

Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge

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Abstract

Biogeographical and ecological theory suggests that species distributions should be driven to higher altitudes and latitudes as global temperatures rise. Such changes occur as growth improves at the poleward edge of a species distribution and declines at the range edge in the opposite or equatorial direction, mirrored by changes in the establishment of new individuals. A substantial body of evidence demonstrates that such processes are underway for a wide variety of species. Case studies from populations at the equatorial range edge of a variety of woody species have led us to understand that widespread growth decline and distributional shifts are underway. However, in apparent contrast, other studies report high productivity and reproduction in some range edge populations. We sought to assess temporal trends in the growth of the widespread European beech tree (*Fagus sylvatica*) across its latitudinal range. We explored the stability of populations to major drought events and the implications for predicted widespread growth decline at its equatorial range edge. In contrast to expectations, we found greatest sensitivity and low resistance to drought in the core of the species range, whilst dry range edge populations showed particularly high resistance to drought and little evidence of drought-linked growth decline. We hypothesize that this high range edge resistance to drought is driven primarily by local environmental factors that allow relict populations to persist despite regionally unfavourable climate. The persistence of such populations demonstrates that range-edge decline is not ubiquitous and is likely to be driven by declining population density at the landscape scale rather than sudden and widespread range retraction.

Keywords: biogeography, climate change, distribution, forest, growth decline, resilience, stability, tree rings

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Introduction

Environmental changes are altering the performance and distribution of species across the globe (Walther *et al.*, 2002; Parmesan, 2006). Contemporary plant range changes have been readily identified in woody species, with upward and poleward range expansion and an increase in population density resulting from enhanced growth and reproduction as the climate warms (Sturm *et al.*, 2001; Harsch *et al.*, 2009). Increased temperatures are expected to be accompanied by altered hydrology, and increasing frequency and severity of extreme events (Schar *et al.*, 2004; IPCC, 2007; Harris *et al.*, 2010). Lower water availability is expected to reduce productivity and increase mortality, particularly at range edges that lie in the equatorial direction (Bigler *et al.*, 2007; Sarris *et al.*, 2007; Allen *et al.*, 2010; Carnicer *et al.*, 2011; Linares *et al.*, 2011; Sanchez-Salguero *et al.*, 2012). Indeed, recent evidence from populations at the equatorial range edge of forest-forming tree species has

shown mortality and growth decline linked to rising temperatures and drought stress over the last half-century (Allen & Breshears, 1998; Jump *et al.*, 2006; Van Mantgem & Stephenson, 2007; Beckage *et al.*, 2008; Piovesan *et al.*, 2008). Given the importance of climate in determining the distribution of plant species globally, distributions are expected to shift poleward and upward as the climate warms, with increased productivity, reproduction and landscape-scale population density at the leading margin of a species distribution contrasting with declining performance at the opposite edge (Hickler *et al.*, 2012; Rabasa *et al.*, 2013).

However, estimates of forest productivity gained from remote sensing have indicated a widespread increase in productivity (Pan *et al.*, 2011). In Europe, forest productivity has increased in northern and central regions, with more spatially variable increases in parts of southern Europe (Spiecker, 1999; Boisvenue & Running, 2006). At the species level, responses vary (Huntley, 1991; Barbeta *et al.*, 2013; Rabasa *et al.*, 2013; Herrero & Zamora, 2014): range retractions are less frequently reported than range expansions, whilst negative impacts of increased temperature and water stress

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are not limited to species' equatorial margins (Broadmeadow *et al.*, 2005; Allen *et al.*, 2010; Kuhn *et al.*, 2015). Furthermore, relict populations of species associated with past climates persist locally, despite climates that are regionally unfavourable for the species (Hampe & Jump, 2011).

The general movement of species ranges is a useful biogeographical model to understand climate change responses at the global scale, but is an oversimplification when the probability of population persistence and loss is considered regionally (Jump *et al.*, 2009; Rabasa *et al.*, 2013; Galvan *et al.*, 2014). The disparity between prediction and observed response is partly due to the emphasis on trends of increasing temperatures driving the predicted movement of species ranges. However, extreme events play a major role in demographic responses at the population level, driving pulsed reductions of forest growth and elevated mortality (Ciais *et al.*, 2005; Adams *et al.*, 2009; Barbeta *et al.*, 2013; Cavin *et al.*, 2013; Herrero & Zamora, 2014; Allen *et al.*, 2015; Meir *et al.*, 2015). In contrast, topographic complexity and other local environmental factors can increase individual population resistance to regionally elevated temperatures (Hampe & Jump, 2011; Adams *et al.*, 2014; Tegel *et al.*, 2014), a particularly important factor at equatorial range edges where species typically occur at higher altitudes than elsewhere in their distribution. However, we know little about how drought resistance and resilience vary across a species' range, despite indications from experimental work that such factors underpinning population stability can vary between populations (Alberto *et al.*, 2013; Bansal *et al.*, 2015).

There is, therefore, a need to assess population stability throughout species ranges in order to identify regional patterns of drought resistance and postdrought recovery. Such a range-wide approach allows us to move beyond the aggregation of individual case studies with risks of publication bias, towards the identification of regional patterns of risk based on random population sampling. Here, we focus on the western European distribution of European beech, *Fagus sylvatica* L., one of Europe's most common late successional forest-forming tree species. *Fagus sylvatica* is drought sensitive (Fotelli *et al.*, 2001; Leuschner *et al.*, 2001; Granier *et al.*, 2007) and is expected to be particularly sensitive to deteriorating water balance as temperatures rise. Recent research in this species has identified predominantly decreasing trends of growth and productivity across Europe (Dittmar *et al.*, 2003; Jump *et al.*, 2006; Piovesan *et al.*, 2008; Bontemps *et al.*, 2009, 2010; Charru *et al.*, 2010; Scharnweber *et al.*, 2011; but see Tegel *et al.*, 2014 for a counterexample). Most attribute the observed growth patterns primarily to environmental change,

with increasing drought stress leading to reductions in radial growth or increases in climate sensitivity (Peuke *et al.*, 2002; Gessler *et al.*, 2004; Meier & Leuschner, 2008; Jump *et al.*, 2010). Modelling studies have forecast changes in the distribution of *F. sylvatica* more widely across its range, alongside reductions in primary productivity (Rennenberg *et al.*, 2004; Broadmeadow *et al.*, 2005; Gessler *et al.*, 2007; Meier *et al.*, 2011).

To identify regional patterns of drought stability and examine the assumptions underpinning predicted range shifts in this species, we asked: (i) Does the importance of high summer temperature and low precipitation in limiting growth of this species increase approaching its equatorial range edge? (ii) Is growth response to climate more consistent at the range edges? (iii) To what extent does absolute aridity of a site affect population drought response, compared to aridity that is extreme relative to mean site conditions? (iv) Which are the regions of the species' distribution that are most resistant and resilient to drought?

Materials and methods

Sampling network

Forty six sites were sampled without prior knowledge of stand characteristics other than that *F. sylvatica* was the dominant or codominant species in the stand. Sites were distributed from 58.5° to 40.8°N, and from 5.8° to 11.8°E (Table S1). For each site, a mean of 29 and minimum of 16 canopy dominant or codominant trees were selected for coring. Two cores were taken per tree using a 4.3-mm-diameter increment borer and prepared using standard dendroecological methods. Diameter at breast height (dbh) was recorded at 1.3 m above ground level. Ring widths were measured using COORECORDER v7.5 (Larsson, 2003a), with the assistance of a stereomicroscope. Using the programme CDENDRO v7.5 (Larsson, 2003b), samples were cross-dated visually by the comparison of growth curves and statistically validated using the interseries comparisons of correlations of chronology segments. For the final cross-dated chronologies, a mean ring width value was calculated for each year for each tree. In total, 2550 cores from 1316 trees were included in the final 46 tree ring chronologies.

Chronologies were detrended using a cubic smoothing spline with a frequency cut-off of 50% and rigidity of 2/3 of the total series curve length to remove long-term trends related to ageing and disturbances (Cook & Kairiukstis, 1990). In order to remove autocorrelation, and as an additional filter to remove the effects of disturbance, the ring width indices were modelled as autoregressive (AR) processes (Cook, 1987). The ring width series were then prewhitened by deducting the modelled autocorrelation structure from the ring width indices. Finally, the detrended and prewhitened ring width indices from each population were then combined into mean chronologies for each site, using Tukey's biweight robust mean (Mosteller & Tukey, 1977). All stages of chronology

building (and further analyses) were performed using R and the package dplR (Bunn, 2010; R Development Core Team, 2012). The resulting ring width indices were used in all ring width based analyses below.

Summary statistics

Summary statistics of mean sensitivity (MS) (Douglas, 1920), mean interseries correlation (Cook & Kairiukstis, 1990) and expressed population signal (Wigley *et al.*, 1984) were calculated to enable the evaluation of the validity of the tree ring chronologies (Table S2).

Climate data

Daily climate variables were obtained for all sites from the high-resolution E-OBS gridded data set: daily mean temperature, maximum temperature, minimum temperature and precipitation (Haylock *et al.*, 2008). This data set has grid spacing at $0.25^\circ \times 0.25^\circ$ resolution (approximately 17.25 km^2) and covers the period from 1950 to 2014. To adjust temperatures for altitude, a linear lapse rate adjustment of $6.0 \text{ }^\circ\text{C per km}$ was applied. This method has been shown to be accurate, compared to a neutral stability algorithm (Dodson & Marks, 1997), although it cannot fully account for potential local effects on lapse rate in spatially complex mountain environments (Rolland, 2003; Minder *et al.*, 2010). The spread of climate stations used in the E-OBS network is uneven, which can lead to interpolated values being oversmoothed (Hofstra *et al.*, 2010). This problem manifests itself most acutely at the southern edge of the study region. Whilst in this region, the E-OBS grid reproduces most climatological features well, it has limitations with regard to extreme indicators (Herrera *et al.* 2012). E-OBS remains the best gridded data set for European studies currently available (Herrera *et al.* 2012); however, it is better suited to regional analyses such as those presented here, whilst individual population-level analyses should be interpreted cautiously.

Bioclimatic variables were calculated using the raw E-OBS daily data. The variables calculated were as follows: annual mean temperature; total annual precipitation; mean maximum temperature of the warmest month; mean minimum temperature of the coldest month; summer precipitation, defined as May to August; continentality index (the difference in mean temperatures of the warmest and coldest months); potential evapotranspiration (PET) calculated using the Thornthwaite method (Thornthwaite, 1948); PET calculated for the summer months (May to August), again using the Thornthwaite method and hereafter referred to as summer PET; aridity index, precipitation divided by PET (UNEP, 1992) calculated for the summer months (May to August), hereafter referred to as summer aridity index (SAI).

Multivariate analysis

To identify geographical structure in both climate and growth response for *F. sylvatica*, multivariate techniques were applied to analyse climatic and growth data. Agglomerative

hierarchical clustering analysis and discriminant coordinate analysis were used to partition sites into regional clusters based on bioclimatic variables (annual mean temperature, total annual precipitation, mean maximum temperature of the warmest month, mean minimum temperature of the coldest month, continentality index and summer potential evapotranspiration). Agglomerative hierarchical cluster analysis was used with rotated principal components analysis to assess regional clustering of sites based on ring width data. Full details of the analysis performed can be found in Appendix S3. Cluster means of bioclimatic variables for the regions identified by multivariate analysis of growth and environmental data are given in Table S4.

Climate–growth analysis

In order to establish the relationships between climate and the growth response of *F. sylvatica*, climate–growth analysis was performed using annual ring width index chronologies and climate data. Monthly climate data were used, comprising a 17-month period from May of the year prior to ring formation, up until September of the year of ring formation. This period includes the previous year's growing season, intervening winter/spring and the growing season during the year of ring formation. This is a standard approach in tree ring analysis since it allows an evaluation of any effects of preconditioning by climate before the growing season (Cook & Kairiukstis, 1990; Biondi & Waikul, 2004). Pearson's correlation coefficients were calculated for each site compared to 34 climate variables, that is each of 17 months for both temperature and precipitation (Blasing *et al.*, 1984). Significance was tested using 1000 bootstrap replicates and with 95% confidence intervals, using the R package bootRes (Zang & Biondi, 2013). Results for each of the sites were then partitioned into the five biogeographical clusters identified by multivariate analysis. Mean correlation function values were calculated for each cluster, in order to identify the climate responses of each group.

Drought indices

The E-OBS data were used to identify drought by calculating the multiscalar standardized precipitation evapotranspiration index (SPEI) (Vicente-Serrano *et al.*, 2010). SPEI is a drought index with flexible temporal integration from one up to 24 months and has been demonstrated to be effective in the study of tree responses to climate (Pasho *et al.*, 2011; Cavin *et al.*, 2013). The index is calculated using PET and precipitation and so includes the effects of both temperature and water balance. SPEI was calculated for all sites using a 12-month timescale (therefore encompassing both current and previous year water availability), with PET derived from the Thornthwaite equation (Thornthwaite, 1948), log-logistic distributed indices and parameters fitted using unbiased probability weighted moments. This measure of drought is relative to conditions at the site for which it is calculated, with a value of 0 representing mean drought conditions, positive values representing higher than average water availability, negative

values representing lower than average water availability and a standard deviation of 1. For a measure of drought that enables the comparison of drought severity between sites, annual SAI (i.e. precipitation divided by potential evapotranspiration) was calculated for each site over the period 1950–2010.

Pointer years

Identification of pointer years (years where an abrupt growth increase or decrease is recorded in a tree ring chronology relative to mean growth) can be used to facilitate study of the environmental conditions that influenced the growth of a population in that year (Schweingruber *et al.*, 1990; Lebourgeois *et al.*, 2005; Neuwirth *et al.*, 2007). To identify pointer years, annual ring width values for each individual tree within each site chronology were transformed into Cropper values, through division by their 11-year moving average values (Cropper, 1979). Cropper values were then normalized to a mean of 0 and standard deviation of 1. To evaluate the normalized values, threshold values described by Neuwirth *et al.* (2007) were followed: 'extreme' > 1.645, 'strong' > 1.28 and 'weak' > 1, as derived from the probability density function of the standardized normal distribution. The weak threshold value was used, to maximize the number of years for further analysis. Where $\geq 50\%$ of all trees within a chronology exceed the defined threshold, the year was considered a pointer year.

In order to identify which pointer years coincided with drought periods, each pointer year identified above within the time period 1951–2004 was compared to SPEI values during the growing period of May–August for that year. Where SPEI fell below -1 in any of those 4 months, the pointer year was classed as a drought-linked pointer year. This approach does not account for the fact that during any of these event years, multiple interacting factors will have influenced growth.

Quantifying growth stability

Age affects tree ring width, with ring width declining over time (Fritts, 1976). To circumvent this problem, basal area increment (BAI) can be used as a metric of tree growth for which increasing or stable trends are found in mature trees (Phipps & Whiton, 1988; Leblanc, 1990; Leblanc *et al.*, 1992). Decline in BAI is commonly interpreted as representing declining tree growth (Pedersen, 1998; Jump *et al.*, 2006). Here, BAI was calculated by using raw, nondetrended ring widths and circumferences to calculate the area of wood added to a cross-section of the tree at breast height (1.3 m) annually:

$$\text{BAI} = \pi(R_n^2 - R_{n-1}^2)$$

where R is the radius of the tree, and n is the tree ring year. Each individual site chronology was truncated to the time period for which number of replicates was greater than or equal to five trees.

The effect of disturbance, such as drought, on tree growth can be evaluated using stability indices described by Lloret *et al.* (2011). These indices quantify the resistance, recovery, resilience and relative resilience of trees in response to

environmental factors and are used here to describe the impact of drought events for the drought-induced pointer years. The indices evaluate tree growth (BAI) during a disturbance relative to growth in the 5 years before and after the disturbance, here the drought-induced pointer year.

Resistance describes the severity of the impact of the disturbance in the year it occurred:

$$\text{Resistance} = \text{Drought}/\text{Predrought}$$

Recovery measures the ability to recover from disturbance relative to its severity. High values reflect a large increase in growth postdisturbance relative to growth during the disturbance:

$$\text{Recovery} = \text{Postdrought}/\text{Drought}$$

Resilience is the ability to regain predisturbance levels of growth, assuming stable climate between the 5-year periods either side of the disturbance. Low values correspond to low resilience:

$$\text{Resilience} = \text{Postdrought}/\text{Predrought}$$

Relative resilience is the resilience weighted by severity of the disturbance in the event year, high levels of damage in the disturbance event act to increase this index:

$$\text{Relative Resilience} = (\text{Postdrought} - \text{Drought})/\text{Predrought}$$

The stability indices above were calculated for each drought-induced pointer year. Pointer years that occurred within 5 years of each other were omitted. Where drought-induced pointer years occurred for a site in successive years, the mean BAI of the 2 years was used to give a single drought BAI for use in calculating resilience indices. As the intention here is to use stability indices to compare the effect of drought stress across multiple locations, we normalized BAI by dividing the BAI of each year by precipitation in that year.

Given the large geographical range covered by this research, spatial and temporal heterogeneity in both the occurrence and severity of drought episodes makes the comparison of individual drought years across sites difficult. Therefore, the stability index values for all drought-induced pointer years at all sites were pooled into a single data set. The resulting data set was analysed using generalized additive modelling (GAM). GAM was conducted using the *mgcv* package in R (Wood, 2011). The values for the smoothing parameters were estimated using generalized cross-validation, which is a modified version of ordinary cross-validation and has been shown to have computational advantages (Zuur *et al.*, 2009). Values of effective degrees of freedom (edf) indicate the degree of linearity of the smoother: higher values of edf represent stronger nonlinear smoothing splines. Results were smoothed using a regression spline with shrinkage. Explanatory variables used were as follows: chronology age in the year of disturbance; latitude; elevation; site aridity, that is mean SAI 1950–2012; relative drought intensity, that is the minimum SPEI in May–August of the drought year; absolute drought intensity, that is SAI of the drought year; relative drought intensity of the previous summer; absolute drought intensity of the previous summer. Explanatory variables were checked for collinearity using paired plots, correlation

coefficients and VIF. The model was refined using a stepwise deletion of nonsignificant terms.

Modelling temporal trends in growth

Basal area increment chronologies were further truncated to the 1966 to 2009 time period common to all 46 sites. To examine growth trends rather than compare absolute growth between sites, BAI for each year was divided by the mean site BAI, to give a dimensionless BAI index. The BAI data were then aggregated into regional data sets, based on the regions determined through the multivariate analysis described above. GAM was then performed on the regional BAI index data, with the sole predictor variable of year of growth, in order to examine temporal trends in BAI. Therefore, the model is of the form:

$$BAI_i = \alpha + f(\text{Year}_i) + \varepsilon_i \text{ where } \varepsilon_i \sim N(0, \sigma^2)$$

where α is the intercept, f is a smoothing spline, and ε represents the residuals. Smoothing parameters were estimated using generalized cross-validation, and the results were smoothed using a regression spline with shrinkage. This approach aimed to identify and describe any nonlinear temporal trends in radial growth across the five biogeographical regions identified here, and so the GAM described above was applied to the five regions separately.

Results

Multivariate analysis

Detailed description of the results of the multivariate analysis can be found in Appendix S3. The final clusters derived from joint analysis of bioclimatic and ring width data were as follows: north-west (no. of sites = 10), range core temperate ($n = 19$), range core continental ($n = 7$), wet south ($n = 3$) and dry south ($n = 7$) (Fig. 1).

Ring width indices

The ring width indices for the north-west display high variability between sites ($\bar{r} = 0.101$), with most years having sites recording both high (index values > 1) and low (index values < 1) growth (Fig. 2). Negative growth indices occurred for all sites in this cluster in 1976, which was an exceptional drought year over much of western Europe. The minimum values of ring widths during periods of low growth were not extreme, with all index values for all sites being >0.5. The core temperate region has the highest within-region homogeneity in growth ($\bar{r} = 0.575$), with frequent synchronized growth reductions throughout the period shown. Near-universal negative ring width indices were recorded across this cluster for the years 1976, 1989–1990, 1995 and 2004. Index values for individual sites

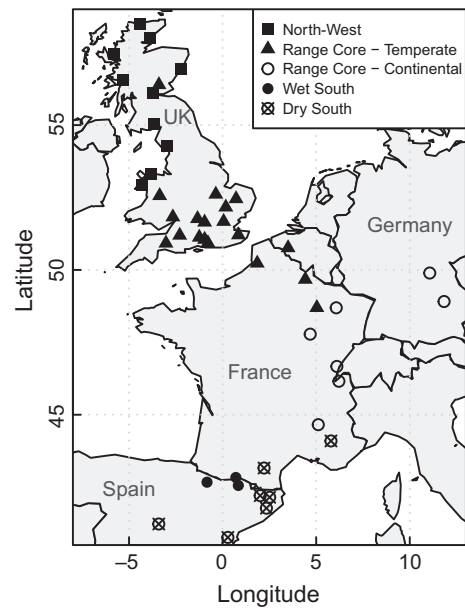


Fig. 1 Biogeographical clusters of *Fagus sylvatica* identified by multivariate analysis and locations of the individual study sites.

were frequently below 0.5 during these synchronized growth suppressions. The core continental region shows similar, although weaker, characteristics ($\bar{r} = 0.489$). Ring index values were higher, although strong region-wide growth suppressions were evident. Finally, the dry south region had high variability in growth between sites in individual years ($\bar{r} = 0.266$). Region-wide growth suppressions were recorded in 1979, 1999 and 2004, although these were smaller than those experienced in the core temperate and core continental regions.

Climate–growth analysis

As with the high variability found between sites for ring width indices, correlation functions for the north-west region failed to display any coherent regional signal in growth response to climate, with high between-site variability (Fig. 3a, b). No features of climate appear to strongly influence year-to-year variation in growth within this cluster. The core temperate region has a strong regional signal, with a negative association between growth and temperature in the summer prior to ring formation. A weaker effect of temperature in the year of growth exists (Fig. 3c). Summer precipitation, both in the year of growth and previous year, positively influences growth (Fig. 3d). For the core continental region, summer temperature is negatively correlated with growth, both in the year of growth and previous year, whilst high summer precipitation in the current growing season boosts growth (Fig. 3e, f).

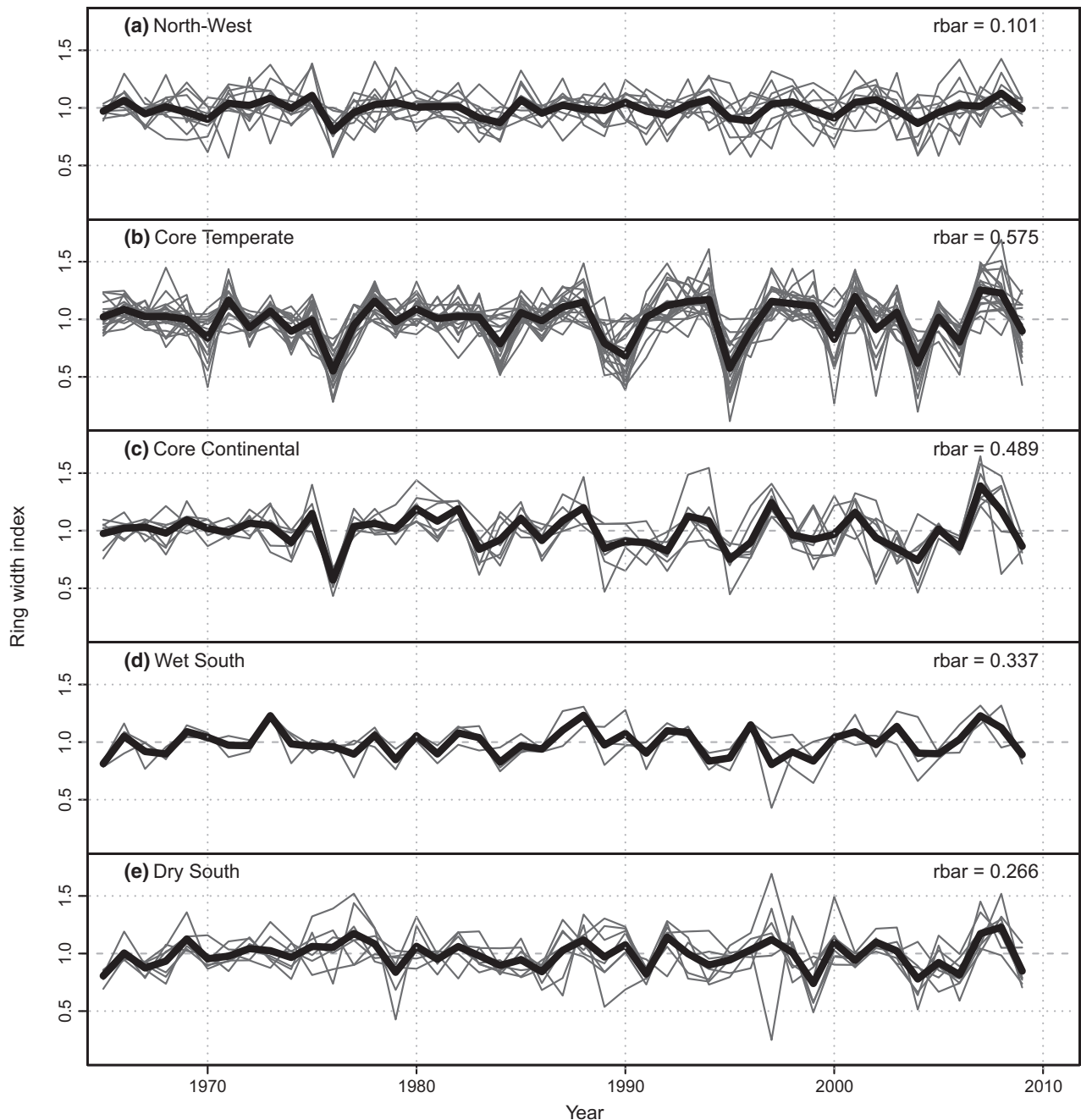


Fig. 2 Detrended and prewhitened ring width chronologies for the 46 sites sampled for *Fagus sylvatica*. Sites are partitioned into regional clusters, and a mean region chronology plotted in bold. \bar{r} is the mean series intercorrelation for each region.

Whilst the core continental region has a largely coherent signal, variability in site correlation coefficients is high for winter precipitation, with significant positive correlations with winter precipitation in greater than one-third of sites. The correlation functions for both the core temperate and core continental groups indicate sensitivity to summer drought conditions. The wet south region has low variation in correlations

between the sites; however, the sample size is low ($n = 3$). Common *F. sylvatica* climate–growth relationships are visible, that is negative effects of summer temperature and positive effects of summer precipitation (Fig. 3g, h). However, the strength of these relationships is weak: wet south sites show no indications of being strongly affected by drought. Finally, for the dry south sites, climate–growth correlations generally have

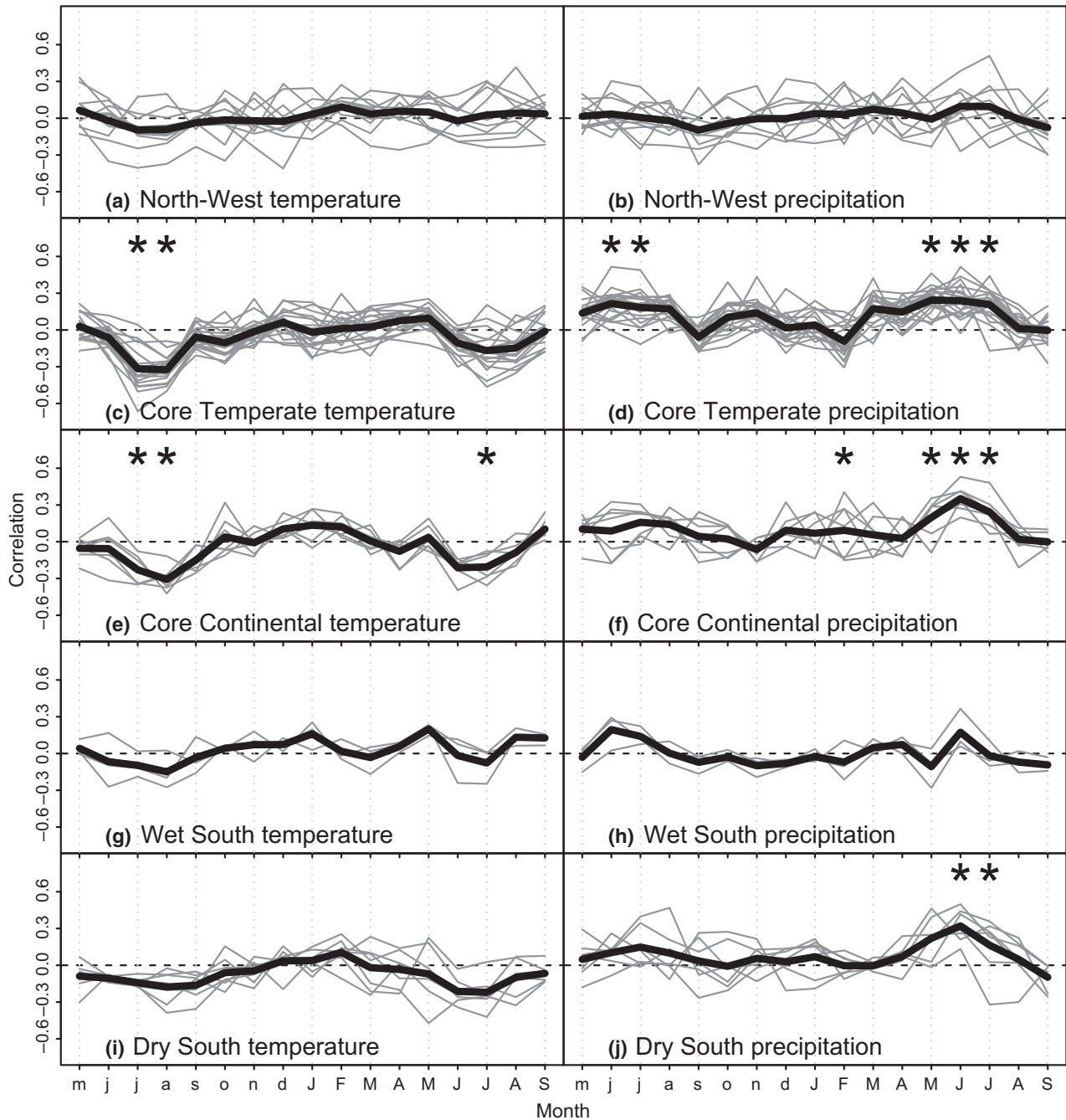


Fig. 3 Climate–growth analysis, showing correlation coefficients for annual radial growth and climate factors in the year of ring formation, and previous year. Climate data used are for the period 1950–2009, and monthly factors plotted on the x-axis are May to December of the year prior to ring formation (lower case m – d), and January to September in the year of ring formation (upper case J – S). The 46 sites sampled are plotted in five biogeographical clusters. Months where significant correlations occurred for >1/3 of sites in each region are marked *.

high variability between sites. Negative correlations for summer temperature (year of growth and previous year) are visible, but weak (Fig. 3i), whereas a strong region-wide signal of positive relationship between summer precipitation and growth exists (Fig. 3j).

Drought indices

The spatial extent of the 1976 drought was limited to the three most northerly regions, with no regional-scale drought in 1976 for the two southernmost regions

(Fig. 4). Drought in 1989–1990 affected all but the most northerly group, yet this only translated into anomalous low growth in the range core groups (Fig. 2). Neither 1989–1990, nor the range-wide drought in 2003 resulted in anomalous low growth for the wet south and dry south groups. The drought of 2003 resulted in widespread drought-induced pointer years in 2004 for the north-west (30% of sites), core temperate (47%) and core continental (57%) groups (Fig. 5).

Using SAI to examine absolute drought conditions and compare water availability between sites (Fig. 6), sites in the dry south group experience the driest conditions, with near constant aridity at levels equivalent to that only experienced for all other groups during drought events. The core temperate region experienced the second highest aridity, particularly for the sites in south-east UK (sites 12, 14–24). For the north-west group, aridity was the lowest of all clusters; however, regional droughts in 1976, 1983 and 1995 did result in aridity for a limited number of sites at a level comparable to the more arid groups.

Growth stability

Of a total of 121 drought-induced pointer years, 90 were selected for further analysis: 23 were removed due to occurring within a 5-year window of each other, and eight occurred in consecutive years and thus were combined into single events (Fig. 5). The GAM models explained a moderate degree of variation in the stability indices: $R^2(\text{adj})$ ranged from 25% for resilience to 55% for resistance (Table 1).

For resistance, age, latitude and previous year SAI were the significant explanatory variables. Both young and old forests experienced smaller reductions of growth in pointer years and hence higher resistance (Fig. 7a), whilst mature forests (~150 years old) experienced larger reductions. However, confidence intervals indicate that effects could be small in magnitude for young and mature forests. Two key features of the relationship between latitude and resistance are high resistance for southern range edge populations (<43°), and low resistance for sites in the range of 51–53° latitude, corresponding to the south-east of the UK. For previous year SAI and resistance, high previous year aridity (i.e. low SAI values) results in low resistance, whilst lower aridity results in higher resistance (Fig. 7a). For recovery (Fig. 7b), age was a significant factor, with higher recovery for trees between 140 and 180 years old. Forests at low latitudes (<43°) had low recovery. However, the P -value for latitude was 0.049 and, given the uncertainty of P values in the range 0.02–0.05 for smoothing functions using estimated degrees of freedom (Zuur *et al.*, 2009), the effect of latitude must therefore be

interpreted with caution. Absolute aridity (SAI) in the year previous to the pointer year had a positive relationship with recovery: more arid conditions resulted in higher recovery values, whilst less arid conditions resulted in lower recovery. For resilience (Fig. 7c), young forests (<60 years) had higher values, and forests between around 100–130 years old had lower values. Latitudes covering the core continental region had higher resilience, whilst those relating to the core temperate region had lower resilience, although the caveat regarding the P -value for the latitude effect must be noted, as above. Finally, for relative resilience (Fig. 7d), the curve for age shows that forests around 150–180 years old were best able to recover performance, weighted by the strength of the drought impact, the oldest trees (>230) show high resistance, yet low recovery and the lowest relative resilience. Equatorial range edge forests had the lowest relative resilience, whilst latitudes relating to the core continental group had higher relative resilience. The relationship with aridity (previous year SAI) showed that higher aridity resulted in higher relative resilience, and lower aridity resulted in lower relative resilience.

Modelling temporal trends in growth

Models (GAM) fitted to the five regions were statistically significant, with R^2 of between 0.11 and 0.24, despite including year as the only predictor variable (Table 2). The estimated degrees of freedom (Table 2) indicate strongly nonlinear temporal trends in the core temperate (Fig. 8g) and core continental regions (Fig. 8h). The temporal trend for these regions is increasing radial growth. However, strong growth suppressions are present in both regions centred on 1976 & 2004. Both of these years correspond to regional-scale drought events. Radial growth for the north-west region is strongly linear, with a trend of increasing growth (Fig. 8f). No periodic disturbances in the increasing trend were recorded, although the variability in radial growth between sites was high, particularly from the mid-1990s onwards (Fig. 8a). For the two equatorial range edge regions, radial growth rose to a peak at around 1990 (Fig. 8i, j) before beginning a slight decline. Broadly, however, BAI at the equatorial range edge was stable over the period examined when considered at the regional scale.

Discussion

Based on an unbiased sampling of 46 *F. sylvatica* populations throughout the latitudinal distribution of this species in western Europe, we identified unexpected patterns of drought sensitivity and growth stability. In

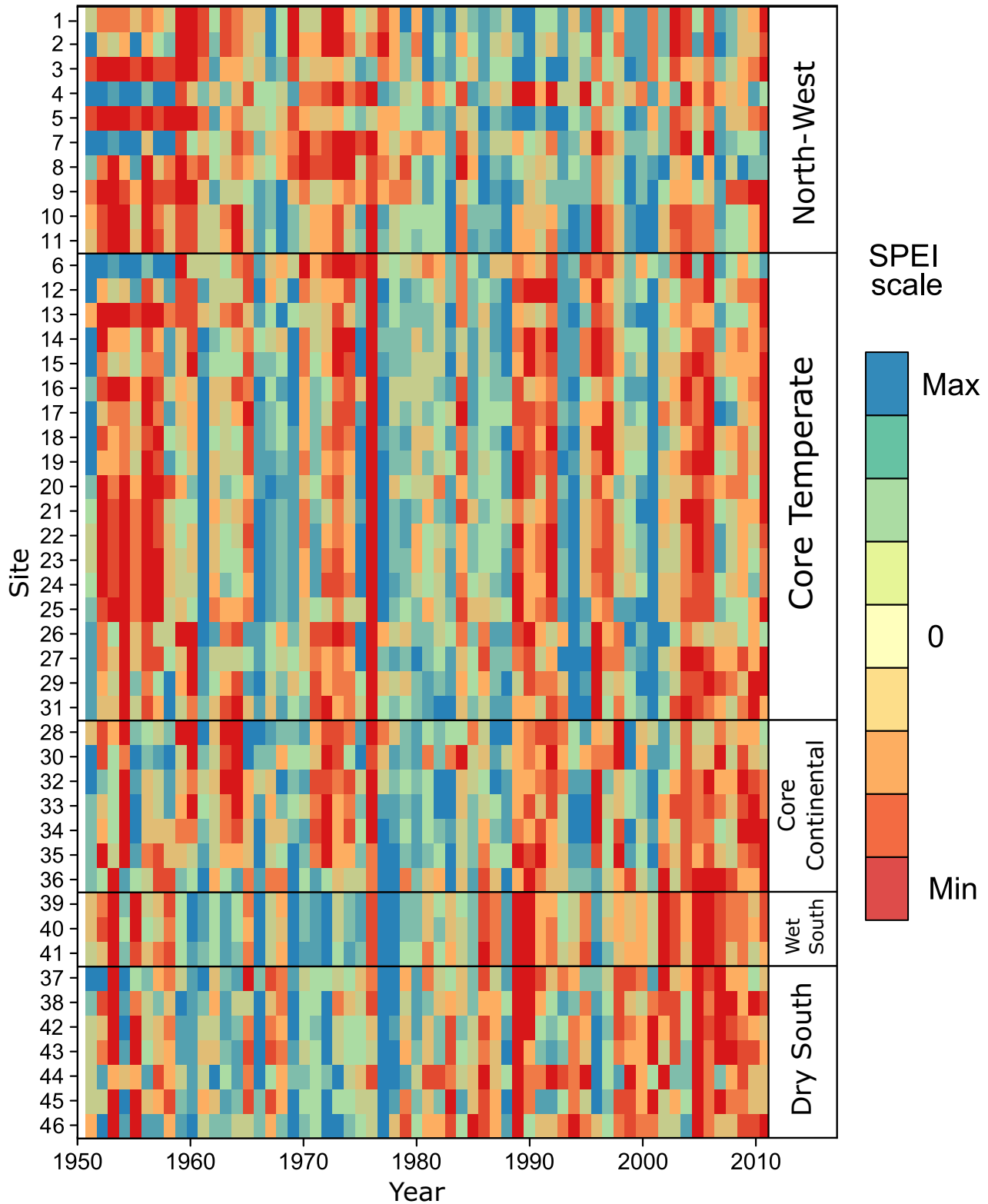


Fig. 4 Time series plot of the standardized precipitation evapotranspiration index (SPEI) drought index for the sampling network. Annual values are plotted for the period 1951–2012. Sites are numbered 1 to 46 in order of descending latitude, that is site 1 is the most northerly and site 46 the most southerly. Values represent drought relative to conditions at each site individually, allowing the comparison of spatial and temporal drought occurrence, but not severity between sites.

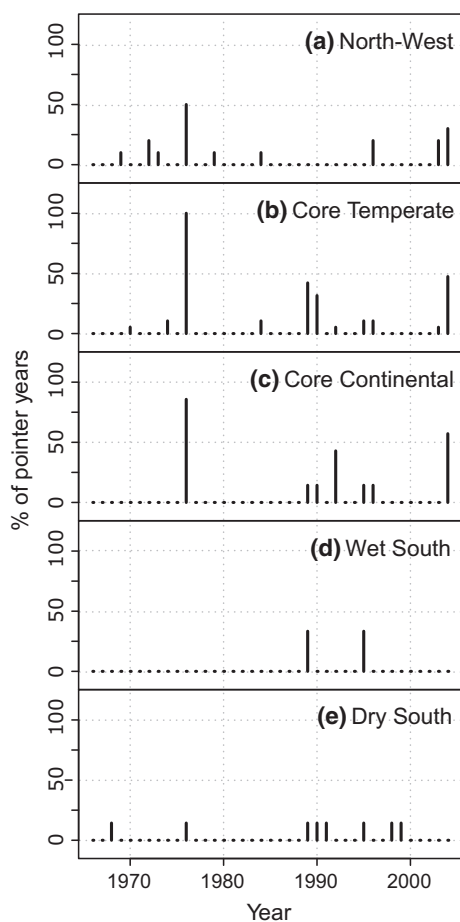


Fig. 5 Percentages of site chronologies showing drought-induced pointer years from 1966 to 2004 for biogeographical regions of *Fagus sylvatica* in western Europe.

contrast to expectations of low stability and widespread growth decline at the equatorial range edge of the species, we found high resistance to drought and approximately stable growth at the equatorial range edge. However, although resistance is high, recovery is poor if growth impacts occur, such that equatorial range edge populations are not resilient to drought. The greatest resilience to drought is instead seen in the core continental populations sampled from northern and central France and southern Germany. Remarkably, whilst the entire range core is highly drought sensitive, it is the core temperate portion of this species' range and specifically southern UK stands that show the poorest drought stability. The strongest signals of low drought resistance and resilience and reductions of growth in response to drought are witnessed in this core temperate region. In contrast, but in agreement with expectations, the poleward range edge of this species shows a sustained increase in growth and little contribution of drought impacts to overall growth patterns.

Spatial patterns of growth stability vary with latitude and site aridity

In addition to the assessment of regional variation in climate–growth relationships (Fig. 3), analysis of growth stability connected to drought-induced pointer years using GAM allowed for an evaluation of specific factors that influence the response of *F. sylvatica* to drought. Latitudinal variation in growth stability corroborates the regional variation in climate–growth relationships and drought pointer year occurrence. *Fagus sylvatica* forest stands at the equatorial range edge (latitude $<45^\circ$) experience lower initial drought impacts in the event year (Fig. 7a). North continental stands recovered well relative to drought damage and predrought growth levels (Fig. 7c, d). Of the regions considered in this study, forest stands in southern UK were highlighted as experiencing especially elevated reductions in growth performance in drought years (Fig. 7a, c), consistent with the high drought sensitivity identified from the climate–growth analysis.

The youngest chronologies were associated with low reductions in growth during drought episodes (Fig. 7a) and high postdrought growth levels relative to predrought performance (Fig. 7c). Stands of mature trees (>130 years chronology length) experienced only small reductions in growth during drought (Fig. 7a) and high recovery (Fig. 7b) and hence relative resistance. Whilst greater drought sensitivity has been reported for older forest stands for many species (Wang *et al.*, 2006; Klos *et al.*, 2009; Linares *et al.*, 2013), this study finds that, for the very oldest stands (over approximately 210 years), there is high resistance to drought, but low recovery and relative resilience if impacts occur.

The reduction in growth in the drought year was primarily influenced by aridity in the previous, rather than the drought year. Absolute aridity (SAI) in the previous year was identified as a major driver of drought impact, whereas relative drought (SPEI) was nonsignificant. The relationship of increasing recovery and relative resilience with increasing previous year's aridity is most likely due to the effect of a larger drought year growth reduction on the calculation of these indices. Since recovery is calculated as the ratio of postdrought growth to growth in the event year and relative resilience is resilience weighted by the severity of disturbance in the drought year, lower growth during the event year will elevate the value of these indices. Likewise, whilst stands at the equatorial range edge show lower recovery and relative resilience, this is likely related to low drought impacts on growth in this region, as these indices are both decreased in the case of low reduction in BAI for the drought year (see formulae above).

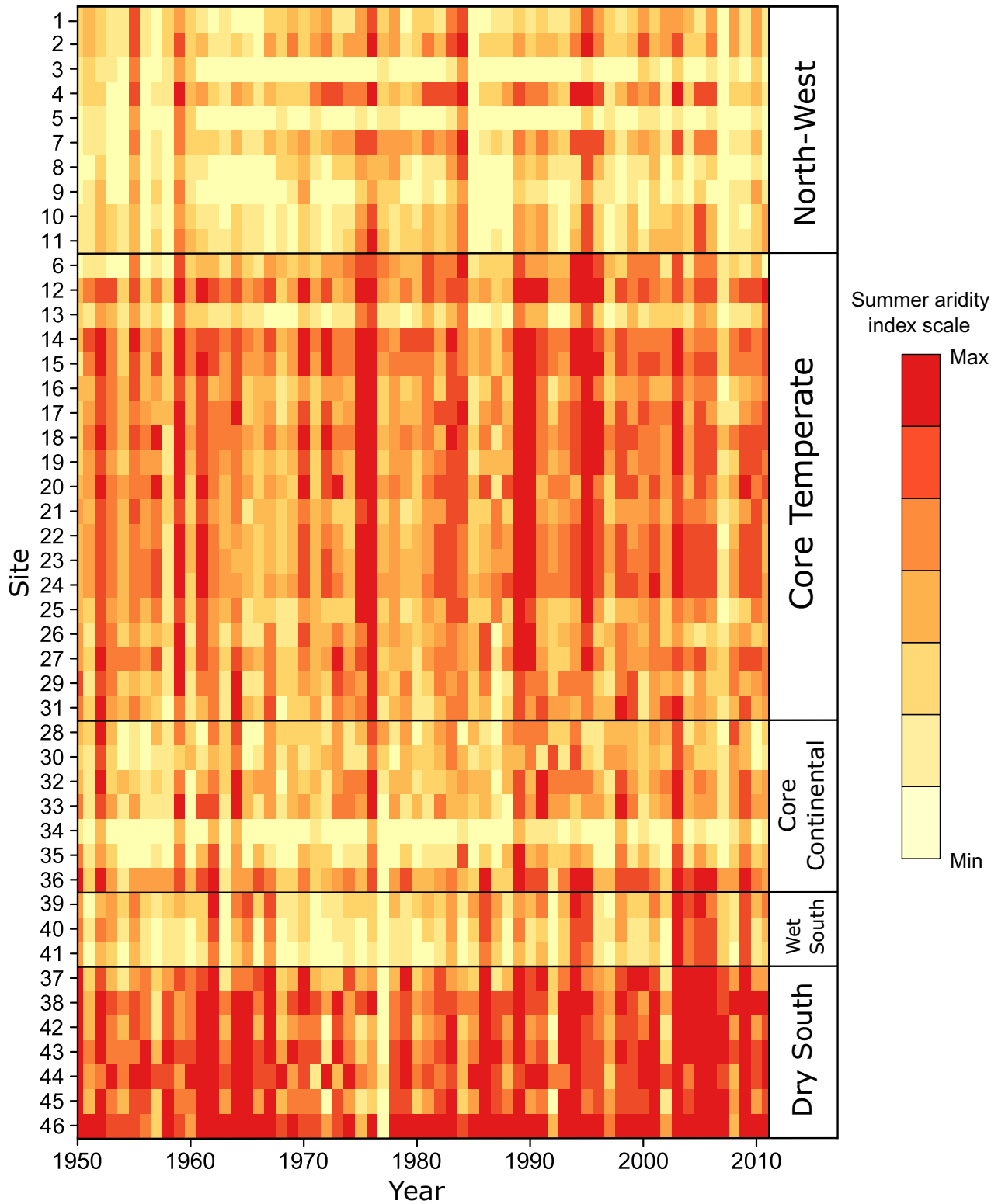


Fig. 6 Time series plot of summer aridity index [precipitation/potential evapotranspiration (PET) calculated for the months May to August]. Annual values are plotted for the period 1950–2011. Sites are numbered as Fig. 4. Values represent absolute aridity, allowing the comparison of aridity and drought severity between sites.

Table 1 Generalized additive model results of stability indices and predicting factors across the western European distribution of *Fagus sylvatica*

Drought impact index	Factor	e.d.f.	F	P	R ² (adj)
Resistance	Age	3.52	6.66	<0.001	
	Latitude	4.94	3.12	0.008	
	Previous year SAI	5.65	6.29	<0.001	
	Whole model				0.554
Recovery	Age	4.27	3.04	0.014	
	Latitude	4.31	2.33	0.049	
	Previous year SAI	4.81	7.97	<0.001	
	Whole model				0.471
Resilience	Age	2.7	4.20	0.006	
	Latitude	8.76	2.25	0.027	
	Whole model				0.252
Relative resilience	Age	4.35	3.19	0.010	
	Latitude	5.22	2.86	0.014	
	Previous year SAI	1.35	17.51	<0.001	
	Whole model				0.393

SAI, summer aridity index.

Greater synchronicity of climate response in the range core

The general pattern of climate–growth relationships we identify for *F. sylvatica* (Fig. 3) is in agreement with previously published studies (Di Filippo *et al.*, 2007; Jump *et al.*, 2007; Maxime & Hendrik, 2011; Scharnweber *et al.*, 2011). Broadly, the response can be described as drought sensitive: positive relationships between summer precipitation and growth, and negative relationships between summer temperature and growth. High variability in climate–growth relationships occurs at both the poleward (Fig. 3a, b) and equatorial range edge (Fig. 3i, j) of this species. This pattern is consistent with a general recent relaxation of cold stress on this species at its poleward limits with recent climatic warming. However, it is in apparent contrast with predictions of increased drought stress at the equatorial range edge, which should lead to highly synchronous drought-induced growth suppression.

This apparent disparity is, however, consistent with forests where stand-level environmental conditions are driving growth, rather than regional-scale climate. Instead, it is the range core populations that typically show regional-scale suppression of growth in synchrony with major drought events. The results presented here reveal variation in the strength of climate–growth relationships across the latitudinal range of the species in western Europe: sites categorized as

being from the range core display greater sensitivity of growth to regional climate (summer temperature and precipitation). Predictably for a region characterized by extremely high annual precipitation (1277 mm, see Appendix S3 Table 2), populations from the most poleward area of the species distribution showed no significant regional climate–growth relationships and high variability in climate–growth correlations.

Low drought sensitivity of *F. sylvatica* growth at its equatorial range edge could be the result of local adaptation of these populations to arid conditions, comparable to genetic clines which have been demonstrated to correspond to aridity gradients for this and other species (Rehfeldt *et al.*, 1999; St Clair *et al.*, 2005; Thiel *et al.*, 2014; Pluess *et al.*, 2016). However, the observed pattern of low drought sensitivity in combination with high interpopulation divergence in climate–growth response is likely to include an effect of population-scale site conditions diverging from regional climate. In this scenario, such populations represent climate relicts – occurring predominantly in sites where fine-scale environmental conditions favour their persistence. Indeed, the climate–growth relationships described here (Fig. 3i, j) can be interpreted as demonstrating the degree of disconnect between regional-scale climate and the conditions experienced by trees at the stand scale (Hampe & Petit, 2005; Jump *et al.*, 2009; Hampe & Jump, 2011). Furthermore, stand-scale soil properties such as nutrient status and water holding capacity not captured by SPEI and SAI are known to significantly modify climate–growth responses in this and other species (Lévesque *et al.*, 2016).

Impacts of drought events across the range of Fagus sylvatica

Immediate comparisons of the drought response of populations within the network of sites are complicated by the variability in both timing and location of droughts across the latitudinal range. Nonetheless, some key events allow regions to be contrasted. Across our sites drawn from the western European distribution of *F. sylvatica*, the drought and growth suppression of 2004 is the universal event affecting all regions. Whilst the heat wave of 2003 has been reported to affect the primary production of European vegetation (Ciais *et al.*, 2005), the study of tree rings has revealed a minor impact in this year, attributed to the effect of spring precipitation alongside preconditioning from previous year conditions (Pichler & Oberhuber, 2007). This finding is corroborated by this study, with reductions in growth primarily associated with a 2004 drought identified using SPEI at 12-month resolution. This temporal resolution incorporated both previous summer conditions, alongside dry spells in 2004. However, despite

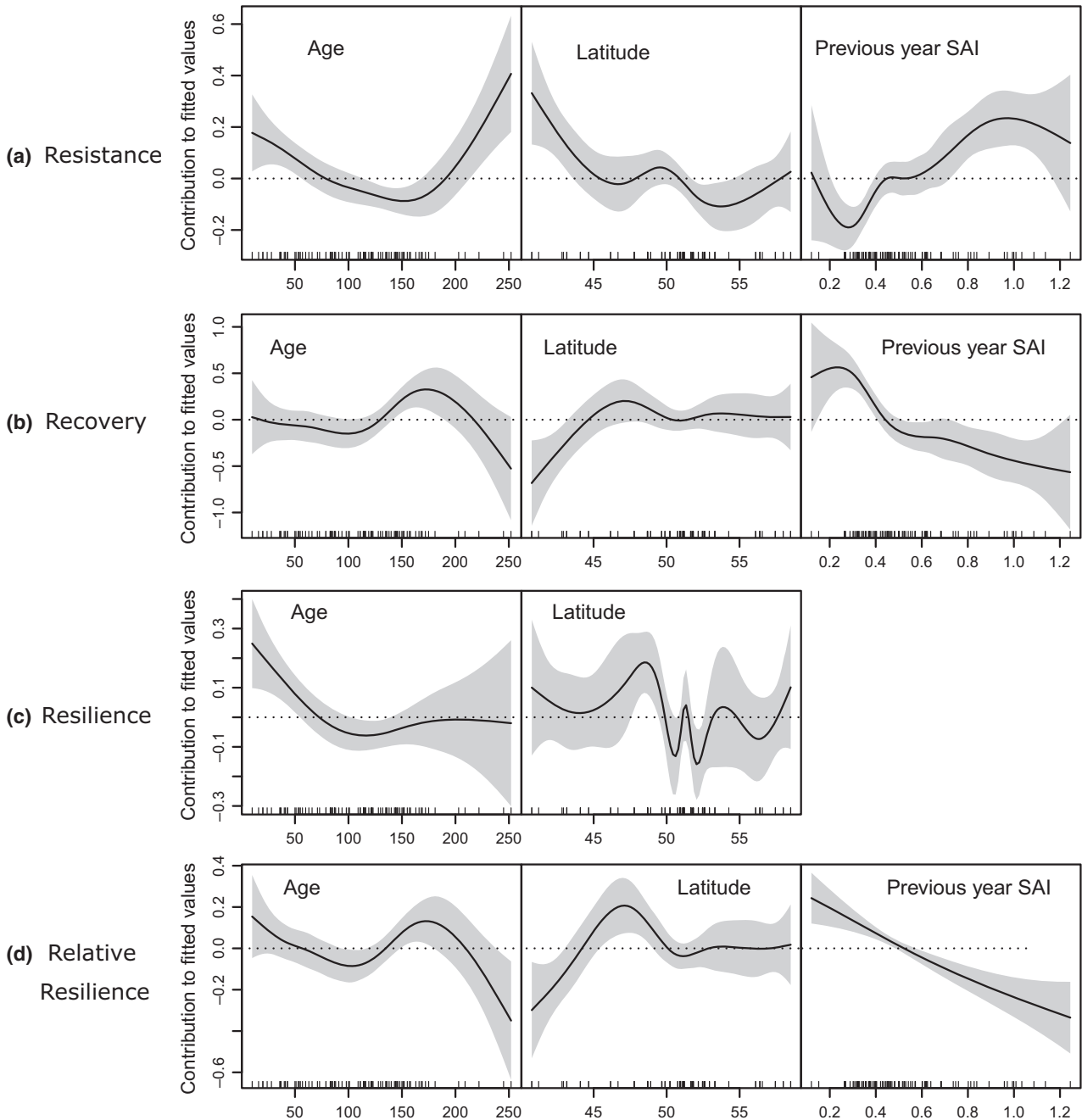


Fig. 7 Generalized additive modelling (GAM) analysis for four growth stability indices throughout the western European distribution of *Fagus sylvatica*: (a) resistance, the reduction in growth during a disturbance, (b) recovery, ability to recover from damage after a disturbance, (c) resilience, the ratio between pre- and postdisturbance growth levels, (d) relative resilience, resilience weighted by the severity of growth reduction during the disturbance. Smoothed curves for significant factors for each index are plotted, with 95% confidence intervals. Notches on the upper side of the x-axis represent the values for individual samples.

the universal scope of the 2004 event within the network, the effects of this drought were not universal: anomalous low growth (Fig. 2) affected primarily the mid-latitude forests and to a lesser extent northern range edge forests. In contrast to expectations, at the southern range edge, both for the arid and wetter

regions, regional-scale drought did not result in regional-scale growth suppressions. For the mid-latitudes, where drought events occurred in synchrony (e.g. 1976, 1990 and 2004: Fig. 4), reductions in growth were near universal and of a higher magnitude than for other regions (Fig. 2b, c).

Table 2 Generalized additive model results of temporal growth basal area increment (BAI) trends for bioclimatic regions of the western European distribution of *Fagus sylvatica*

Region	Factor	e.d.f.	F	P	R ² (adj)
North-west	Year	1.63	64.31	<0.001	0.241
Core temperate	Year	8.83	13.62	<0.001	0.125
Core continental	Year	8.42	8.73	<0.001	0.196
Wet south	Year	6.52	3.50	0.001	0.158
Dry south	Year	5.71	5.70	<0.001	0.11

For the poleward range edge forests, between-site growth variability was high even in drought years. Consequently, regional-scale variation in annual water availability does not result in regional-scale synchronization of tree growth. The one exception is the drought event in 1976, where all poleward range edge sites recorded low growth (Fig. 2a). For poleward range edge sites, the general lack of drought impact on growth is predictable given that precipitation for this region (1277 mm per annum, see Appendix S3 Table 2) is far in excess of the 500 mm minimum threshold considered to represent a hygric constraint (Bolte *et al.*, 2007) and that poleward edge populations for plant species are more generally affected by low temperature (Woodward, 1987).

Growth stability at the equatorial range edge

Equatorial range edge sites displayed both low magnitude (in the wet south region, Fig. 2d) and high between-site variability (in the dry south region, Fig. 2e) of growth response to regional-scale drought episodes. Despite significant drought conditions relative to mean site hydrological conditions, and the most extreme aridity relative to conditions throughout the network of sites, populations at the equatorial range edge were little affected by drought. For the southern portion of the range, GAM analysis of BAI shows that growth was broadly stable (Fig. 8). This stability of growth, combined with the lower climate sensitivity for equatorial range edge sites (Fig. 3i, j), rarer occurrence of pointer years (Fig. 5), and lower magnitude of growth reductions (Fig. 2), implies that equatorial range edge populations may be more robust than previously thought.

These results are in contrast to individual case studies linking reduced water availability at southern range edge populations for *F. sylvatica* to general reductions in growth (Jump *et al.*, 2006; Piovesan *et al.*, 2008). Stabilizing factors may play an important role in ameliorating increasing drought stress for equatorial range edge forests, such as the quality of sites to which the species is already restricted at the range edge, along

with greater stress tolerance of range edge populations (Lloret *et al.*, 2012). For many species at their equatorial range edge, populations are already restricted to sites at which local conditions buffer them from regional climate (Hampe & Jump, 2011). The results presented here support this expectation and suggest that the reported growth declines for southern range edge populations could be due to generally elevated drought stress in individual locations studied, rather than regional-scale drought events.

Whilst some studies have found equatorial range edge populations for multiple species to exhibit low climate sensitivity (Herrero *et al.*, 2013), many others have reported strong sensitivity to precipitation and growth reductions (Weber *et al.*, 2007; Thabeet *et al.*, 2009; Martín-Benito *et al.*, 2010). The results presented here for the equatorial range edge represent the integration of tree ring data from 10 separate sites, and thus transcend the limitations of case studies, and any potential publication bias towards dramatic results indicating forest decline. However, it should be noted that equatorial range edge populations are still performing poorly relative to other regions of the species range based on mean BAI data (Fig. S5) and ring width (Table S2).

Recent climate models have predicted an increase in both the frequency and severity of drought events in the western Mediterranean (Giorgi & Lionello, 2008). These increasingly arid conditions are expected to impact upon the growth and mortality of tree species within the region (Linares *et al.*, 2011; Granda *et al.*, 2013), with European beech forests, highlighted as at risk from increases in both the frequency and severity of drought stress (Lindner *et al.*, 2010; Milad *et al.*, 2011; Zimmermann *et al.*, 2015). Future climatic conditions are likely to breach threshold values resulting in unexpected and long-lasting reductions in growth (Cavin *et al.*, 2013; Lloyd *et al.*, 2013; Zimmermann *et al.*, 2015), which are strongly linked to subsequent tree mortality (Berdanier & Clark, 2016). Consequently, the apparent stability of southern *F. sylvatica* forests to 20th- and early 21st-century climate change cannot be assumed to continue indefinitely. The implications for future biogeographical changes are that range changes will occur at least initially through a landscape-scale reduction in population density rather than sudden, widespread range retraction (Jump *et al.*, 2009).

Increasing growth in the range core and poleward range edge

For the range core regions, growth has increased over the period studied (Fig. 8). These results contrast with other dendroecological studies, which have reported declining *F. sylvatica* growth for Flanders (Kint *et al.*,

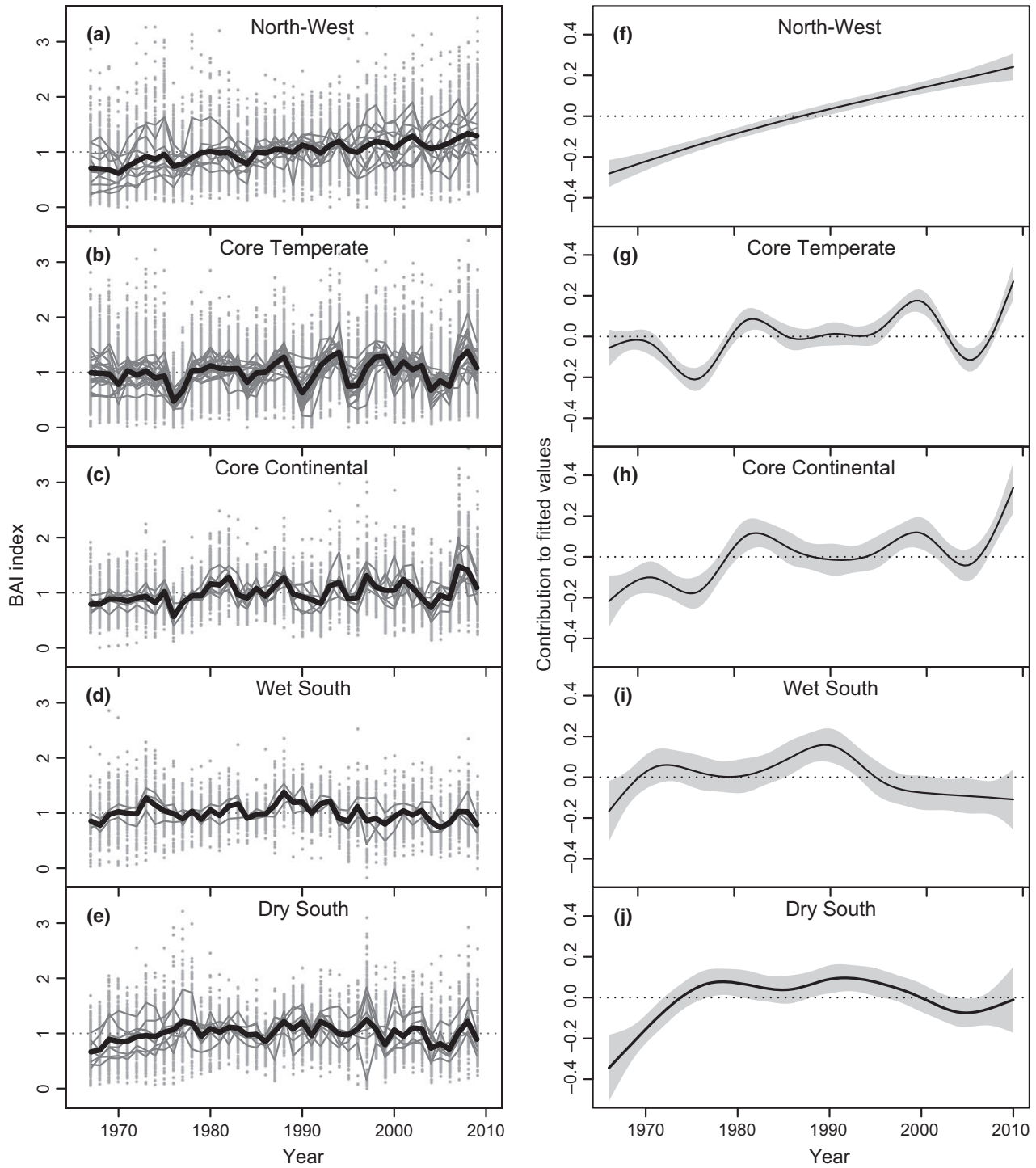


Fig. 8 Basal area increment (BAI) chronologies and generalized additive modelling (GAM) model smoothing curves for the five bioclimatic regions of the western European distribution of *Fagus sylvatica*. Left panels show individual BAI index values per site as points, site BAI curves in grey and regional mean BAI in black. Right panels show the GAM smoothers, with 95% confidence intervals. The regions depicted are north-west (plots a and f), core temperate (b and g), core continental (c and h), wet south (d and i) and dry south (e and j).

2012), across north-eastern France (Bontemps *et al.*, 2010; Charru *et al.*, 2010), and for high altitude central European forests (Dittmar *et al.*, 2003). Thus, fears of a

widespread decline for *F. sylvatica* across its entire range core distribution in Europe are not supported by the large-scale, multisite study presented in this paper.

However, periodic reductions in growth have occurred, tied to regional-scale drought events. This finding of periodic growth reductions highlights high and increasing sensitivity to climate (and specifically drought). A continent-wide assessment of tree growth for Europe reported similarly that the sensitivity of tree growth to drought was higher in central Europe and the south of the UK compared to the Mediterranean region (Babst *et al.*, 2013). Recent work has also highlighted the elevated response to drought conditions for *F. sylvatica* forests growing at mesic sites, compared to dry sites (Weber *et al.*, 2013), and to increases in drought sensitivity at wetter sites over recent years alongside increases in the occurrence of years during which growth is suppressed (Friedrichs *et al.*, 2009; Scharnweber *et al.*, 2011). Therefore, the forecast increases in water stress across many central European regions in the 21st century are likely to have significant negative impacts on *F. sylvatica* forests (Zimmermann *et al.*, 2015).

Crucially, this study reveals that *F. sylvatica* populations in the mesic range core and specifically the south of the UK are the most drought sensitive of the regions studied. Modelling has already identified this as a region where the primary productivity of *F. sylvatica* is likely to be severely compromised under future climate scenarios (Broadmeadow *et al.*, 2005). In this region, climate sensitivity is highest, absolute aridity is higher than for any region beyond the Mediterranean basin, and drought-induced reductions in growth are the highest throughout the regions sampled here. Previous work has identified extreme and long-lasting drought impacts within this region (Peterken & Mountford, 1996; Cavin *et al.*, 2013).

Overall, the results of this study suggest that the negative impacts of drought on the growth and productivity of *F. sylvatica* are likely to become considerably more widespread as the climate warms. Whilst some populations at the equatorial range edge appear buffered against rising drought stress to some degree, their recovery is particularly poor when drought impacts occur. Furthermore, the high sensitivity and low stability of core populations in response to drought should urge us towards a more nuanced view of risk and caution us against assuming that vulnerability to climate change is primarily a property of the range edge.

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References

- Adams HD, Guardiola-Claramonte M, Barron-Gafford GA *et al.* (2009) Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *PNAS*, **106**, 7063–7066.
- Adams HR, Barnard HR, Loomis AK (2014) Topography alters tree growth-climate relationships in a semi-arid forested catchment. *Ecosphere*, **5**. doi: 10.1890/es1814-00296.00291.
- Alberto FJ, Aitken SN, Alía R *et al.* (2013) Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology*, **19**, 1645–1661.
- Allen CD, Breshears DD (1998) Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. *PNAS*, **95**, 14839–14842.
- Allen CD, Macalady AK, Chenchouni H *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.
- Allen CD, Breshears DD, McDowell N (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, **6**, 1–55.
- Babst F, Poulter B, Trouet V *et al.* (2013) Site- and species-specific responses of forest growth to climate across the European continent. *Global Ecology and Biogeography*, **22**, 706–717.
- Bansal S, Harrington CA, Gould PJ, St Clair JB (2015) Climate-related genetic variation in drought-resistance of Douglas-fir (*Pseudotsuga menziesii*). *Global Change Biology*, **21**, 947–958.
- Barbeta A, Ogaya R, Peñuelas J (2013) Dampening effects of long-term experimental drought on growth and mortality rates of a Holm oak forest. *Global Change Biology*, **19**, 3133–3144.
- Beckage B, Osborne B, Gavin DG, Pucko C, Siccama T, Perkins T (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *PNAS*, **105**, 4197–4202.
- Berdanier AB, Clark JS (2016) Multiyear drought-induced morbidity preceding tree death in Southeastern U.S. forests. *Ecological Applications*, **26**, 17–23.
- Bigler C, Gavin DG, Gunning C, Veblen TT (2007) Drought induces lagged tree mortality in a subalpine forest in the Rocky Mountains. *Oikos*, **116**, 1983–1994.
- Biondi F, Waikul K (2004) DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences*, **30**, 303–311.
- Blasing TJ, Solomon AM, Duvick DN (1984) Response functions revisited. *Tree-Ring Bulletin*, **44**, 1–15.
- Boisvenue C, Running SW (2006) Impacts of climate change on natural forest productivity – evidence since the middle of the 20th Century. *Global Change Biology*, **12**, 862–882.
- Bolte A, Czajkowski T, Kompa T (2007) The north-eastern distribution range of European beech – a review. *Forestry*, **80**, 413–429.
- Bontemps JD, Hervé JC, Dhôte JF (2009) Long-term changes in forest productivity: a consistent assessment in even-aged stands. *Forest Science*, **55**, 549–564.
- Bontemps JD, Hervé JC, Dhôte JF (2010) Dominant radial and height growth reveal comparable historical variations for common beech in north-eastern France. *Forest Ecology and Management*, **259**, 1455–1463.
- Broadmeadow MSJ, Ray D, Samuel CJA (2005) Climate change and the future for broadleaved tree species in Britain. *Forestry*, **78**, 145–161.
- Bunn AG (2010) Statistical and visual crossdating in R using the dplR library. *Dendrochronologia*, **28**, 251–258.
- Carnicer J, Coll M, Ninyerola M, Pons X, Sánchez G, Peñuelas J (2011) Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *PNAS*, **108**, 1474–1478.
- Cavin L, Mountford EP, Peterken GF, Jump AS (2013) Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Functional Ecology*, **27**, 1424–1435.
- Charru M, Seynave I, Morneau F, Bontemps JD (2010) Recent changes in forest productivity: an analysis of national forest inventory data for common beech (*Fagus sylvatica* L.) in north-eastern France. *Forest Ecology and Management*, **260**, 864–874.
- Ciais P, Reichstein M, Viovy N *et al.* (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.
- Cook ER (1987) The decomposition of tree-ring series for environmental studies. *Tree-Ring Bulletin*, **1987**, 37–59.

- Cook ER, Kairiukstis LA (1990) *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Publishers, Dordrecht.
- Cropper JP (1979) Tree ring skeleton plotting by computer. *Tree-Ring Bulletin*, **39**, 47–60.
- Di Filippo A, Biondi F, Čufar K *et al.* (2007) Bioclimatology of beech (*Fagus sylvatica* L.) in the Eastern Alps: spatial and altitudinal climatic signals identified through a tree-ring network. *Journal of Biogeography*, **34**, 1873–1892.
- Dittmar C, Zech W, Elling W (2003) Growth variations of common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe – a dendroecological study. *Forest Ecology and Management*, **173**, 63–78.
- Dodson R, Marks D (1997) Daily air temperature interpolated at high spatial resolution over a large mountainous region. *Climate Research*, **8**, 1–20.
- Douglas AE (1920) Evidence of climatic effects in the annual rings of trees. *Ecology*, **1**, 24–32.
- Fotelli M, Gessler A, Peuke A, Rennenberg H (2001) Drought affects the competitive interactions between *Fagus sylvatica* seedlings and an early successional species, *Rubus fruticosus*: responses of growth, water status and $\delta^{13}C$ composition. *New Phytologist*, **151**, 427–435.
- Friedrichs D, Trouet V, Büntgen U, Frank D, Esper J, Neuwirth B, Löffler J (2009) Species-specific climate sensitivity of tree growth in Central-West Germany. *Trees*, **23**, 729–739.
- Fritts HC (1976) *Tree Rings and Climate*. Academic Press, London, UK.
- Galvan JD, Camarero JJ, Ginzler C, Buentgen U (2014) Spatial diversity of recent trends in Mediterranean tree growth. *Environmental Research Letters*, **9**, 084001. doi: 10.1088/1748-9326/9/8/084001.
- Gessler A, Keitel C, Nahm M, Rennenberg H (2004) Water shortage affects the water and nitrogen balance in Central European beech forests. *Plant Biology*, **6**, 289–298.
- Gessler A, Keitel C, Kreuzwieser J, Matyssek R, Seiler W, Rennenberg H (2007) Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees – Structure and Function*, **21**, 1–11.
- Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. *Global and Planetary Change*, **63**, 90–104.
- Granda E, Camarero JJ, Gimeno TE, Martínez-Fernández J, Valladares F (2013) Intensity and timing of warming and drought differentially affect growth patterns of co-occurring Mediterranean tree species. *European Journal of Forest Research*, **132**, 469–480.
- Granier A, Reichstein M, Breda N *et al.* (2007) Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. *Agricultural and Forest Meteorology*, **143**, 123–145.
- Hampe A, Jump AS (2011) Climate relicts: past, present, future. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 313–333.
- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.
- Harris GR, Collins M, Sexton DMH, Murphy JM, Booth BBB (2010) Probabilistic projections for 21st century European climate. *Natural Hazards and Earth System Sciences*, **10**, 2009–2020.
- Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, **12**, 1040–1049.
- Haylock MR, Hofstra N, Klein Tank AMG, Klok EJ, Jones PD, New M (2008) A European daily high-resolution gridded data set of surface temperature and precipitation for 1950–2006. *Journal of Geophysical Research*, **113**. doi: 10.1029/2008JD010201.
- Herrera S, Gutiérrez JM, Ancel R, Pons MR, Frías MD, Fernández J (2012) Development and analysis of a 50 year high-resolution daily gridded precipitation dataset over Spain. *International Journal of Climatology*, **32**, 74–85.
- Herrero A, Zamora R (2014) Plant responses to extreme climatic events: a field test of resilience capacity at the southern range edge. *PLoS One*, **9**, e87842.
- Herrero A, Rigling A, Zamora R (2013) Varying climate sensitivity at the dry distribution edge of *Pinus sylvestris* and *P. nigra*. *Forest Ecology and Management*, **308**, 50–61.
- Hickler T, Vohland K, Feehan J *et al.* (2012) Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. *Global Ecology and Biogeography*, **21**, 50–63.
- Hofstra N, New M, McSweeney C (2010) The influence of interpolation and station network density on the distributions and trends of climate variables in gridded daily data. *Climate Dynamics*. doi: 10.1007/s00382-009-0698-1.
- Huntley B (1991) How plants respond to climate change – migration rates, individualism and the consequences for plant communities. *Annals of Botany*, **67**, 15–22.
- IPCC (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163–2174.
- Jump AS, Hunt JM, Peñuelas J (2007) Climate relationships of growth and establishment across the altitudinal range of *Fagus sylvatica* in the Montseny Mountains, northeast Spain. *Ecoscience*, **14**, 507–518.
- Jump AS, Matyas C, Peñuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology & Evolution*, **24**, 694–701.
- Jump AS, Cavin L, Hunter PD (2010) Monitoring and managing responses to climate change at the retreating range edge of forest trees. *Journal of Environmental Monitoring*, **12**, 1791–1798.
- Kint V, Aertsen W, Campioli M, Vansteenkiste D, Delcloo A, Muys B (2012) Radial growth change of temperate tree species in response to altered regional climate and air quality in the period 1901–2008. *Climatic Change*, **115**, 343–363.
- Klos RJ, Wang GG, Bauerle WL, Rieck JR (2009) Drought impact on forest growth and mortality in the southeast USA: an analysis using Forest Health and Monitoring data. *Ecological Applications*, **19**, 699–708.
- Kuhn AR, Grill S, Baumgarten M, Ankerst DP, Matyssek R (2015) Daily growth of European beech (*Fagus sylvatica* L.) on moist sites is affected by short-term drought rather than ozone uptake. *Trees-Structure and Function*, **29**, 1501–1519.
- Larsson L-A (2003a) CoRecorder: Image Co-Ordinate Recording Program. Available at: <http://www.cybis.se> (accessed 20 April 2016).
- Larsson L-A (2003b) CDendro: Cybis Dendro Dating Program. Available at: <http://www.cybis.se> (accessed 20 April 2016).
- Leblanc DC (1990) Relationships between breast-height and whole-stem growth indexes for red spruce on Whiteface Mountain, New York. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **20**, 1399–1407.
- Leblanc DC, Nicholas NS, Zedaker SM (1992) Prevalence of individual tree growth decline in red spruce populations of the Southern Appalachian mountains. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **22**, 905–914.
- 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 – Structure and Function*, **19**, 385–401.
- Leuschner C, Backes K, Hertel D, Schipka F, Schmitt U, Terborg O, Runge M (2001) Drought responses at leaf, stem and fine root levels of competitive *Fagus sylvatica* L. and *Quercus petraea* (Matt.) Liebl. trees in dry and wet years. *Forest Ecology and Management*, **149**, 33–46.
- Lévesque M, Walthert L, Weber P (2016) Soil nutrients influence growth response of temperate tree species to drought. *Journal of Ecology*, **104**, 377–387.
- Linares JC, Delgado-Huertas A, Carreira JA (2011) Climatic trends and different drought adaptive capacity and vulnerability in a mixed *Abies pinsapo*–*Pinus halepensis* forest. *Climatic Change*, **105**, 67–90.
- Linares JC, Taiqui L, Sanguesa-Barreda G, Seco JI, Camarero JJ (2013) Age-related drought sensitivity of Atlas cedar (*Cedrus atlantica*) in the Moroccan Middle Atlas forests. *Dendrochronologia*, **31**, 88–96.
- Lindner M, Maroschek M, Netherer S *et al.* (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *Forest Ecology and Management*, **259**, 698–709.
- Lloret F, Keeling EG, Sala A (2011) Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos*, **120**, 1909–1920.
- Lloret F, Escudero A, Iriondo JM, Martínez-Vilalta J, Valladares F (2012) Extreme climatic events and vegetation: the role of stabilizing processes. *Global Change Biology*, **18**, 797–805.
- Lloyd AH, Duffy PA, Mann DH (2013) Nonlinear responses of white spruce growth to climate variability in interior Alaska. *Canadian Journal of Forest Research*, **43**, 331–343.
- Martin-Benito D, Río M, Cañellas I (2010) Black pine (*Pinus nigra* Arn.) growth divergence along a latitudinal gradient in Western Mediterranean mountains. *Annals of Forest Science*, **67**, 401–401.
- Maxime C, Hendrik D (2011) Effects of climate on diameter growth of co-occurring *Fagus sylvatica* and *Abies alba* along an altitudinal gradient. *Trees – Structure and Function*, **25**, 265–276.
- Meier IC, Leuschner C (2008) Genotypic variation and phenotypic plasticity in the drought response of fine roots of European beech. *Tree Physiology*, **28**, 297–309.
- Meier ES, Edwards TC Jr, Kienast F, Dobbertin M, Zimmermann NE (2011) Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. *Journal of Biogeography*, **38**, 371–382.

- Meir P, Mencuccini M, Dewar RC (2015) Drought-related tree mortality: addressing the gaps in understanding and prediction. *New Phytologist*, **207**, 28–33.
- Milad M, Schaich H, Burgi M, Konold W (2011) Climate change and nature conservation in Central European forests: a review of consequences, concepts and challenges. *Forest Ecology and Management*, **261**, 829–843.
- Minder JR, Mote PW, Lundquist JD (2010) Surface temperature lapse rates over complex terrain: lessons from the Cascade Mountains. *Journal of Geophysical Research*, **115**, D14122. doi: 10.1029/2009JD013493.
- Mosteller F, Tukey JW (1977) *Data Analysis and Regression*. Addison-Wesley, Reading.
- Neuwirth B, Schweingruber FH, Winiger M (2007) Spatial patterns of central European pointer years from 1901 to 1971. *Dendrochronologia*, **24**, 79–89.
- Pan Y, Birdsey RA, Fang J *et al.* (2011) A large and persistent carbon sink in the world's forests. *Science*, **333**, 988–993.
- Parnesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- Pasho E, Camarero JJ, De Luis M, Vicente-Serrano SM (2011) Impacts of drought at different time scales on forest growth across a wide climatic gradient in north-eastern Spain. *Agricultural and Forest Meteorology*, **151**, 1800–1811.
- Pedersen BS (1998) Modeling tree mortality in response to short- and long-term environmental stresses. *Ecological Modelling*, **105**, 347–351.
- Peterken GF, Mountford EP (1996) Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. *Forestry*, **69**, 125–136.
- Peuke AD, Schraml C, Hartung W, Rennenberg H (2002) Identification of drought-sensitive beech ecotypes by physiological parameters. *New Phytologist*, **154**, 373–387.
- Phipps RL, Whiton JC (1988) Decline in long-term growth trends of white oak. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **18**, 24–32.
- Pichler P, Oberhuber W (2007) Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. *Forest Ecology and Management*, **242**, 688–699.
- Piovesan G, Biondi F, Di Filippo A, Alessandrini A, Maugeri M (2008) Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology*, **14**, 1265–1281.
- Pluess AR, Frank A, Heiri C, Lalagüe H, Vendramin GG, Oddou-Muratario S (2016) Genome-environment association study suggests local adaptation to climate at the regional scale in *Fagus sylvatica*. *New Phytologist*, **210**, 589–601.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org> (accessed 20 April 2016).
- Rabasa SG, Grandá E, Benavides R *et al.* (2013) Disparity in elevational shifts of European trees in response to recent climate warming. *Global Change Biology*, **19**, 2490–2499.
- Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton DA (1999) Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs*, **69**, 375–407.
- Rennenberg VH, Seiler W, Matyssek R, Gessler A, Kreuzwieser J (2004) European beech (*Fagus sylvatica* L.) – a forest tree without future in the south of Central Europe? *Allgemeine Forst Und Jagdzeitung*, **175**, 210–224.
- Rolland C (2003) Spatial and seasonal variations of air temperature lapse rates in alpine regions. *Journal of Climate*, **16**, 1032–1046.
- Sanchez-Salguero R, Navarro-Cerrillo RM, Swetnam TW, Zavala MA (2012) Is drought the main decline factor at the rear edge of Europe? The case of southern Iberian pine plantations. *Forest Ecology and Management*, **271**, 158–169.
- Sarris D, Christodoulakis D, Körner C (2007) Recent decline in precipitation and tree growth in the eastern Mediterranean. *Global Change Biology*, **13**, 1187–1200.
- Schar C, Vidale PL, Luthi D, Frei C, Haberli C, Liniger MA, Appenzeller C (2004) The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332–336.
- Schamweber T, Manthey M, Criegee C, Bauwe A, Schroder C, Wilmking M (2011) Drought matters – declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. *Forest Ecology and Management*, **262**, 947–961.
- Schweingruber FH, Eckstein D, Bacht S, Bräker OU (1990) Identification, presentation and interpretation of event years and pointer years in dendrochronology. *Dendrochronologia*, **8**, 9–38.
- Spiecker H (1999) Overview of recent growth trends in European forests. *Water, Air & Soil Pollution*, **116**, 33–46.
- St Clair JB, Mandel NL, Vance-Borland KW (2005) Genecology of Douglas fir in western Oregon and Washington. *Annals of Botany*, **96**, 1199–1214.
- Sturm M, Racine C, Tape K (2001) Climate change: increasing shrub abundance in the Arctic. *Nature*, **411**, 546–547.
- Tegel W, Seim A, Hakelberg D, Hoffmann S, Panev M, Westphal T, Buntgen U (2014) A recent growth increase of European beech (*Fagus sylvatica* L.) at its Mediterranean distribution limit contradicts drought stress. *European Journal of Forest Research*, **133**, 61–71.
- Thabert A, Venetier M, Gadbin-Henry C, Denelle N, Roux M, Caraglio Y, Vila B (2009) Response of *Pinus sylvestris* L. to recent climatic events in the French Mediterranean region. *Trees*, **23**, 843–853.
- Thiel D, Kreyling J, Backhaus S *et al.* (2014) Different reactions of central and marginal provenances of *Fagus sylvatica* to experimental drought. *European Journal of Forest Research*, **133**, 247–260.
- Thornthwaite CW (1948) An approach toward a rational classification of climate. *Geographical Review*, **38**, 55–94.
- UNEP (1992) *World Atlas of Desertification*. Edward Arnold, London.
- Van Mantgem PJ, Stephenson NL (2007) Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters*, **10**, 909–916.
- Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A multiscale drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of Climate*, **23**, 1696–1718.
- Walther G-R, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Wang GG, Chhin S, Bauerle WL (2006) Effect of natural atmospheric CO₂ fertilization suggested by open-grown white spruce in a dry environment. *Global Change Biology*, **12**, 601–610.
- Weber P, Bugmann H, Rigling A (2007) Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. *Journal of Vegetation Science*, **18**, 777–792.
- Weber P, Bugmann H, Pluess AR, Walther L, Rigling A (2013) Drought response and changing mean sensitivity of European beech close to the dry distribution limit. *Trees*, **27**, 171–181.
- Wigley TML, Briffa KR, Jones PD (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology*, **23**, 201–213.
- Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, **73**, 3–36.
- Woodward FI (1987) *Climate and Plant Distribution*. Cambridge University Press, Cambridge.
- Zang C, Biondi F (2013) Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. *Dendrochronologia*, **31**, 68–74.
- Zimmermann J, Hauck M, Dulamsuren C, 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.
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Site details for 46 sites sampled for *Fagus sylvatica* along a latitudinal gradient in western Europe.

Table S2. Summary statistics for *Fagus sylvatica* tree ring chronologies from 46 sites sampled along a latitudinal gradient in western Europe.

Appendix S3. Supplementary methods for bioclimatic and growth-based zonation of the western European distribution of *Fagus sylvatica*.

Table S4. Cluster means of bioclimatic variables for the regions identified by multivariate analysis of growth and environmental data.

Figure S5. Boxplots of the basal area increment (BAI) for the sites and regions sampled for *Fagus sylvatica* along a latitudinal gradient in western Europe.