- Vilà, M., Vayreda, J., Comas, L., Ibáñez, J. J., Mata, T. and Obón, B. 2007. Species richness and wood production: a positive association in Mediterranean forests. – *Ecol. Lett.* 10: 241–250.
- Way, D. A. and Oren, R. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. – *Tree Physiol.* 30: 669–688.
- Zhang, Y., Chen, H. Y. H. and Reich, P. B. 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis: diversity and productivity relationships. – *J. Ecol.* 100: 742–749.
- Zimmermann, J., Hauck, M., Dulamsuren, C. and Leuschner, C. 2015. Climate warming-related growth decline affects *Fagus sylvatica*, but not other broad-leaved tree species in central European mixed forests. – *Ecosystems* 18: 560–572.